

LIMITED GEOGRAPHIC VARIATION IN THE VOCALIZATIONS OF A NEOTROPICAL FURNARIID, *SYNALLAXIS ALBESCENS*

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ABSTRACT.—I recorded and analyzed vocalizations of *Synallaxis albescens* from three populations in Venezuela, two continental and one island, to assess the extent of geographic variation for a species of the family Furnariidae. Previous work on geographic variation in suboscines has focused on species of the Tyrannidae. I also tested the sound environment hypothesis. From nine vocalization characters I created discriminant functions that best separated the three populations. I then used classification analyses to determine how well the discriminant function models assigned individuals to their home populations. Classification analyses using discriminant functions created from first songs of recorded individuals correctly assigned individuals to their home populations 74.1% of the time and 66.7% of the time for functions created from arbitrarily chosen sixth songs. The island population was significantly more variable than either of the continental populations for the first syllable length but not for the frequency-modulated portion of the second syllable. The results demonstrate that geographic variation exists among populations although a sufficient amount of similarity prevents unequivocal classification of $\frac{1}{4}$ to $\frac{1}{3}$ of individuals to their home populations. The results regarding vocalization variability provide weak support for the sound-environment hypothesis. Received 30 June 1997, accepted 9 Feb. 1998.

The avian order Passeriformes comprises two suborders, the oscines, suborder Passeri, and the suboscines, suborder Tyranni. The oscines developed the ability to learn vocalizations and now produce songs that are strongly influenced by environmental experience (Kroodsma and Baylis 1982). In contrast, the suboscines do not demonstrate vocal learning and generally produce songs that are stereotyped and little affected by the environment (Nottebohm 1972). For example, laboratory work with a suboscine species, the Eastern Phoebe (*Sayornis phoebe*) showed that its song was relatively unaffected by environmental influence (Kroodsma 1985, 1989; Kroodsma and Konishi 1991).

One result of the flexibility of the oscine vocal learning process is geographic variation of songs within species (Marler and Tamura 1962; reviewed in Mundinger 1982, Shy 1983, Tubaro et al. 1993, Tubaro and Segura 1995). If the lack of learning by the Eastern Phoebe extends to the majority of suboscines, the expectation is that their songs will not vary geographically to the extent observed in oscines because the environment will be unable to influence a learning process. This reasoning does not preclude the possibility that

geographic variation may arise through restricted gene flow between populations, genetic drift, or natural selection for “fitting” vocalizations to the environment, but it does remove a potentially major source of variation. Studies that systematically investigated geographic variation in suboscine song have found little evidence that it exists, although the studies have all involved species of the family Tyrannidae (Lanyon 1978, Payne and Budde 1979, Johnson 1980). The present analysis is the first systematic investigation of geographic variation in the vocalizations of a Furnariid.

In this study I also compare the variability of vocalizations of an island population with that of two mainland populations, allowing a test of Marler’s (1960) sound environment hypothesis. This hypothesis predicts that species inhabiting areas with few other species, the island population in this case, will be less constrained to produce rigid species-specific vocalizations than species inhabiting areas with many other competitors for vocal space, like the continental populations. The study species was the Pale-breasted Spinetail (*Synallaxis albescens*) which has an extensive distribution, ranging from Central America through central Argentina (Vaurie 1980).

STUDY AREA AND METHODS

Recordings of Pale-breasted Spinetails were made at three locations in Venezuela (Fig. 1). Hato Masaguaral, a wildlife preserve/cattle ranch in the state of Guarico

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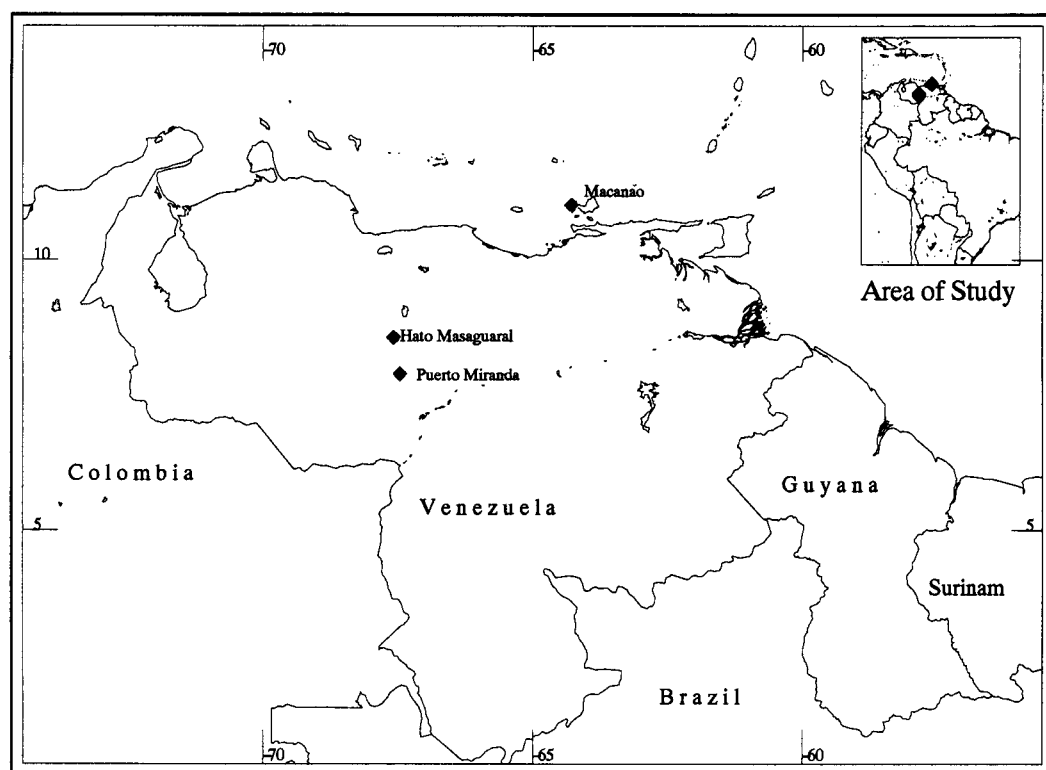


FIG. 1. Sites where vocalizations were recorded.

in central Venezuela, is located at $8^{\circ} 34' \text{ N}$, $67^{\circ} 35' \text{ W}$. The second site was a rice farm, Puerto Miranda, in the state of Apure, $7^{\circ} 54' \text{ N}$, $67^{\circ} 28' \text{ W}$. The third site was the southern shore of the peninsula of Macanao on Margarita Island, off the northern coast of Venezuela, at $11^{\circ} 00' \text{ N}$, $64^{\circ} 17' \text{ W}$. Masaguaral is approximately 90 km from Miranda and 450 km from Margarita Island. Miranda is approximately 480 km from Margarita Island. Recordings were made at Masaguaral 19–20 April 1993, at Miranda 23 April 1993 and at Margarita Island, 29 April 1993. Eleven birds were recorded at Masaguaral, 10 at Miranda, and 6 at Margarita Island. Recordings were made passively, as I walked through sites and heard individuals singing. Male and female Pale-breasted Spinetails are monomorphic and it is likely that both sing as is the case with other Furnariids such as *Synallaxis brachyura* and *Phacellodomus rufifrons* (Skutch 1996). I used a TC-D5 Pro II Sony tape recorder and Dan Gibson P 650 parabolic microphone to make the recordings.

I made sonagrams for the first 11 songs per individual unless any of those songs did not produce a legible figure. When sonagrams were not legible, successive songs were used to obtain a total of 11 songs per bird. For one bird of the Margarita Island population only nine songs were usable. The sonagrams were produced with a Kay Elemetrics DSP Sonagraph, Model 5500.

Time measurements were taken from sonagrams with a 300 Hz filter bandwidth and frequency measurements from sonagrams with a 59 Hz filter bandwidth. Following previous studies (Payne and Budde 1979, Johnson 1980, Kroodsma 1984, Baptista and Schuchmann 1990, Handford and Loughheed 1991, Tubaro and Segura 1995), I measured a number of variables for each song: the frequency immediately before the abrupt rise in frequency near the end of the first syllable (F1), the maximum frequency of the abrupt rise (F2), the maximum frequency of the second syllable (F3), the duration of the first syllable excluding the abrupt rise in frequency toward the end of the syllable (T1), the duration of the first syllable (T2), the duration of the interval between the first and second syllables (T3), the duration of the second syllable (T4), the duration of the first five frequency modulations after the maximum frequency of the second syllable (T5), and the duration of the entire vocalization (T6; Fig. 2).

Measurements taken from the first recorded songs of each individual were used in analyses to determine whether the three populations had distinctive song characteristics that could be used to classify individuals as belonging to one population or another. Similar analyses were carried out with the arbitrarily chosen sixth songs and the results using the first and sixth songs were compared. For the above models, I used

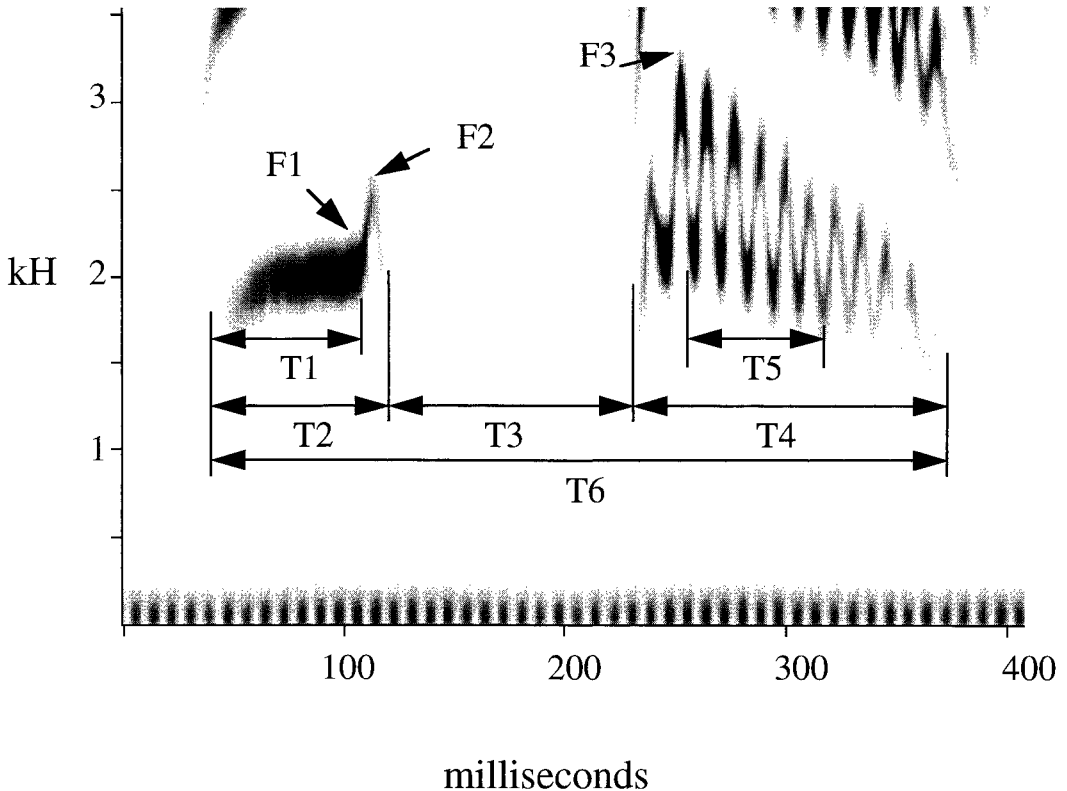


FIG. 2. Temporal and frequency variables that were measured from sonagrams of vocalizations of *Synallaxis albescens*.

stepwise Multivariate Analysis of Variance procedures to choose the song characteristics that could be used to create discriminant functions (Rencher 1995). The discriminant functions are linear combinations of the chosen variables that provide the best separation between groups. Once I determined the variables to be used in each model, the discriminant analyses were conducted. The same models were then used in classification analyses to determine how well the models classified an individual as belonging to a particular population.

Coefficients of variation provide a means to compare the variability of a character across populations. To test the sound environment hypothesis I determined coefficients of variation for the two uncorrelated vocal characters that were most useful in discriminating among the populations. Since the island population of Pale-breasted Spinetails shares vocal space with only one half the number of species as the mainland populations, the expectation was that the vocal characters should be more variable for the island population. All statistical analyses were performed with SYSTAT 5.2 for the Macintosh (SYSTAT 1992).

RESULTS

The song of *Synallaxis albescens* is composed of two notes and is usually repeated fre-

quently by an individual. The song shows similarities to those of the Eastern Phoebe and the Willow Flycatcher (*Empidonax traillii*). Two to three harmonics were visible in most spectrograms with more energy typically concentrated in the second harmonic than in the fundamental frequency. Measurements of the nine variables for individuals of the three populations are given in Table 1.

The duration of the first syllable, the duration of the first syllable excluding the abrupt rise in frequency toward the end, the duration of the frequency-modulated portion of the second syllable, and the frequency near the end of the first syllable showed significant differences among populations in one-way ANOVAs using the first songs and then the sixth songs of individuals. However, some of these variables were significantly correlated. For first and sixth songs, the durations of the first syllable and the frequency-modulated portion of the second syllable were two uncorrelated

TABLE 1. Descriptive statistics for vocalizations of *Synallaxis albescens* from three populations.

Variable	Hato Masaguaral	Margarita Island	Puerto Miranda
No. individuals	11	6	10
T1 ^a	88.25 ± 9.00 ^b	93.45 ± 14.66	102.29 ± 12.88
T2	102.35 ± 9.00	107.42 ± 13.67	116.13 ± 12.70
T3	95.04 ± 8.23	103.79 ± 14.71	92.16 ± 7.45
T4	166.41 ± 17.65	167.61 ± 9.66	172.27 ± 16.64
T5	53.85 ± 5.48	58.90 ± 2.78	51.75 ± 3.45
T6	360.99 ± 12.75	377.80 ± 32.72	380.64 ± 30.61
F1 ^c	2320.00 ± 151.46	2145.25 ± 171.50	2294.18 ± 143.07
F2	2949.75 ± 175.96	2672.83 ± 301.08	3027.09 ± 400.02
F3	3249.18 ± 212.82	3204.92 ± 229.47	3320.55 ± 249.25

^a T1 is the duration of the first syllable, excluding the abrupt rise in frequency at the end of the syllable; T2 is the duration of the first syllable; T3 is the duration of the interval between the first and second syllables; T4 is the duration of the second syllable; T5 is the duration of the first five frequency modulations after the maximum frequency of the second syllable; T6 is the duration of the entire vocalization; F1 is the frequency immediately before the abrupt rise in frequency near the end of the first syllable; F2 is the maximum frequency of the abrupt rise; F3 is the maximum frequency of the second syllable. Time variables are in milliseconds.

^b Values are mean ± standard deviation. Means are based on 11 songs per individual except for one individual from the Margarita Island population for which I used 9 songs. I calculated a mean for each individual and then calculated a second order mean for each population using the individual means.

^c Frequency variables are in Hertz.

variables that showed significant differences among populations ($F_{2,24} = 4.66$, $P < 0.025$, and $F_{2,24} = 4.50$, $P < 0.025$, respectively, for first songs; $F_{2,24} = 3.54$, $P < 0.05$, and $F_{2,24} = 4.05$, $P < 0.05$, respectively, for sixth songs). For first and sixth songs, the duration of the first syllable did not differ between the populations of Masaguaral and Margarita Island or between the populations of Miranda and Margarita Island, although it was significantly longer for the Miranda population compared to the Masaguaral population (Tukey-Kramer test for unplanned comparisons among means: $P > 0.05$, > 0.05 , and $= 0.02$,

respectively, for first songs; $P > 0.05$, > 0.05 , and $= 0.04$, respectively, for sixth songs). The duration of the frequency-modulated portion of the second syllable did not differ between the populations of Masaguaral and Margarita Island or between the populations of Masaguaral and Miranda, although it was significantly longer for the population of Margarita Island compared to the population of Miranda (Tukey-Kramer test for unplanned comparisons among means: $P > 0.05$, > 0.05 , and $= 0.02$, respectively, for first songs; $P > 0.05$, > 0.05 , and $= 0.03$, respectively, for sixth songs).

Stepwise MANOVA variable selection and discriminant analyses for the first songs revealed that the duration of the first syllable and the frequency near the end of the first syllable were most important in distinguishing individuals from different populations. For the sixth songs, the duration of the frequency-modulated portion of the second syllable, the duration of the first syllable, and the frequency near the end of the first syllable were most important (Table 2). Subsequent classification analyses using the discriminant models correctly classified an individual bird to its home population 74.1% of the time for the first song model and 66.7% of the time for the sixth song model.

For the duration of the first syllable, the Margarita Island population had a significantly greater coefficient of variation than either

TABLE 2. Discriminant models constructed to distinguish vocalizations from three populations.

Variables	Correlation with discriminant	
	function 1	function 2
First Songs		
T2 ^a	0.61355	0.78965
F1	0.48997	-0.87174
Sixth Songs		
T5 ^b	-0.48905	0.89350
T2	0.31557	0.40472
F1	0.39433	-0.76115

^a T2 is the duration of the first syllable; F1 is the frequency immediately before the abrupt rise in frequency near the end of the first syllable. Both variables make significant contributions to model, T2 at $P < 0.025$ and F1 at $P < 0.025$. Model has overall Wilks' Λ of 0.492, $F_{4,46} = 4.90$, and $P < 0.005$.

^b T5 is the duration of the first five frequency modulations after the maximum frequency of the second syllable. All three variables make significant contributions to model, T5 at $P < 0.05$, T2 at $P < 0.01$, and F1 at $P < 0.05$. Model has overall Wilks' Λ of 0.364, $F_{6,44} = 4.82$, and $P < 0.001$.

the Masaguaral population ($\bar{x} = 4.74 \pm 0.62\%$ SD vs. $3.67 \pm 1.40\%$, respectively; Mann-Whitney U -test; $N_1 = 11$, $N_2 = 6$, $U = 55$, $P < 0.025$) or the Miranda population ($2.87 \pm 1.13\%$, Mann-Whitney U -test; $N_1 = 10$, $N_2 = 6$, $U = 55$, $P < 0.005$). For the coefficients of variation of the duration of the frequency-modulated portion of the second syllable, there were no significant differences between the Margarita Island and Masaguaral populations ($2.28 \pm 2.07\%$ vs $1.76 \pm 0.81\%$, respectively; Mann-Whitney U -test; $N_1 = 11$, $N_2 = 6$, $U = 34$, $P > 0.05$) or between the Margarita Island and Miranda populations ($1.74 \pm 0.61\%$; Mann-Whitney U -test; $N_1 = 10$, $N_2 = 6$, $U = 34$, $P > 0.05$).

DISCUSSION

Previous researchers of furnariid vocalizations have concluded that little, if any, geographic variation exists, although the conclusions were not based on systematic analyses of songs (Vaurie and Schwartz 1972, Vaurie 1980). For example, Vaurie and Schwartz (1972) presented sonagrams for various members of the genus *Synallaxis* but their conclusion of no variation in the song of several species, including *S. albescens*, was based on "the extensive field experience of Schwartz". With regard to suboscines of families other than the Furnariidae, Payne and Budde (1979), in their investigation of song differences and distance between territorial Acadian Flycatchers (*Empidonax virescens*), reported a lack of correlations between the degree of similarity of any of the song characters and distance between birds, although they conducted their study over a limited geographic scale (< 30 km). Lanyon (1978) in a revision of the genus *Myiarchus*, reported no geographic variation in vocalizations for 7 of the 11 species studied. For 1 of the 11 species he had no data, and of the 3 for which he did report some variation, 2 showed variation in carrier frequency that he found to be inversely correlated with body size (bigger body = lower frequency). The geographic variation Johnson (1980) described for two other species of flycatchers, *E. difficilis* and *E. flavescens*, may be a result of interspecific, rather than intraspecific variation (Kroodsma 1988). The results here demonstrate some identifiable differences between the populations although not

all the patterns are consistent with the expectation that the closest populations, Masaguaral and Miranda, should be the most similar. Although these populations were similar in the duration of the frequency-modulated portion of the second syllable, they were significantly different in the duration of the first syllable. The Margarita Island population showed no differences from the Masaguaral population in these two variables while it did differ from the Miranda population in the duration of the frequency-modulated portion of the second syllable. These results indicate that some vocal characters differ among populations, but that the patterns of difference are not consistent from character to character, and that distance between sites is not a good predictor of the degree of similarity between populations. It is unlikely that population differences can be attributed to different motivational states because all individuals were recorded during approximately the same time of year, late in the dry season before breeding had begun.

The discriminant models demonstrate that combinations of variables can be used to classify individuals to one population or another, although not with a great deal of accuracy; 74.1% of individuals were correctly classified with the first song model and 66.7% were correctly classified with the sixth song model. An observer is hard put to distinguish differences among the populations in the field (pers. obs.), although a few subtle differences among populations were evident from the sonagrams. In contrast, research of oscine vocalizations sometimes reveals striking patterns of song differences over distance (Marler and Tamura 1962, McGregor 1980, Rothstein and Fleischer 1987). Baptista and King (1980) for example, found seven song types and numerous distinctive variations of these types for White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the western U.S. The results presented here indicate that the variability that exists between populations is less than that found in several oscine species that have been studied, and support the idea that environmental influence on song is limited.

The greater variability of the duration of the first syllable for the Margarita Island population, compared to either of the mainland populations, supports the sound environment hypothesis of Marler (1960) that predicts vocal-

izations are less species-specific in environments with fewer other species. Approximately 147 resident species occur on Margarita Island (Yepez Tamayo 1963), while nearly 300 occur in central Venezuela, where the Masaguaral and Miranda populations are located (Thomas 1979). Kroodsma and co-workers (1987) found little support for the sound environment hypothesis in a comparison of the variability of songs of the Cocos Flycatcher (*Nesotriccus ridgwayi*) with songs of the closely related Mouse-colored Tyrannulet (*Phaeomyias murina*), which lives in a more species-rich environment. However, a comparison of the vocalizations of one species in several environments provides a stronger test of the hypothesis. The duration of the frequency-modulated portion of the second syllable, in contrast to the duration of the first syllable, was not more variable in the island population than the continental populations, indicating that different song characters vary in their flexibility. If the duration of the frequency-modulated portion of the second syllable is a more significant variable with regard to species-specific recognition than the duration of the first syllable, it may be that such characters are highly conserved, even in species-poor environments. A more definitive test of the hypothesis will include assessments of the importance of the characters to the birds' species-recognition abilities and determination of the strength and mechanisms of interspecific influences on song.

Suboscine families such as the Furnariidae and the Tyrannidae are speciose (>200 species and >350 species, respectively), yet several authors have suggested a link between vocal learning and high rates of speciation. Marler (1970) suggested that vocal learning was an evolutionary response to the demands of species-specific recognition in passerines, necessitated by high rates of speciation and high degrees of sympatry in the group. Kroodsma (1988) indicated that high speciation rates among oscines may be a result of vocal learning, if vocal learning promotes genetic isolation of populations. Nottebohm (1972:130) also recognized a relationship between rapid speciation and the ability to learn vocalizations, although he stated, "In no case is it possible to say whether vocal learning preceded and aided rapid speciation or resulted from it;

the correlation between the two may be accidental." He also noted exceptions to the pattern of speciose groups being vocal learners, for example, the tyrannids and furnariids mentioned above. Ames (1971), in his analysis of syrinx characters and their relevance to passerine systematics, documented the uniform morphology of the oscine syrinx and the highly variable nature of the suboscine syrinx. While vocal learning, associated cultural evolution, and geographic variation in song may be linked to rapid speciation in oscines, perhaps morphological evolution of the syrinx and accompanying divergence in song is linked to high speciation rates in suboscine groups. The constraints of the evolutionary histories of the two groups may have resulted in different strategies to insure species-specific song and reproductive isolation.

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