



Individuality in songs of Acadian flycatchers and recognition of neighbours

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Acadian flycatchers, *Empidonax virescens*, like many other tyrant flycatchers (Tyrannidae), sing complex songs with little variation among individuals. Measurements of frequency and timing revealed that individuals' songs included consistent but slight individual differences. A comparison of differences between songs of territorial neighbours and between more distant males revealed no evidence that neighbours learn the features of each other's songs. Playbacks of neighbours' and strangers' songs for 30 min at predetermined distances from singing subjects provided marginal evidence that territorial birds recognize these differences. Playbacks for only 2 min provided no such evidence, although similar experiments with hooded warblers, *Wilsonia citrina*, and Kentucky warblers, *Oporornis formosa*, in the same forest had provided clear evidence for recognition of individual neighbours. The slight differences in individuals' songs and the degradation of songs during propagation in a forest must make this discrimination difficult for Acadian flycatchers. In tyrant flycatchers, complex songs with innate developmental constraints might evolve by sexual selection for species recognition despite disadvantages for individual recognition.

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The complex sounds used by territorial birds for long-range communication perhaps always include consistent differences among individuals, although in some species these differences are small (Hutchison et al. 1968; Miller 1978; Wooller 1978; Moseley 1979; Cavanagh & Ritchison 1987; Galleotti et al. 1993; Robisson et al. 1993; Peake et al. 1998; Delpont et al. 2002; Lovell & Lein 2004a). Furthermore, birds can use these differences to discriminate between categories of conspecifics. Simple experiments with playbacks of tape-recordings have shown that many territorial species can discriminate between neighbours and strangers on the basis of individual differences in their vocalizations (Weeden & Falls 1959; Beer 1970; Falls 1982; Lamprechts & Dhondt 1995; Stoddard 1996; Rebbeck et al. 2001; Bee & Gerhardt 2002), and more elaborate experiments have shown that at least some species can distinguish among multiple individual neighbours (Brooks & Falls 1975; Wiley & Wiley 1977; Godard 1991; Stoddard et al. 1991; Godard & Wiley 1995).

Both individual distinctiveness in vocalizations and recognition of neighbours by their vocalizations recur in other organisms as well. Experiments with frogs, for

instance, indicate capabilities at least superficially similar to those of territorial birds (Bee & Gerhardt 2002). Primates also have similar capabilities (Cheney & Seyfarth 1988; Mitani et al. 1996). Humans of course can distinguish many conspecific individuals by vocalizations alone, although the limits of this capability have never been well studied.

Because it seems so natural to us, it is easy for us to assume that all species have the ability to recognize conspecific individuals. Nevertheless, some species, especially birds that do not learn their songs, have complex repertoires of vocalizations with minimal individual differences. This combination of complexity and minimal individual differentiation in signals might limit the possibilities for individual recognition. The psychology of learning suggests that large repertoires (which could increase the number of discriminations that must be learned) and subtle cues (which could increase the difficulty of attending to the differences) should increase the difficulty of recognition. Furthermore, full individual recognition is an inherently complex task. Recognition of neighbours as a whole, as opposed to strangers, requires association of a response with a familiar conspecific signal. Recognition of multiple individuals, on the other hand, requires association of several different responses with each of several approximately equally familiar signals.

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Thus the evolution of complexity and individual distinctiveness in signals might require some compromises.

The tyrant flycatchers (Tyrannidae) illustrate these issues. They produce frequency-modulated songs, in many cases rivalling the complexity of oscines' learned songs. Yet available evidence indicates they do not learn their songs. Flycatchers reared in acoustic isolation or even deafened at an early age sing songs within the normal range for the species (Kroodsma 1984; Kroodsma & Konishi 1991). Consequently, all individuals in a population sing similar patterns. Nevertheless, there are slight but consistent individual differences in flycatchers' songs (Westcott 1997; Lovell & Lein 2004a). At least in species with small territories or open habitats, flycatchers can recognize neighbours by these slight differences in songs (Westcott 1997; Lovell & Lein 2004b). These differences become even less apparent at long range, particularly in forests where reverberation degrades rapidly modulated signals (Wiley & Richards 1982; Wiley 1991, 1994; Naguib 2003).

This study addresses the possibility of neighbour-stranger discrimination by Acadian flycatchers, *Empidonax virens*, common inhabitants of mature bottomland forests in eastern North America. It provides a comparison with similar studies of hooded warblers, *Wilsonia citrina*, and Kentucky warblers, *Oporornis formosa*, that defend territories overlapping the flycatchers in the same forests. These warblers presumably learn features of their songs, which include clear individual differences, and they can recognize individual neighbours' songs (Godard 1991, 1993a; Godard & Wiley 1995).

First, I document consistent individual differences in the songs of Acadian flycatchers. Second, I consider whether the songs of neighbouring territorial birds are more or less similar than those of more distant birds. Experiments with birds in acoustic isolation (Kroodsma 1984; Kroodsma & Konishi 1991) do not eliminate the possibility that individuals might learn details of their songs as a result of interactions with neighbouring conspecifics. Although one study failed to find any small-scale geographical variation in Acadian flycatchers' songs (Payne & Budde 1979), it did not specifically address the question of whether or not immediate neighbours might learn from each other.

Third, I conducted two series of playbacks to assess capabilities for neighbour-stranger discrimination. The first in 1996, following procedures in previous experiments with the warblers just mentioned, presented a 2-min playback near each subject's territorial boundary. The absence of discrimination in this experiment prompted a second one, designed to maximize the chances for subjects to hear and to respond to the playbacks. This experiment in 2002 presented 30-min playbacks at predetermined distances from the subjects.

METHODS

General Observations

In most years during 1994–2002, I conducted 50-min observations at intervals of 2–4 days on 10–20 territories in 80 ha of mature and late successional bottomland forest

within Mason Farm Biological Reserve and the adjoining New Hope Gamelands near Chapel Hill, North Carolina, U.S.A. Observations of four banded birds in 1995 revealed that Acadian flycatchers in this population sang in mutually exclusive areas. In subsequent years, to avoid exposing subjects to playbacks before my experiments, I discontinued capturing males for marking. Instead I relied on their daily presence and routine behaviour in delimited areas to identify males. No behaviour suggested territorial replacement on any subject's territory preceding or during the experiments. In addition, I could often recognize by ear the slight differences between individuals' songs, as described below, and thus could confirm a male's occupation of its territory throughout any one season.

Individual Variation in Daytime Songs

A preliminary study of songs in this population (Georgitis 1996) led to conclusions similar to those of more extensive studies in subsequent years. Here I report only the results of a study of 13 individuals, which included all those recorded during multiple sessions at least 2 h apart in 2002. From each recording session, I selected the first clearly recorded song. There were two to five such songs for each subject. For seven individuals these songs were recorded on at least 2 days each; for the remaining four individuals they were from two separate sessions at least 2 h apart on the same day. For each song, I measured seven frequencies and six intervals as follows.

Songs digitized at 22.05 kHz with 16-bit accuracy were displayed as spectrograms with WildSpectra (version 020502, 128-point transform size, Hanning window, 50% overlap, Wiley & Wiley 2002). The frequency and time coordinates at seven points in the song were then obtained with the cursor (resolution 344 Hz, 2.90 ms, see Fig. 1). Most songs included five inflections (maxima) of frequency; the seven points measured included these five inflections, in addition to the beginning and end of the song. The start and end of the song were probably identified less accurately than the peaks, because the apparent start or end of a note depends on the intensity of the display. The seven points in each song were used to compute nonoverlapping intervals and the total duration of the song.

After inspection of the data for outliers, I used ANOVA to compare the between- and within-individual variances in both frequencies and intervals in songs. In order to compare subsets of these features for relative accuracy in identifying individuals, the frequencies or intervals that differed significantly among individuals were entered into discriminant function analyses. For this objective, all of the data were used to compute discriminant functions. An absolute measure of accuracy in classification, which would depend not only on a separation of samples for learning and testing, but also on the numbers of songs and individuals included in each sample, was not an objective of this analysis.

To compare differences in songs of neighbours with those of more distant birds, I computed the absolute differences in these frequencies and intervals for single

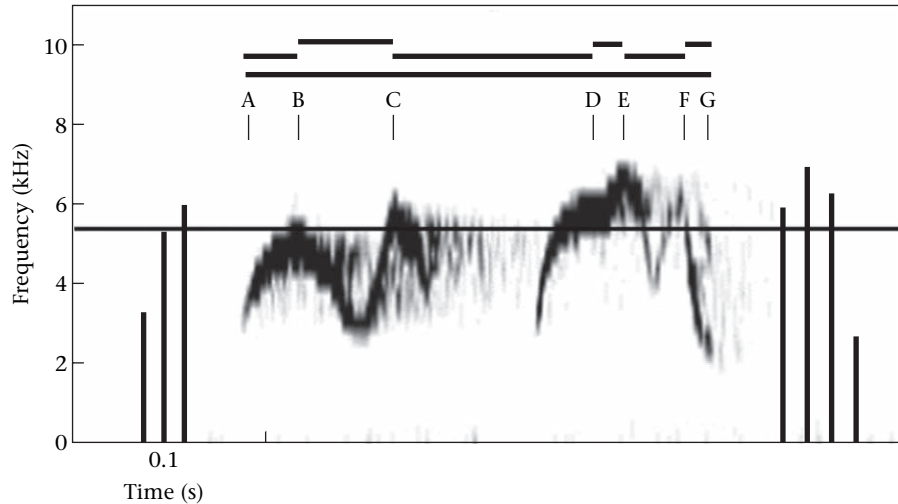


Figure 1. Measures of Acadian flycatchers' songs: seven measures of duration (horizontal bars) and seven measures of frequency (vertical bars) derived from seven points (A–G).

songs selected at random from each of two subjects. Altogether I had 22 such comparisons: six pairs of immediate neighbours, 10 pairs of neighbours once removed (with one mutually contiguous territory intervening between the two subjects), and six pairs with territories at least thrice removed (with the full diameters of at least two territories and a discontinuity of habitat intervening). Each individual was included only once in each category of proximity. ANOVA then compared the variances within and between these categories (JMP 3.2.6, SAS Institute, Cary, North Carolina, U.S.A.). Because these comparisons all yielded negative results, I computed the first principal component of the features of songs, and then used ANOVA to compute a single measure of power for a test of differences between the three categories of neighbours.

Two Series of Playback Experiments

In 1996, playbacks were presented to eight subjects between 22 May and 4 June, and in 2002, to 14 subjects between 28 May and 3 June.

The playbacks in 1996 followed the procedures for previous experiments with territorial hooded and Kentucky warblers (Godard & Wiley 1995; Wiley & Godard 1996). Tapes were played for 2 min (seven songs total) from locations 5–10 m inside the previously mapped areas used by subjects while singing. Unlike the warblers, the flycatchers usually failed to approach these playbacks, although they often sang in response from a distance.

The playbacks in 2002 incorporated changes intended to evoke a more definite response. Tapes were played 50–75 m from a singing male for 30 min (four songs/min). In both series the playbacks were presented in a direction appropriate for an immediate neighbour of the subject, but in the second series the speaker was placed within a predetermined range of distances from the subject and continued for a longer time than in the first series.

Preparation of Tapes for Playback

Separate playback tapes were prepared from one or two examples of each subject's and several nearby birds' songs (18 exemplars, 1996; 24 exemplars, 2002). These songs were recorded with a Sony TCD-ProII recorder and Sennheiser ME67 ultradirectional microphone from distances of 4–8 m in order to reduce degradation during propagation. After digitizing the songs at 22.05 kHz and 16-bit accuracy, I standardized the maximal amplitude. Copies of each song were then combined with intervening silent intervals to produce sequences with four songs/min but with slightly varying intervals that matched the intervals used by a male while singing naturally at this rate. Four songs/min was the modal rate for males singing undisturbed on their territories in late May. For playback of a neighbour's songs, I randomly chose a tape of a male with an immediately contiguous territory. For a stranger's songs I chose a tape of a male recorded well beyond the subject's range of hearing (>500 m away, with three territories and a habitat discontinuity intervening).

Procedures for Playback

Playbacks began between 0630 and 1230 hours Eastern Daylight Time, at least 15 min after the end of dawn singing and before the hottest part of the afternoon. For each experiment the speaker was fastened to a small branch about 2 m above ground and aimed towards the subject (and thus away from the nearest neighbour). After the apparatus was in place, I selected a tape or track for playback at random (by rolling a die), subject to the constraints of the experimental design. On separate days, 2–4 days apart, each subject received playbacks of a neighbour's and a stranger's songs in random order (equal numbers heard neighbours and strangers first). Playback always began within 2 min of hearing the subject or its mate at the appropriate distance (see below), provided the nearest neighbour could not be heard. Neighbouring

subjects were tested 1–2 days apart (usually 1 day apart in 1996 and 2 days apart in 2002). I terminated playbacks if a neighbour approached the speaker (twice in 1996, three times in 2002). These aborted experiments were later repeated with the same subject at a new location.

In 1996, the speaker was placed near the limit of the subject's range for singing (<10 m inside the limit of the observed locations for singing) in the direction of the appropriate neighbour. When playback began the subject or his mate was 50–100 m away. In 2002, the speaker was placed 25–50 m from the subject in the direction of the neighbour, regardless of distance from the limits of the subject's locations for singing. The distance inside the limit of the subject's singing range varied from 10 to 50 m, but in all cases was less than 1/6 of the diameter of the subject's territory.

Calibration of Playback Intensity

Tapes were played on a Sony TCD-ProII cassette recorder (1996) or a Sony Discman portable CD player (2002). In each case the line output was led through an AmpliVox portable amplifier (15 V) to a Realistic tweeter horn (frequency response, 3–15 kHz \pm 3 dB). This speaker was highly directional (for broadcasts of flycatchers' songs, -13 ± 1 dB at 90° from the axis, -17 dB \pm 1 at 180°, measured with a Realistic sound pressure level (SPL) metre, C weighting, fast response, 2 m above ground in a forest). I set the amplifier so that songs on a playback tape were broadcast at a level close to that of natural songs (as judged by equal readings on the VU metre of the same Sony TCD-ProII recorder and Sennheiser ME67 microphone when monitoring either the playback or natural songs at distances of 8 or 12 m at a height of 1.5–2 m above ground in a forest). This setting produced SPLs of $80\text{--}88 \pm 1$ dB at 1 m for the different normalized playbacks. These SPLs are lower than those of many oscines' songs. Although the files used for playback all had the same maximal amplitudes as measured in the digitized sound, the energy as a function of time varied among songs. Consequently, the SPL metre (C weighting, fast response) responded differently to the maxima in these songs (± 4 dB). To my ear all playbacks sounded normal in intensity and timbre.

Responses of Subjects

The behaviour of subjects and their mates was recorded from 5 min before until 15 min after playback. From a distance of about 10–15 m from the speaker, I could hear all songs and wheep/wheeu calls within 75–100 m and could see birds and hear trills and triplets within 10 m of the speaker (vocalizations are described below). Birds never appeared to respond to my presence and often perched within 2–3 m in the course of their movements near the speaker. When not singing, males often uttered wheep calls. Females instead usually produced wheeu calls. During playbacks, when I knew the location of the subject as judged by regular singing, I never heard his mate utter songs, trills, or triplets. Wheep/wheeu calls

were often uttered rapidly enough and far enough away that I could not reliably count them. Instead I determined how many minutes of observation included these calls from the subject or his mate.

In addition, I noted the subject's distance from the speaker each time it vocalized within 10 m. From these notes I determined the amount of time to the nearest minute that the subject spent within 10 m and within 3 m in a horizontal direction from the speaker. The subject often perched 4–15 m above ground, sometimes almost directly above the speaker. In addition, I determined the number of flights by the subject within 10 m of the speaker. The subject's mate almost never approached within 10 m of the speaker (only in one experiment each year), so I did not attempt to assess distances and numbers of flights for females.

In each 5-min period before, during and after playback (or in 1996, 2-min period during playback), I recorded the number of the subject's songs, the number of trills, the number of triplet calls, the number of minutes spent within 10 m of the speaker, and the number of minutes in which the male or his mate uttered wheep/wheeu calls. As many of these measures were associated with each other, I computed their principal components for use in statistical tests. All statistical tests were calculated with JMP 3.2.6. For Wilcoxon signed-ranks matched-pairs tests, JMP reported the larger of the two observed minus expected summed ranks (labelled T' here).

RESULTS

Territoriality, Mates and Vocalizations

Territorial neighbours often sang simultaneously while 100–200 m apart and only infrequently approached each other at mutual boundaries. Song was almost always produced by males, although on several occasions a female near her nest appeared to sing once. Each male sang from an irregular area 100–300 m in maximal diameter (for similar densities in other populations, see: Mumford 1964; Whitehead & Taylor 2002). Females often called regularly when off the nest. During these times, a female usually remained within the area used frequently by the male for singing, well away from boundaries.

Close-range interactions between individuals other than mates occurred in three circumstances: infrequent but sometimes prolonged encounters between neighbouring pairs near boundaries in the week following the first arrivals in spring; brief interactions between a mated pair and a third individual usually deep inside a territory during nest building; and daily countersinging in dim light at dawn.

During dawn countersinging (about 30 min before until 20 min after sunrise), male Acadian flycatchers sang from perches 15–50 m from neighbours, often the same perches in successive days. During this time, males sang a combination of two brief syllables, neither one like daytime songs. No chase or contact was ever observed. Once it was light enough to see well in the understory, males sang only their daytime songs, at rates of two to six songs/min, with pauses

lasting a few minutes to an hour. Singing rates decreased once young hatched. Dawn singing thus did not provide opportunities for neighbours to learn each other's daytime songs, the subject of the experiments reported here.

Singing by male Acadian flycatchers resembled that by male hooded warblers (Wiley et al. 1994) in its confinement to mutually exclusive territories and its division into distinctive dawn and daytime modes. Both species occurred in approximately the same densities in the study area, often in overlapping locations in mature forest, and occupied territories about the same sizes, 2–10 ha. Unlike the flycatcher, the warblers sang a repertoire of 5–10 patterns during the day and used patterns at dawn identical to those used later.

In addition to song, Acadian flycatchers produced several other vocalizations either alone or in encounters with conspecifics (Mumford 1964; Whitehead & Taylor 2002). Males often uttered a quiet trill between songs, usually during flights to new perches. Both sexes produced short notes, often 4–15/min for long periods. These notes took two forms (wheep and wheeu) with some intermediates. The latter were used more frequently by females and when individuals approached each other. A female frequently repeated these notes in long bouts during nest building and during breaks in incubation while her mate sang repeatedly 25–100 m away (less often both used these calls repeatedly at similar separations). Thus it was often possible to keep track of the movements of a male and his mate simultaneously.

Two other distinctive vocalizations occurred during intense interactions. One was a burst of two to four notes (often a triplet, t–t–t), usually uttered when one bird flew near its mate or a rival. Triplets were most frequent before incubation began, whenever a male swooped close past his mate. They also occurred when one male flew towards another in boundary encounters and sometimes near a speaker in response to playbacks. A second distinctive vocalization, a brief doubled harsh note, was occasionally appended to wheeu calls by females (wheeu-kchr), apparently when aroused by proximity of a mate or rival. Triplets and wheeu-kchr were produced mostly by males and females respectively, although each occasionally produced the other as well.

Individual Differences in Daytime Songs

Males' daytime songs consist of three purely tonal notes with rapid frequency modulations (Figs 1, 2). ANOVA revealed highly consistent differences among individuals in both frequencies and intervals in songs. Five of the seven measured frequencies differed highly significantly among individuals (frequencies B, C, D, E and G; see [Statistical Appendix](#), section 1). The total length of the song and the intervals of the two gaps in the song (intervals AG, CD and EF) also differed highly significantly among individuals. The interval between peaks in the second note (interval DE) also differed among individuals ($P < 0.002$). Only the lengths of the initial upsweeps and the final downsweep (intervals AB, BC and FG) provided no evidence for individual differences (see [Statistical](#)

[Appendix](#), section 2). These intervals, as mentioned above, were probably the least accurately measured. With careful attention at close range, I could hear consistent individual differences in both pitch and timing.

The four measures of songs that differed most among individuals were the frequencies of the first and third peaks (the initial peaks of the first two notes) and the durations of the gaps between the notes. If these four measures were entered in a discriminant function analysis, all songs in the sample of 36 were attributed to the correct individual. If only the two frequencies were used, the discriminant function analysis made 12 errors in classification (33%). If only the two intervals were used, there were seven errors (19%). Thus a combination of frequencies and intervals allowed the most accurate identification of individuals' songs in this sample of 13 individuals.

Some of the measures of songs were strongly correlated. Among nonoverlapping intervals in songs, only the two that included gaps (intervals CD and EF) were highly correlated (0.45, other pairs of intervals < 0.40). Frequencies B, C and D, the three internal peaks in songs, were also highly correlated (0.55–0.86, other pairs of frequencies < 0.45). No frequency correlated highly with any interval in songs (< 0.25).

Differences in Daytime Songs in Relation to Proximity

No significant differences appeared in the songs of neighbours, near neighbours and distant birds ($P > 0.4$ for all measures but two; see [Statistical Appendix](#), sections 3, 4; Fig. 2). The measure that came closest to statistical significance, the frequency at the end of the song (frequency G), had a lower mean difference (greater similarity) among distant pairs of birds than among immediate and near neighbours. The first principal component of the features of songs likewise showed no differences among the three categories of neighbours (see [Statistical Appendix](#), section 5). There is thus no evidence that neighbours were more likely than distant birds to sing similar songs.

Responses to 2-min Playbacks

In the first series of experiments (1996), subjects received brief playbacks (2 min) from speakers near their territorial boundaries. In these circumstances there were no indications that males or pairs responded differently to neighbours' and strangers' songs. The subjects clearly responded to the playbacks overall as shown by a significant decrease in singing during the 2 min of playback in comparison with the 2 min before (Wilcoxon matched-pairs signed-ranks test: $T' = 21.5$, $N = 9$ (16 playbacks to 8 subjects, 7 ties), $P = 0.008$; Fig. 3). Only one subject approached the speaker during or after the playback. No comparisons of vocalizations during or after the playback revealed differences between responses to neighbours' and strangers' songs.

A principal component analysis of the subjects' and their mates' responses included five measures of response

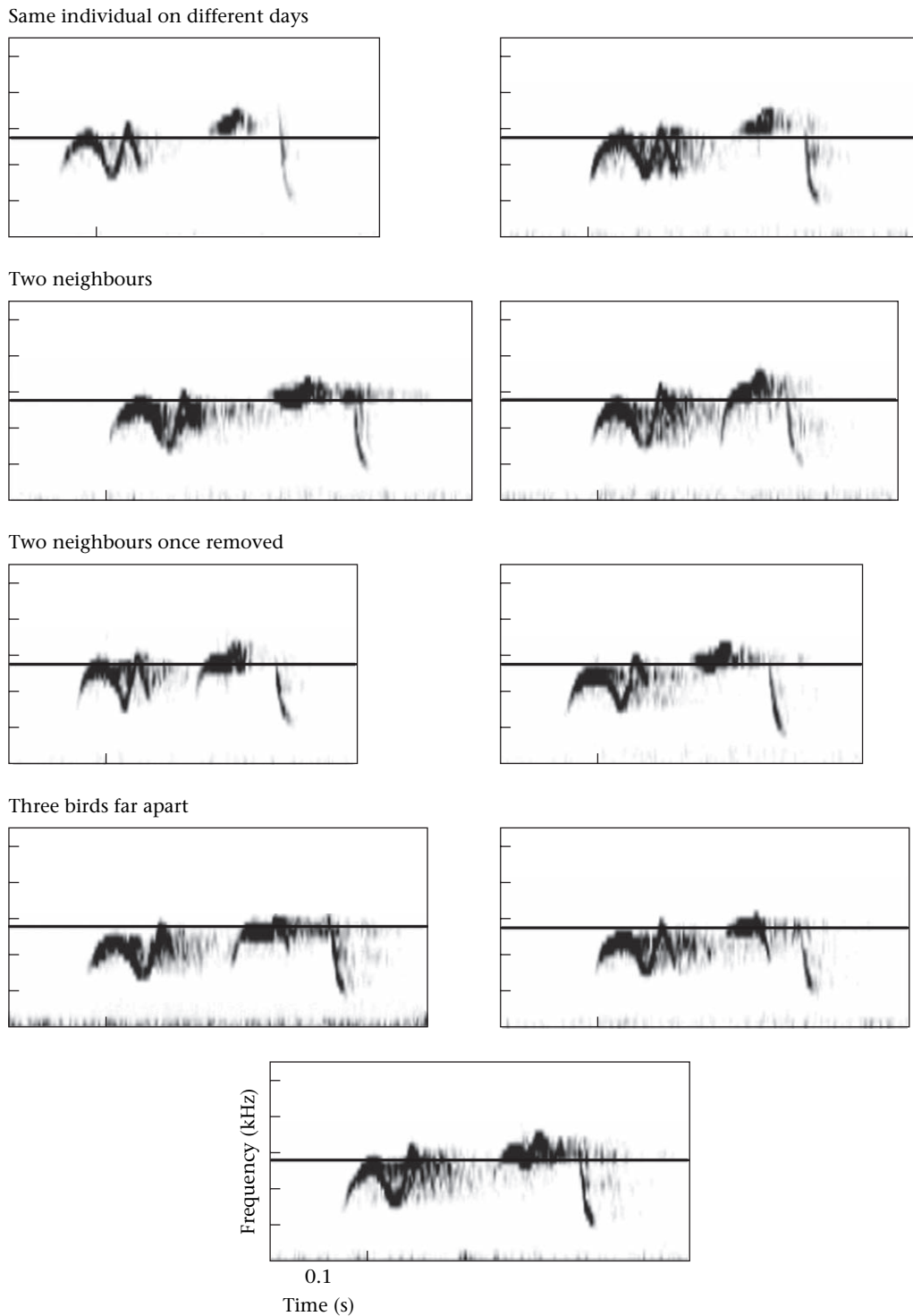


Figure 2. Spectrograms of songs of Acadian flycatchers (see text for details): comparison of typical examples of songs by the same bird, by territorial neighbours, by once-removed neighbours, and by more distant birds.

in each of four intervals of time: numbers of songs, minutes spent within 10 m of the speaker, number of trills, number of triplet calls and number of minutes with mates' calls during playback and during each of three 5-min periods afterwards. The first six principal components had eigenvalues greater than 1, the first explained 29% of the variance in responses, and the first four explained 75%

of the variance. For each of the first four principal components, differences between the scores for responses to neighbours' and strangers' tapes were all close to zero (see [Statistical Appendix](#), section 6).

Following neighbours' playbacks, subjects' singing rates increased progressively until the mean rate during the third 5-min period after playback (12 songs/5 min) was nearly

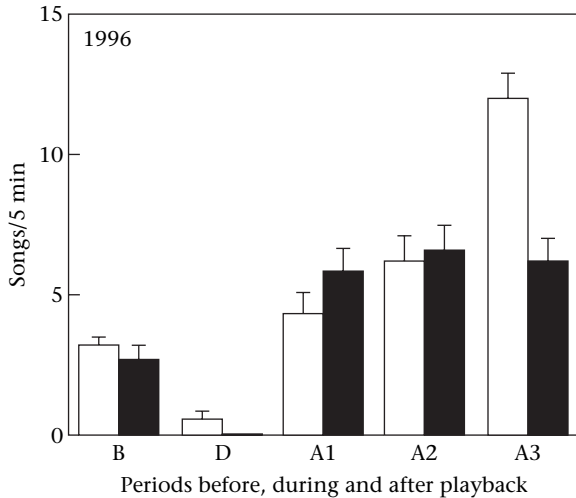


Figure 3. Numbers of songs/5 min before (B), during (D), and in three periods after (A1–A3) playbacks in 1996. □: responses to neighbours' songs; ■: responses to strangers' songs.

twice that during this period following strangers' playbacks (6.25 songs/5 min). Nevertheless, in paired tests, this difference fell short of statistical significance (Wilcoxon matched-pairs signed-ranks test: $T' = -10.5$, $N = 8$, $P = 0.09$; Fig. 3). In addition, subjects' total songs during the three periods after playback did not differ consistently between neighbours' and strangers' songs ($T = -3.5$, $N = 8$, $P = 0.34$). Only four subjects uttered triplet calls during or after playbacks, in no particular pattern.

Responses to 30-min Playbacks

The second series of playbacks (in 2002) was designed to allow more time for subjects to hear and to respond to the playbacks. Not only did the playbacks last longer but the speakers were placed at predetermined distances from the subjects (50–75 m), rather than at predetermined distances from boundaries. The sample size was also larger.

As in the previous experiment, rates of singing decreased when playbacks began. They then increased progressively during the 30 min of playback, more so in response to neighbours' songs than to strangers' (Fig. 4), although this difference did not reach statistical significance (repeated measures MANOVA: $F_{1,26} = 3.37$, Wilkes' lambda = 0.885, $P = 0.08$; Fig. 4). For 15 min following the termination of playback, singing rates decreased or stabilized at a level apparently higher than before playback.

A principal component analysis included five measures of response during each of six equal periods during playback. Six principal components had eigenvalues greater than 1, the first five of which explained more than 75% of variance in responses. The first principal component explained 37% of variance, over twice as much as any other. It had moderately heavy weightings (>0.2) on the subjects' singing rates, time spent within 10 m of the speaker, and trill rates in most of the six periods during playback.

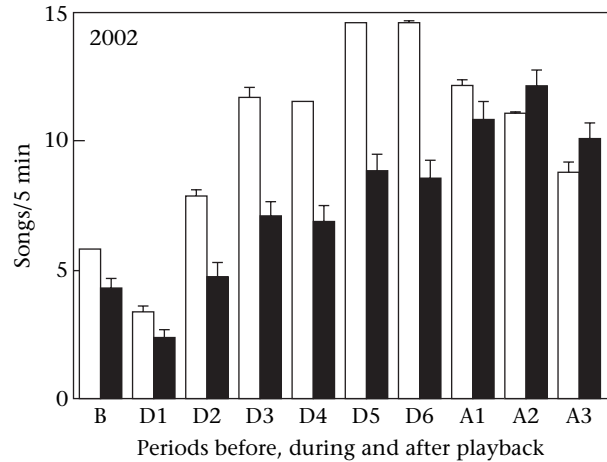


Figure 4. Numbers of songs/5 min before (B), in six periods during (D), and in three periods after (A1–A3) playbacks in 2002. □: responses to neighbours' songs; ■: responses to strangers' songs.

For the first principal component, 4 of 14 subjects had lower scores for responses to strangers' than to neighbours' songs (in comparison, PC2, 10/14; PC3, 6/14; PC4, 8/14). In paired comparisons of responses to neighbours' and strangers' songs, the differences in the first principal component scores failed to reach statistical significance (Wilcoxon matched-pairs signed-ranks test: $T' = -27.5$, $N = 14$, $P = 0.09$).

In comparisons of the differences in the total songs in response to neighbour and stranger playbacks, the lower response to strangers was almost statistically significant (Wilcoxon matched-pairs signed-ranks test: $T' = -27$, $N = 14$, $P = 0.059$; Fig. 4). The differences in total triplet calls, the calls used in close-range encounters, were greater to stranger than to neighbour playbacks ($T = 26.5$, $N = 11$ (excluding 3 ties), $P = 0.017$; Fig. 5). Totals for the other

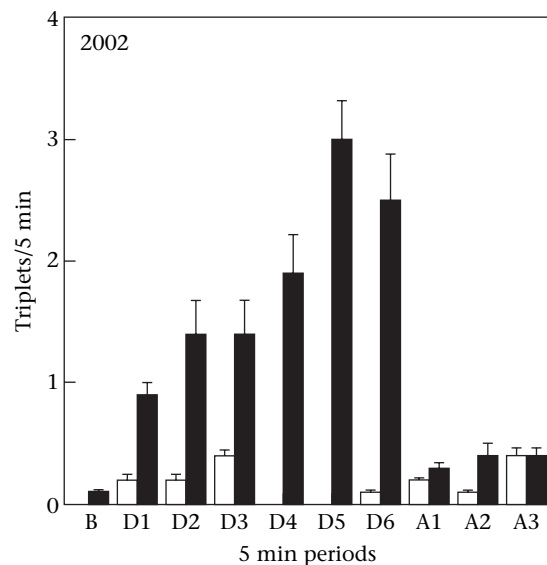


Figure 5. Numbers of triplets/5 min before (B), in six periods during (D), and in three periods after (A1–A3) playbacks in 2002. □: responses to neighbours' songs; ■: responses to strangers' songs.

three measures of response revealed no significant differences between responses to neighbours and strangers.

When I adjusted the alpha level for statistical significance by Bonferroni's correction ($0.05/5 = 0.01$), the difference in total triplet calls did not reach statistical significance. On the other hand, triplet calls and close approach were the two characteristic responses to natural territorial intrusions. When I used this information to restrict the focus to two statistical tests, the difference in triplet calls reached significance. Either way, the evidence for discrimination between neighbours' and strangers' songs is marginal.

During the six 5-min periods following playback, the differences between responses to neighbours' and strangers' songs increased progressively. For the first three periods following playback, there were no consistent differences in any measure of response.

DISCUSSION

Conspecific Recognition by Tyrant Flycatchers

This study has shown that songs of Acadian flycatchers differ consistently among individuals, although the differences are slight. There was no evidence that neighbours' songs differ more or less than those of more distant birds and thus no suggestion that these flycatchers adjust the details of their songs to match those of their neighbours.

Responses of territorial birds to neighbours' and strangers' songs during the second series of experiments provided only marginal evidence for discrimination. These experiments, in comparison with the first series, included longer playbacks and also controlled the distance of playback from the subject. They might thus have increased the opportunities for subjects to recognize their neighbours' songs. On the other hand, the density of Acadian flycatchers in 2002 was about one-third lower than in 1996. If the lower density reduced the opportunities to hear their neighbour's songs, the subjects' ability to recognize neighbours might also have been reduced. Furthermore, if both neighbours and strangers were less of a threat, there could be less advantage for learning these distinctions. Nevertheless, in both years, all subjects had at least one immediate neighbour with which they regularly interacted at close range, and all playbacks of neighbours' songs were of immediate neighbours.

Possible discrimination between neighbours' and strangers' songs appeared only in subjects' use of calls associated with high-intensity interactions. Paired comparisons of subjects' overall behaviour in these two situations, as indicated by scores on the first principal component of all measures of response, provided no evidence for discrimination. The rate of singing during playbacks almost reached statistical significance in the longer experiments in 2002, but not in the shorter experiments in 1996. In both experiments, subjects sang less in response to strangers than neighbours. In contrast, subjects used triplets more in response to strangers than neighbours. Thus it seems possible that Acadian flycatchers in natural situations recognize strangers' songs but only after some time.

At least one other species of *Empidonax* can distinguish neighbours' and strangers' songs, the alder flycatcher, *E. alnorum* (Lovell & Lein 2004b). This species occupies shrubby habitats where the birds sing above the level of most of the vegetation on small contiguous territories. Thus the degradation of songs during propagation between birds or between speaker and listener is limited primarily to frequency-dependent attenuation. Irregular amplitude fluctuations probably degrade these brief vocalizations only minimally, and presumably little reverberation occurs in this open environment (Wiley & Richards 1982). Another tyrannid that can discriminate between neighbours and strangers, the ochre-bellied flycatcher, *Mionectes oleagineus*, forms small leks in tropical forest, where interacting individuals are often much closer together than are singing territorial Acadian flycatchers (Westcott 1997). Acadian flycatchers, separated by large distances in the interiors of forests, must face greater challenges in recognizing familiar neighbours than do either of these species.

Another suboscine, the spotted antbird, *Hylophylax naevioides*, which occupies large territories in tropical forests and has slight individual differences in songs, has failed to differentiate neighbours and strangers by song (Bard et al. 2002). Slight differences in signals are presumably difficult to recognize when communication occurs over long distances in acoustically complex environments.

Contrasts with Conspecific Recognition by Oscines

Marginal neighbour-stranger discrimination by Acadian flycatchers contrasts with clear recognition of multiple individual neighbours by hooded and Kentucky warblers in the same area (Godard 1991; Godard & Wiley 1995). Both the flycatchers and the warblers occupy territories in the understory of mature bottomland forests. Males of all three species often sing in the more open layer between the shrubs in the understory and the canopy, about 2–10 m above ground.

The experiments in 1996 followed the procedures used in earlier experiments with warblers. Samples sizes ($N = 8$) and playback procedures were similar. Although the experiments with warblers compared responses to different neighbours' songs (rather than to neighbours and strangers' songs), Wilcoxon tests indicated much stronger differences in responses ($T = 0$ in comparisons of the first principal components of responses for both species). The difference in responses was readily apparent in the field. In contrast, the flycatchers did not respond differently to neighbours' and strangers' songs. Consequently, it seems unlikely that they would be able to recognize multiple individual neighbours, a more complex task.

The warblers presumably learn aspects of their songs but nevertheless include clear individual differences in their songs. The flycatchers show no signs of learning in the development of their songs. The close resemblance between individuals' songs is instead a result of innate development (Kroodsma 1984, 1985; Kroodsma & Konishi 1991). The slight differences in the songs of individual

Acadian flycatchers, combined with the acoustically complex environment, must make it difficult to learn neighbours' songs.

Proximate Mechanisms of Recognition

Lower responses to neighbours than to strangers could result from habituation to familiar sounds (Wiley & Wiley 1977; Richards 1979; Stoddard 1996; Bee & Gerhardt 2002). Even differences in responses to neighbours' songs in an unexpected place could result from site-specific habituation (Wiley & Wiley 1977; Bee & Gerhardt 2002). Nevertheless, at least in birds, evidence suggests that these forms of recognition involve associative learning, not just habituation (Richards 1979; Godard 1991). The flycatchers respond to neighbours by singing more but by uttering triplets less, an indication that the response to strangers is stronger than to neighbours. The warblers also frequently stop singing and utter high-intensity aggressive calls in response to playbacks. In this regard, the flycatchers seem to respond in ways similar to the warblers, but with less evidence of recognizing neighbours' songs. These responses do not represent simple habituation, as some measures of behaviour increase while others decrease.

Responses to neighbours' songs vary among and even within species. Another species in the same area, the red-eyed vireo, *Vireo olivaceus*, has failed to discriminate between different neighbours' songs (Godard 1993b). These vireos sing large repertoires (about 40 patterns) of phrases in irregular order, and neighbours often share patterns. The larger repertoires and greater sharing presumably make it more difficult for these vireos than for the warblers to learn neighbours' songs. The tufted titmouse, *Baeolophus bicolor*, also in the same area, sings repertoires of moderate size (about 10 patterns) like the hooded warbler, but neighbours share nearly all of their patterns. This species has also failed to recognize different neighbours' songs, although they readily differentiated neighbours from strangers (Schroeder & Wiley 1983).

At least two oscines are also known to recognize neighbours in some circumstances but not in others. Resident populations of song sparrows, *Melospiza melodia*, in Washington failed to differentiate between neighbours and strangers following an occasion when predation created unusual flux in territorial boundaries (Stoddard et al. 1991). Among Carolina wrens, *Thryothorus ludovicianus*, males respond more strongly to strangers during spring when nesting than during autumn when young males are establishing territories (Hyman 2002). In both cases, increased flux in territorial boundaries resulted in reduced discrimination between neighbours and strangers.

In captivity, on the other hand, in experiments with clear signals, no background sound, and rigorous operant conditioning, birds can learn to discriminate any audible differences in acoustic signals. Sometimes this capability is astonishing (Stoddard et al. 1992). These conditions contrast with natural situations, however, where recognition requires discriminations among signals degraded during propagation and classification of conspecifics with imperfectly predictable behaviour. This variability raises

questions about the evolution of complex songs and territorial interactions.

A Trade-off in the Evolution of Conspecific Recognition

In general, individuals should benefit by discriminating among conspecifics that present different levels of threat. Thus when neighbours and strangers differ in this regard, natural selection should promote mechanisms for discrimination, including clear differences among individuals' songs and clear differentiation of responses. The failure of some species to make clear neighbour-stranger discriminations might thus have two general explanations: either neighbours and strangers pose similar threats, or conflicting advantages outweigh those of neighbour-stranger discrimination.

(1) In some circumstances, neighbours and strangers might pose equal threats of usurping territories for singing, so there would be no advantage to discriminating between these rivals (Godard & Wiley 1995; Stoddard 1996). If so, complex or shared vocalizations, without clear individual differences, might evolve in order to promote attraction of mates or assessment by rivals.

A potential problem arises when territorial neighbours are rivals for resources other than territories for singing, including extrapair copulations and extraterritorial food. Nevertheless, these forms of competition between neighbours should have little influence on agreement about boundaries for singing, because advantages of mutual restraint in competition in one arena would accrue to neighbours regardless of continuing competition in other arenas. Territorial neighbours could mutually benefit by respecting boundaries for singing, regardless of whether or not they continue to compete without restraint for other resources. Consequently, differences among species in responses to singing neighbours seem unlikely to result simply from differences in other possible rivalries between neighbours.

Reduced neighbour-stranger discrimination during increased flux in territorial boundaries might make neighbours and strangers equal rivals for singing space. Furthermore, the continual changes in neighbours would increase the challenge of discrimination.

(2) In other circumstances, advantages of complex or shared vocalizations could outweigh advantages of discrimination between neighbours and strangers. In tyrant flycatchers, complex vocalizations subject to innate developmental constraints might preclude the evolution of songs with strong individualities. Instead, complex frequency-modulated songs might evolve as a result of sexual selection by intraspecific or interspecific mate choice, despite disadvantages of reduced discrimination among individuals.

Among visually similar sibling species of flycatchers, elaborate songs are evidently crucial for recognition of conspecifics (Stein 1963; Lanyon 1978; Johnson 1980). Little is known about which features of these songs are important for species recognition or mate choice, or how degradation and background sounds affect their perception

by conspecifics. Consequently, we cannot yet say much about possible trade-offs between advantages of species recognition and individual recognition in these species.

In some oscines, such as red-eyed vireos, complex repertoires or precisely shared songs might also evolve as a result of sexual selection, despite disadvantages in possibilities for individual recognition by song. In others, such as tufted titmice, which occupy year-round territories and have life-long relationships with neighbours, strongly individualized songs might not be needed for recognition. In this case, precise sharing of songs might evolve without consequences for recognition of neighbours.

Territorial Acadian flycatchers are less proficient in neighbour-stranger discrimination than some oscines in similar habitats and with similar behaviour otherwise. This finding raises the question why species differ in their capabilities for recognizing individuals.

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Statistical Appendix

(1) One-way ANOVAs for individual differences in frequencies in songs: frequency B: $F_{12,35} = 10.7$, $P < 0.0001$; frequency C: $F_{12,35} = 7.0$, $P < 0.0001$; frequency D: $F_{12,35} = 12.3$, $P < 0.0001$; frequency E: $F_{12,35} = 9.8$, $P < 0.0001$; frequency F: $F_{12,35} = 1.3$, $P = 0.30$; frequency G: $F_{12,35} = 4.5$, $P = 0.0009$.

(2) One-way ANOVAs for individual differences in intervals in songs: interval AG: $F_{12,35} = 28.0$, $P < 0.0001$; interval BC: $F_{12,35} = 2.1$, $P = 0.06$; interval CD: $F_{12,35} = 11.8$, $P < 0.0001$; interval DE: $F_{12,35} = 4.3$, $P = 0.001$; interval EF: $F_{12,35} = 21.5$, $P < 0.0001$; interval FG: $F_{12,35} = 1.0$, $P = 0.49$.

(3) One-way ANOVAs for differences in frequencies among songs of neighbours, neighbours once removed, and distant individuals: frequency B: $F_{2,19} = 0.25$, $P = 0.79$; frequency C: $F_{2,19} = 0.55$, $P = 0.59$; frequency D: $F_{2,19} = 0.70$, $P = 0.51$; frequency E: $F_{2,19} = 0.09$, $P = 0.91$; frequency F: $F_{2,19} = 0.56$, $P = 0.58$; frequency G: $F_{2,19} = 0.04$, $P = 0.96$.

(4) One-way ANOVAs for differences in intervals among songs of neighbours, neighbours once removed, and distant individuals: interval AG: $F_{2,19} = 2.61$, $P = 0.10$; interval BC: $F_{2,19} = 0.10$, $P = 0.91$; interval CD: $F_{2,19} = 0.86$, $P = 0.44$; interval DE: $F_{2,19} = 0.48$, $P = 0.63$; interval EF: $F_{2,19} = 0.37$, $P = 0.72$; interval FG: $F_{2,19} = 0.63$, $P = 0.54$.

(5) One-way ANOVA for differences in principal component scores for features of songs of neighbours, neighbours once removed, and distant individuals: $F_{2,19} = 0.41$, $P = 0.67$, power = 0.11.

(6) Wilcoxon matched-pairs signed-ranks tests for differences in principal component scores for responses to neighbours' and strangers' songs in 1996: PC1: $T' = 4$, $N = 8$, $P = 0.64$; PC2: $T' = 3$, $N = 8$, $P = 0.74$; PC3: $T' = 4$, $N = 8$, $P = 0.64$; PC4: $T' = -10$, $N = 8$, $P = 0.20$.