

Song variation in a population of Alder Flycatchers

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ABSTRACT. Song variation has been studied extensively over the past 50 yr but almost entirely in oscine passerines. Although learning is an essential component of song development in most, if not all, oscines, there is no definitive evidence for song learning in suboscine passerines. This suggests that the patterns and extent of individual and geographic variation may differ between these groups as well. We examined individual variation in the “fee-bee-o” song in a population of Alder Flycatchers (*Empidonax alnorum*) in southwestern Alberta. Songs of individual males were recorded during the breeding season in 2001. We measured temporal and frequency variables of songs and conducted univariate and multivariate statistical analyses to characterize variation within and among individuals. There was little variation among the songs of an individual male during single recording sessions and across recordings made over the breeding season. All measured variables varied significantly more among than within individuals. Discriminant function analysis assigned 91–100% of songs to the correct individual. Therefore, there was sufficient variation among individual males to identify them statistically and, potentially, to permit individual discrimination by the birds.

SINOPSIS. Variación en el canto de una población de *Empidonax alnorum*

La variación en el canto de las aves ha sido estudiada extensivamente en los últimos 50 años, particularmente en paserinos oscinos. Aunque el aprendizaje es un componente esencial en el desarrollo del canto de la mayoría, si no en todos los oscinos, no hay evidencia para el aprendizaje del canto en paserinos suboscinos. Esto sugiere que el patrón y la amplitud de la variación individual y geográfica pudiera ser diferente entre estos dos grupos. Examinamos la variación individual en el canto “fi-bii-o” de una población de individuos de *Empidonax alnorum* en el suroeste de Alberta. Se grabó el canto de individuos particulares durante la temporada reproductiva de 2001. Medimos variables temporales y de frecuencia y utilizamos análisis estadístico univariable y multivariable para caracterizar la variación en y entre individuos. Se encontró muy poca variación entre individuos machos en una grabación hecha en un momento dado y en grabaciones obtenidas lo largo de la época reproductiva. Todas las variables estudiadas, variaron significativamente más entre individuos que en individuos particulares. El análisis discriminativo de funciones asignó de 91–100% de las canciones al individuo correcto. Por tanto, hubo suficiente variación entre individuos machos para poder identificarlos, utilizando estadísticas, y potencialmente para permitir que las propias aves puedan discriminar entre individuos.

Key words: Alberta, *Empidonax alnorum*, individual variation, song, suboscine

The avian order Passeriformes includes approximately 5700 species or about 60% of living species of birds (Sibley and Monroe 1990). Suboscine passerines (suborder Tyranni) make up approximately 20% (1151 species) of the order and are a dominant part of Neotropical avifaunas (Sibley and Monroe 1990). Despite this, our knowledge of passerine song and its functions is biased heavily toward studies of oscine passerines (suborder Passeri). However, it is known that species in 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 oscine passerines studied (33 families; Kroodsma 1982, 1996; Slater 1989). In contrast, song ontogeny is apparently genetically-programmed

in suboscines (Kroodsma 1984). A potential effect of learning versus non-learning modes of song development may be greater geographic and individual variation in song structure exhibited by oscines than by most suboscines (Kroodsma 1996).

Although little, if any, geographic or individual variation has been described in songs of suboscines (Stein 1963; Lanyon 1978; Payne and Budde 1979; Johnson 1980), visual inspection of published audiospectrograms (e.g., Stein 1963; Payne and Budde 1979; Kroodsma 1984) suggests measurable variation. However, large sample sizes of songs and quantitative analyses have been lacking in most studies of variation in suboscine passerine songs (see Sedgwick 2001 for an exception).

Individual variation in the vocalizations of birds has been documented in many species (re-

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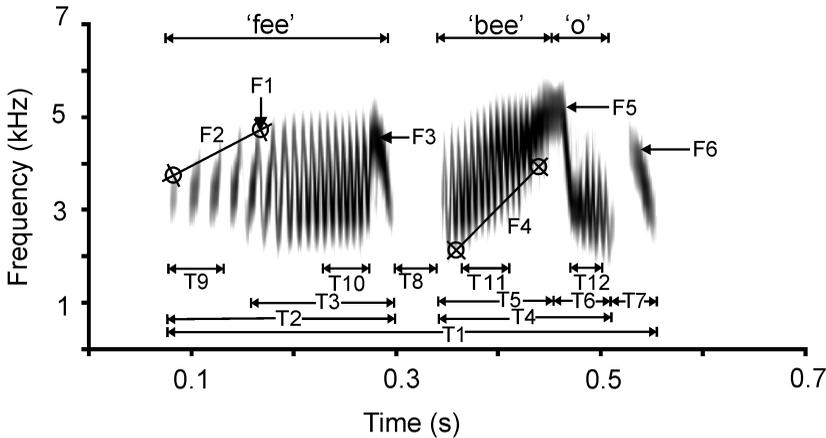


Fig. 1. Audiospectrogram of a “fee-bee-o” song of the Alder Flycatcher. Lines and symbols indicate time (T) and frequency (F) measurements. See Appendix 1 for explanation of measurements.

viewed in Beer 1970; Falls 1982). The few studies that have attempted to characterize individual variation in songs of suboscines (Kelloff and Stein 1953; Payne and Budde 1979; Kroodsma 1984) did not measure enough songs to describe variation within and among individuals in a population adequately and thus were not able to provide a comprehensive quantitative analysis of variation. We recorded and analyzed songs of Alder Flycatchers (*Empidonax alnorum*) to determine whether variation was sufficiently restricted within individuals, but sufficiently great among individuals, to permit us to identify individuals by song.

METHODS

Songs of 13 territorial male Alder Flycatchers were recorded during the breeding season of 2001 at Bryant Creek (51°02'N, 114°47'W) in the foothills of the Rocky Mountains, approximately 80 km west of Calgary, Alberta. Alder Flycatchers breed in willow (*Salix* spp.) and bog birch (*Betula glandulosa*) thickets bordering streams and beaver ponds in the area. Ten males were captured using mist nets, banded, and marked with hair dye on their breast feathers for individual identification. Three unmarked individuals were identified by territory position and their persistent use of specific song perches. Songs were recorded between 03:00 to 08:00 MST using a Nagra 4.2 reel-to-reel tape recorder and a Sennheiser K6-P microphone in a Telinga parabolic reflector. Alder Flycatchers

song repertoires consist of one relatively simple song type (Fig. 1) described verbally as “fee-bee-o” (Stein 1963).

Individual songs were acquired from the original tapes as digital sound files using RTSD Ver. 1.10 and SIGNAL Ver. 3.1 bioacoustical software (Engineering Design, Belmont, MA) with a sample rate of 25 kHz. We wrote a program in the SIGNAL language to assist in measurement of 12 temporal variables and six frequency variables for each “fee-bee-o” song (Fig. 1; measurements defined in Appendix 1). Temporal variables were measured on wideband spectrograms with a resolution of 2.6 ms. Frequency variables were measured on a spectral contour generated from the spectrogram. Spectral contours track the frequency with the maximum sound energy at a given time. This procedure avoided the subjectivity associated with measurement of frequency on a wideband spectrogram. Two data sets were generated. The first included measurements of 10 songs recorded on a single day for each male (within-recordings data set). The second included measurements of single examples of songs from each of a series of recordings made on 4–9 different dates for each male (among-recordings data set).

SYSTAT 9.0 software (SPSS Inc., Chicago, IL) was used in all statistical analyses. We used coefficients of variation (CV) to quantify the magnitude of variability in each measured variable in the within-recordings data set. We calculated within-male coefficients of variation (CV_w) for each male to measure the amount of

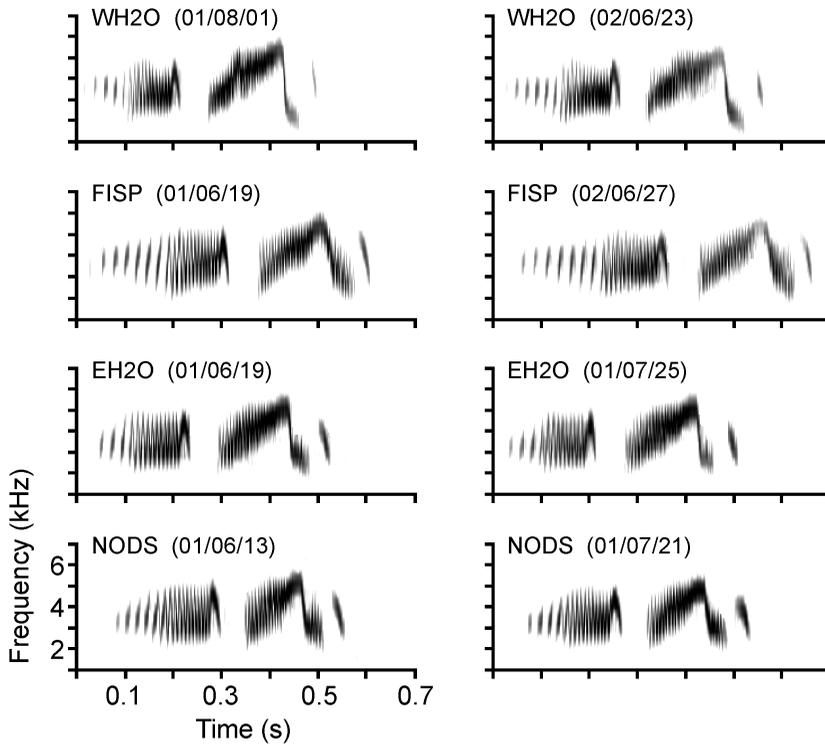


Fig. 2. Audiospectrograms of “fee-bee-o” songs of Alder Flycatchers indicating constancy of songs within individuals and variation among individuals. Each row has two songs of an individual. Note that examples for males FISP and WH2O were recorded in different years.

variation during a recording session and calculated among-male coefficients of variation (CV_a) from the variable means for each male. An ANOVA was conducted on each of the 18 variables in the within-recordings data set to compare within-male and among-male variability in these variables.

Many of the variables measured were correlated with one another. 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. We then used discriminant function analysis (DFA) of principal component scores of songs in each of the two data sets to determine whether songs of individuals could be identified reliably. Results of jack-knifed classifications, in which each song was classified using discriminant functions computed from all songs in the data set except the case being classified, are reported as percentages of songs classified correctly. This technique was used because it is a conservative estimate of the power of the clas-

sification technique and as a way to cross-validate our results (Manly 1994). We also combined the two data sets into a cross-classification data set, conducting an additional DFA to determine whether discriminant functions derived from the among-recordings data set could correctly identify the songs in the within-recordings data set.

RESULTS

Visual inspection of audiospectrograms suggests differences in timing, “shape,” and presence or absence of different elements that characterize songs of different individuals (Fig. 2). Values of mean CV_w ranged from 0.9% for maximum frequency of the terminal note of the “fee-bee-o” song (F6) to 57.8% for rate of frequency change in the “fee” introduction (F2). Values of CV_a ranged from 5.2% for the maximum frequency of the “fee” chevron (F3) to 57.9% for rate of frequency change in the “fee” introduction (F2). Coefficients of variation

Table 1. Descriptive statistics and coefficients of variation for 18 variables measured for 10 “fee-bee-o” songs each for 13 male Alder Flycatchers in the within-recordings data set. See Fig. 1 and Appendix 1 for explanation of variables.

Variable	Mean \pm SD	Mean CV_w (Range)	CV_a	$F_{12, 117}^a$
T1	517.8 \pm 35.4	2.4 (1.1–3.0)	6.8	77.8
T2	234.9 \pm 30.2	4.9 (2.2–6.9)	12.8	63.9
T3	122.7 \pm 12.1	4.7 (3.0–7.9)	9.9	42.7
T4	189.9 \pm 23.4	1.5 (0.9–2.1)	12.3	621.9
T5	136.7 \pm 21.5	2.3 (1.5–4.1)	15.7	421.6
T6	53.3 \pm 7.9	5.3 (3.0–8.7)	15.0	79.2
T7	39.4 \pm 5.9	5.3 (3.1–7.8)	15.0	66.0
T8	53.6 \pm 9.0	3.2 (1.3–5.2)	16.9	257.1
T9	19.1 \pm 1.0	5.1 (3.2–7.8)	5.5	10.9
T10	7.1 \pm 0.6	1.4 (0.8–2.9)	8.3	332.3
T11	6.4 \pm 0.3	2.7 (1.1–6.0)	5.5	29.5
T12	5.9 \pm 0.5	6.0 (2.1–16.3)	7.8	10.6
F1	4064.3 \pm 227.7	4.1 (0.6–7.9)	5.6	15.7
F2	8.5 \pm 4.9	57.8 (21.6–268.8)	57.9	16.4
F3	4344.3 \pm 223.7	1.1 (0.4–2.1)	5.2	189.7
F4	20.9 \pm 5.2	3.1 (3.2–13.7)	25.0	105.8
F5	5053.2 \pm 305.3	1.3 (0.4–5.4)	6.0	103.9
F6	4292.5 \pm 316.4	0.9 (0.7–3.4)	7.4	121.6

^a F -values for ANOVAs comparing within- and among-male variation for each variable; all $P < 0.001$.

among males (CV_a) were greater than coefficients of variation within males (CV_w) for all variables measured (Table 1). ANOVAs revealed that all 18 variables varied significantly more among males than within males (Table 1).

Principal components analyses of the different data sets generated five or six principal components with eigenvalues >1.0 from the original measurements, explaining at least 78% of the variation among individuals (Table 2). MANOVAs conducted as part of DFAs showed highly significant differences among multivariate means for different individuals in all data sets (within-recordings, $F_{72,615} = 114.1$, $P < 0.001$; among-recordings, $F_{35,141} = 26.2$, $P < 0.001$; cross-classification, $F_{42,317} = 92.8$; $P < 0.001$). Jack-knifed classifications correctly identified all 130 songs in the within-recordings

data set and 41 of the 45 songs (91%) in the among-recordings data set. The cross-classification analysis correctly identified all songs from the within-recordings data set using the discriminant functions generated from the among-recordings data set.

DISCUSSION

Our results indicate that there is little variation in songs within individuals, with low mean CV_w values for most variables measured (Table 1). Quantitative analyses (S. Lovell and R. Lein, unpubl. data) and visual examination of songs of two marked males recorded in both 2001 and 2002 (WH2O and FISP, Fig. 2) also indicate that songs of individuals do not change from year to year. This is not surprising, given

Table 2. Sample sizes and results of principal component analyses for data sets measured for “fee-bee-o” songs of Alder Flycatchers.

Data set	No. of males	Songs/male	Number of PCs with eigenvalue > 1.0	Variance explained
Within-recordings	13	10	6	84%
Among-recordings	8	4–9	5	78%
Cross-classification	8	—	6	82%

the evidence that songs of this species are innate (Kroodsma 1984).

Our analyses demonstrate that there is sufficient stereotypy of song features within males in the population at Bryant Creek, but sufficient variation among males, to permit statistical identification of songs of individuals. There also appears to be sufficient variation among males to permit individual recognition of territorial neighbors by the birds. Although such individual recognition seems likely, it has not been demonstrated conclusively for this species or for any suboscine (Stoddard 1996).

Analyses of the type that we used provide a means to assign unknown songs to the correct individual in the absence of information such as color-marking. However, it should be recognized that DFA will assign all unknowns to one of the pre-defined groups. Such a procedure would be valid only if songs of all individuals in the study population were used to calculate the discriminant functions (Terry et al. 2001).

This study is one of the first to document individual variation in songs of a suboscine passerine using quantitative methods. Such variation does not allow us to infer anything about possible functions. Individual variation is a prerequisite for possible neighbor-stranger discrimination and individual recognition by song (Falls 1982). Neighbor-stranger discrimination has been tested in only two suboscine species (Bard et al. 2002; Westcott 1997) with rather ambiguous results. Individual recognition has not been demonstrated conclusively in any suboscine. If found, the logical next step would be to determine the features of songs involved in individual recognition.

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Appendix 1. Description of song variables measured for audiospectrograms of “fee-bee-o” songs of male Alder Flycatchers. See methods for description of procedures used to measure temporal and frequency variables.

Code	Variable
T1	Duration of the entire song (msec)
T2	Duration of the “fee” phrase (msec)
T3	Duration of the frequency modulation (FM) portion of the “fee” phrase (msec)
T4	Duration of the “bee-o” phrase (msec)
T5	Duration of the “bee” portion of the “bee-o” phrase (msec)
T6	Duration of the “o” portion of the “bee-o” phrase (msec)
T7	Duration of the interval between “bee-o” phrase and terminal note (msec)
T8	Duration of the interval between the “fee” and “bee-o” phrases (msec)
T9	Repetition rate of the first four introductory notes of the “fee” phrase (msec)
T10	Repetition rate of last four FMs of the “fee” phrase (msec)
T11	Repetition rate of first four FMs of the “bee” portion of the “bee-o” phrase (msec)
T12	Repetition rate of first four FMs of the “o” portion of the “bee-o” phrase (msec)
F1	Maximum frequency of the “fee” introductory notes (kHz)
F2	Rate of frequency change in the “fee” introduction (Hz/msec)
F3	Maximum frequency of the “fee” chevron (kHz)
F4	Rate of frequency change of the “bee” portion of the “bee-o” phrase (Hz/msec)
F5	Maximum frequency of the “bee-o” phrase (kHz)
F6	Maximum frequency of the terminal note of the “fee-bee-o” song (kHz)