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Source: The Wilson Journal of Ornithology, 129(1):13-24.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/1559-4491-129.1.13
URL: http://www.bioone.org/doi/full/10.1676/1559-4491-129.1.13

The Wilson Journal of Ornithology 129(1):13–24, 2017

VOCAL VARIATION AND SPECIES LIMITS IN THE *SCLERURUS MEXICANUS* COMPLEX

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ABSTRACT.—Phylogeographic analyses have hypothesized that *Sclerurus* (Furnariidae) populations of the rufous-throated clade (*S. rufigularis* and *S. mexicanus* sensu lato) have a long history of evolutionary isolation, particularly within the *S. mexicanus* complex (Tawny-throated Leaftosser). Although it has long been recognized that *S. mexicanus* should be split into two or more species, choosing between alternative species-delimitation schemes is much less clear due to minimal understanding of phenotypic variation and distributional range limits. We explored the extent of vocal variation between all described subspecies of *S. mexicanus* by analyzing spectral and temporal traits of songs and calls. We found five distinct vocal groups within *S. mexicanus* that differ primarily in their songs' maximum frequency, pace, and note shape. Specifically, we found that *mexicanus, pullus, andinus*, and *obscurior* each are vocally distinct from one another and from a group composed of *macconnelli, peruvianus,* and *bahiae*. Song traits of *S. rufigularis* overlapped with those of sympatric *macconnelli* and *peruvianus* and allopatric *obscurior*. The vocal distinctiveness patterns paralleled phylogeographic patterns and support a taxonomic scheme of treating *S. mexicanus* as five different species: *S. mexicanus*, *S. pullus*, *S. obscurior*, *S. andinus*, and *S. macconnelli* (including *peruvianus* and *bahiae*). *Received 18 July 2015. Accepted 3 April 2016.*

Keywords: elevational zonation, Sclerurinae, species limits, suboscine vocalizations, trait conservatism

Sclerurus leaftossers inhabit understory of tropical lowland and lower montane forests from southeastern Brazil to central Mexico (Parker et al. 1996, Remsen 2003) and represent one the most distinct lineages in the Furnariidae radiation (Moyle et al. 2009, Derryberry et al. 2011, d'Horta et al. 2013). Six species currently are recognized, but none are monotypic (Remsen 2003, Clements et al. 2014), suggesting a need for taxonomic revision. Under current taxonomy, each *Sclerurus* is a relatively widespread polytypic species with pronounced phylogeographic structure (d'Horta et al. 2013). Although most of the genetically differentiated populations within the six *Sclerurus* species are allopatric, a few cases of distributional overlap and elevational parapatry are known in *S. scansor* (d'Horta et al. 2011) and *S. mexicanus* (d'Horta et al. 2013, Smith et al. 2014). In addition, lineages of the *S. scansor*-*S. albigularis* pair do not form reciprocally monophyletic groups when inferred from a nuclear locus, whereas phylogenetic relationships of *S. rufigularis* are uncertain with respect to two major clades of *S. mexicanus* (d'Horta et al. 2013).

The large geographic range of *S. mexicanus* is occupied by seven subspecies (Fig. 1; Remsen 2003, Dickinson and Christidis 2014) that show different degrees of phenotypic and genetic differentiation (Remsen 2003, d'Horta et al. 2013). Similar to other taxa that vary subtly and have little known plumage color patterns, subspecies are often not fully diagnosable (as in *S. m. anomalus* and *S. m. certus*; see Remsen 2003). The assignment of individuals to subspecies may be misleading, thus the deduced geographic ranges may show an artificially intricate pattern. Such misallocations resulted in the distribution of *S. mexicanus andinus*, a taxon restricted to the northern Andean foothills (d'Horta et al. 2013), including the tepuis of northern Amazonia (Hilty 2003, Remsen 2003) and the lowlands of central Panama (Wetmore 1972). In turn, *S. obscurior* of the Chocó lowlands was thought to occur in the Darién highlands (Wetmore 1972). Recent phylogeographic studies helped clarify this conundrum and documented old lineage divergence events among populations of the rufous-throated *Sclerurus* clade, particularly within the *S. mexicanus* complex (d'Horta et al. 2013, Smith et al. 2014). d'Horta et al. (2013) suggested that several subspecies be treated as separate species, but revising species limits in the group is complicated by subtle phenotypic variation between lineages and an incomplete understanding of the limits of their distribution.

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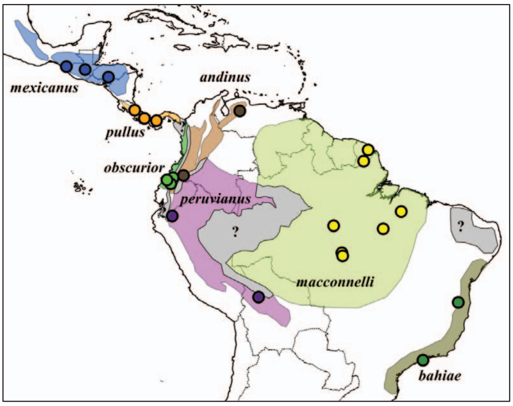

FIG. 1. Distributions of the seven recognized *Sclerurus mexicanus* subspecies based on d'Horta et al. (2013). Points represent georeferenced localities from recordings used in this study (see Table 1). Gray areas (marked with '?') indicate regions in which the subspecies is not known.

Further evidence for underestimated species diversity in *S. mexicanus* exists in the form of elevational parapatry in regions of secondary contact between populations. These elevational replacements involve at least the taxa pairs *obscurior-andinus* along the continuum of humid forests from the Chocó lowlands to the montane slopes of the Western Andes of Ecuador and Colombia, and *macconnelli-peruvianus* of southwestern Amazonia to the eastern slopes of the Andes of southern Peru and Bolivia. In situations where phenotypic differences between putative species can be subtle and confused by individual variation (e.g., *Scytalopus* tapaculos; Krabbe and Schulenberg 1997, Cuervo et al. 2005, Krabbe and Cadena 2010, Avendaño et al. 2015), species diversity and patterns of secondary contact can be easily overlooked.

The patterns of overlapping distributions of evolutionarily distinct lineages, and the lack of support for monophyly utilizing several genetic markers, indicate that changes are warranted to the dominant *status quo* of species taxonomy of *Sclerurus* (d'Horta et al. 2013). Although multiple lines of evidence may clearly indicate that species diversity is underestimated (Peterson 1998, Cadena and Cuervo 2010), delineating species limits in cryptic complexes with subtle vocal and phenotypic characters separating populations is not always straightforward (Mayr and Ashlock 1991, Remsen 2005, Watson 2005, de Queiroz 2007). In *Sclerurus,* taxonomic biases likely have been induced by their overall homogeneous size, shape, and plumage coloration. These issues are compounded by insufficient or inexistent specimen collecting and by a scarcity of phylogenetic studies or assessments of variation in phenotypic or vocal signals. As some species of suboscines have demonstrated that song can be partly or wholly inherited, it has often been used to assist in species delimitation (Kroodsma 1984, 1989; Kroodsma and Konishi 1991; Isler et al. 1998, 1999). In many recent studies of suboscine species complexes, vocal variation has been found to parallel genetic structure (Cuervo et al. 2005, Krabbe and Cadena 2010) and to be a useful character for species delimitation (Isler et al. 1998, 2012; Marantz 2005; Isler and Whitney 2011). Nonetheless, vocal variation must be taken into account with alternative lines of evidence and not treated as a singular character for identifying species groups (Raposo and Höfling 2003). Previous taxonomic assessments within the Furnariidae that have incorporated vocal variation (Robbins and Zimmer 2005) have later been corroborated by genetic data (Derryberry et al. 2011), validating the use of vocalizations to assist in the assessment of suboscine phylogenies.

Here, we analyzed vocalizations from the entire distribution of *Sclerurus mexicanus* to examine geographic variation and determine whether vocalizations could be used to construct species groups that are supported by the phylogenetic data (d'Horta et al. 2013). Furthermore, we assessed whether vocal groups were consistent with currently described subspecies and if vocal attributes could be used to assign an individual's identity to a specific population. We included *S. rufigularis* in the analyses to assess the relative differentiation in vocalizations across *S. mexicanus* lineages and test the robustness of proposed species-level taxonomies. For consistency, *S. mexicanus* populations are listed from north to south for the rest of this manuscript.

METHODS

Songs and calls were obtained from Banco de Sonidos Animales (BSA; Instituto Alexander von Humboldt, Bogotá, Colombia), Macaulay Library of Natural Sounds (ML; Cornell Lab of Ornithology, Ithaca, NY, USA), xeno-canto.org (XC), Avian Vocalizations Center (AVoCet [AV]; Michigan State University, East Lansing, USA), commercial bird sound anthologies (Ross and Whitney 1995; Krabbe and Nilsson 2003; Boesman 2011, 2012), or supplied by field recordists (a full list of recordings is in Appendix 1). Sound recording sampling of *Sclerurus* is geographically biased towards Amazonian localities, and a few subspecies (e.g., nominate *mexicanus*) have insufficient material. The number of recordings available is relatively small but representative of typical songs and calls of all named subspecies. A maximum of five recordings were chosen from each subspecies for analysis, covering the geographic breadth of the complex range. Recordings for which subspecific identity was unclear were excluded from the analyses. We identified recordings of unsolicited natural songs and calls from those made in response to playback stimuli, and discarded low-quality samples. Many recordings include songs ending with rapid trills, and these recordings were not included in the quantitative analyses if the birds seemed agitated or were noted to be recorded after playback. Other individuals incorporated multiple call notes into their sessions; call notes were considered part of a "song" when they were part of the contiguous phrase of notes and not when given in excitement between song bouts.

Up to ten call notes or song bouts were measured per individual, and presented as individual averages. We quantified the individual's song length, pace (notes per second), maximum frequency, frequency range, and first note length. Pace was selected over the gross number of notes as many populations (and even individuals) can vary in the number of notes they deliver, but their song's speed is relatively consistent. Maximum frequency was selected in favor of minimum frequency as maximums are often more clearly defined in spectrograms, and more confidence can thus be placed in their measurements than in frequency minima. Given the descending quality of *Sclerurus* songs, frequency range better reflected the overall 'bandwidth' and character of songs, whereas using minimum and maximum frequency in tandem compares only the extrema of vocalizations. Moreover, using minimum frequency as a variable explained less variation than using frequency range. First note length was used to gather information on the character of individual notes and provide standardization in instances when the number of notes varied significantly. Calls were quantified by their maximum frequency and frequency range to provide a parallel to analyses of the overall songs. We included vocalizations of *S. rufigularis* within the analyses to enable comparisons of the vocal divergence between *S. mexicanus* populations with respect to a closely related species-level taxon. Recordings of *S. rufigularis* were selected from across the range of the species without regard to subspecies.

All recordings were analyzed quantitatively and assessed qualitatively. Spectrograms were quantified in Raven Pro 1.4 (Bioacoustics Research Program 2011) using the default settings. Depending on the amount of background noise present in a recording, brightness and contrast were adjusted to make the note edges more visible to facilitate accurate measurements. The view window was adjusted to provide more clarity on the notes and songs; the measurements of the window were made to cover the entire frequency range of the song and contain the entire song bout within the window at one time. For most songs, this meant a window view incorporated the frequency range from ca. 0–12,000 Hz with a time frame of ca. 4 sec. A similar procedure was performed for calls, with a window of ca. 0–12,000 Hz with a time frame of ca. 1 sec. All measurements were performed by JCC to ensure consistency, and several measurements were repeated to ensure that vocal measures were repeatable. When two channels of audio were present, measurements were taken only from Channel 1. All calculations were performed using R 3.2.0 (R Core Team 2015) using the packages ggplot2 (Wickham 2009), ggbiplot (Vu 2011), and MASS (Venables and Ripley 2002). Given the small sample sizes, we conducted Kruskal-Wallis tests to assess variation within the complex as a whole and Mann-Whitney *U*-tests to assess univariate differences between pairs of populations. We explored the position of each sample in vocal space by means of a Principal Components Analysis (PCA) for comparisons between groups using the entire dataset. These analyses were considered necessary given inherent correlations within song variables. PCAs were derived independently for songs and calls, with song PCAs conducted with and without song pace (which was removed due to "NA" values resulting from birds ending their songs in trills).

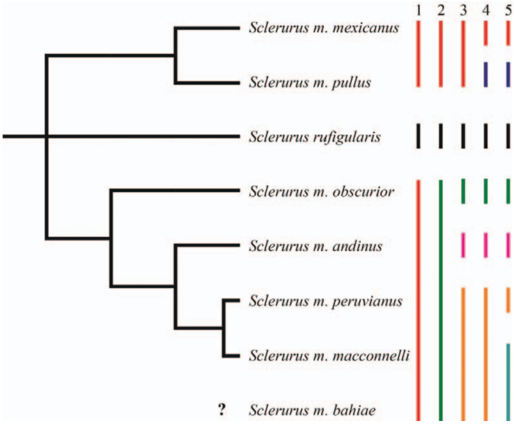

FIG. 2. Proposals tested in this analysis compared with a phylogeny adapted from d'Horta et al. (2013).

We tested the overall distinctiveness of groups via Linear Discriminant Function Analysis (DFA) to assess whether subspecific groups were correctly assigned based on vocal information. These analyses were conducted on the PCAs of song length, maximum frequency, frequency range, and first note length. After loadings were attained, a prediction was made based off of the original recordings to assign them to subspecies. Species group proposals tested were as follows: 1) *S. mexicanus* and *S. rufigularis*; 2) *S. mexicanus* (including *S. m. pullus*), *S. obscurior* (including all South American populations), and *S. rufigularis*; 3) *S. mexicanus* (including *S. m. pullus*), *S. obscurior*, *S. andinus*, *S. macconnelli* (including *S. m. peruvianus* and *bahiae*), and *S. rufigularis*; 4) *S. mexicanus*, *S. pullus*, *S. obscurior*, *S. andinus*, *S. macconnelli* (including *S. m. peruvianus* and *bahiae*), and *S. rufigularis*; and 5) *S. mexicanus*, *S. pullus*, *S. obscurior*, *S. andinus*, *S. peruvianus, S. macconnelli* (including *S. m. bahiae*), and *S. rufigularis* (Fig. 2).

RESULTS

Songs.—Only one song recording of the nominate subspecies was available, consisting of a series of long, drawn out notes that are broadly 'n' shaped (Fig. 3A). The song slows and drops in pitch as the bird sings. The pace (1.6 notes*sec^{-1}) and note shape are similar to the more southerly *S. m. pullus* (1.4 ± 0.11 notes*sec^{-1}, Fig. 3B) but differs in mean maximum frequency (*S. m. mexicanus* 5342.10 Hz, *S. m. pullus* 6959.13 ± 1013.66 Hz). The song of *S. m. pullus* is consistently higher pitched but contains similarly long, broad 'n' shaped notes. *S. m. pullus* and, to a lesser extent, *S. m. mexicanus* are statistically distinct from the South American subspecies (collective maximum frequency 5116.57 ± 191.60 Hz, 3.83 ± 0.49 notes*sec^{-1}).

The Chocó *S. m. obscurior* has a highly pitched (max. freq. 5403.95 ± 401.78 Hz), relatively slow song (3.14 ± 0.29 notes*sec^{-1}), with notes that are relatively flat (freq. range 2595.30 ± 330.29 Hz, Fig. 3C). The pitch is similar to the adjacent *S. m. andinus* (max. freq. 5875.43 ± 564.56 Hz), but is lower than that of *S. m. pullus*. *S. m. andinus* note shape resembles a '~' or sideways 'j' shape (Fig. 3D), but are often faster (4.25 ± 0.95 notes*sec^{-1}) and more musical than those of *S. m. obscurior* (freq. range 3428.50 ± 576.25 Hz).

The Amazonian subspecies *S. m. macconnelli* and *S. m. peruvianus* are reminiscent of *S. m. andinus* and have similarly structured songs (Fig. 3E). *S. m. peruvianus* is unique in having more '/' or reduced '∫' shaped notes, whereas *S. m. macconnelli* has '∫' to '√' shaped notes, with stress on the initial descent and ascent of the notes with cut-off note ends. Both populations are very similar in quality and general sound, although *S. m. peruvianus* averages slower with a higher maximum frequency (*S. m. peruvianus* 2.89 ± 0.16 notes*sec^{-1}, max. freq. 5074.05 ± 263.04 Hz; *S. m. macconnelli* 3.58 ± 0.29 notes*sec^{-1}, max. freq. 4783.79 ± 203.78 Hz).

The Atlantic forest *S. m. bahiae* has songs that are similar to *S. m. macconnelli* of Amazonia in terms of maximum frequency and pace (4793.32 ± 362.23 Hz, 3.90 ± 0.09 notes*sec^{-1}). Its note shape is a short, condensed '√'. Notes have two obvious points of stress during songs, with an initial note start and then louder ascension creating a bi-syllabic sound for most notes.

Lastly, the quality of *S. rufigularis* is most similar to the sympatric *S. m. macconnelli* (max. freq. 4934.63 ± 333.16 Hz, Fig. 3F), but songs are often delivered at a faster pace (5.28 ± 1.74 notes*sec^{-1}). It exhibits wide variation in its songs and is often difficult to distinguish from *S. mexicanus* populations. Unlike syntopic populations of *S. mexicanus*, many *S. rufigularis* end their songs with a higher pitched call note or a rise in pitch of the final song notes.

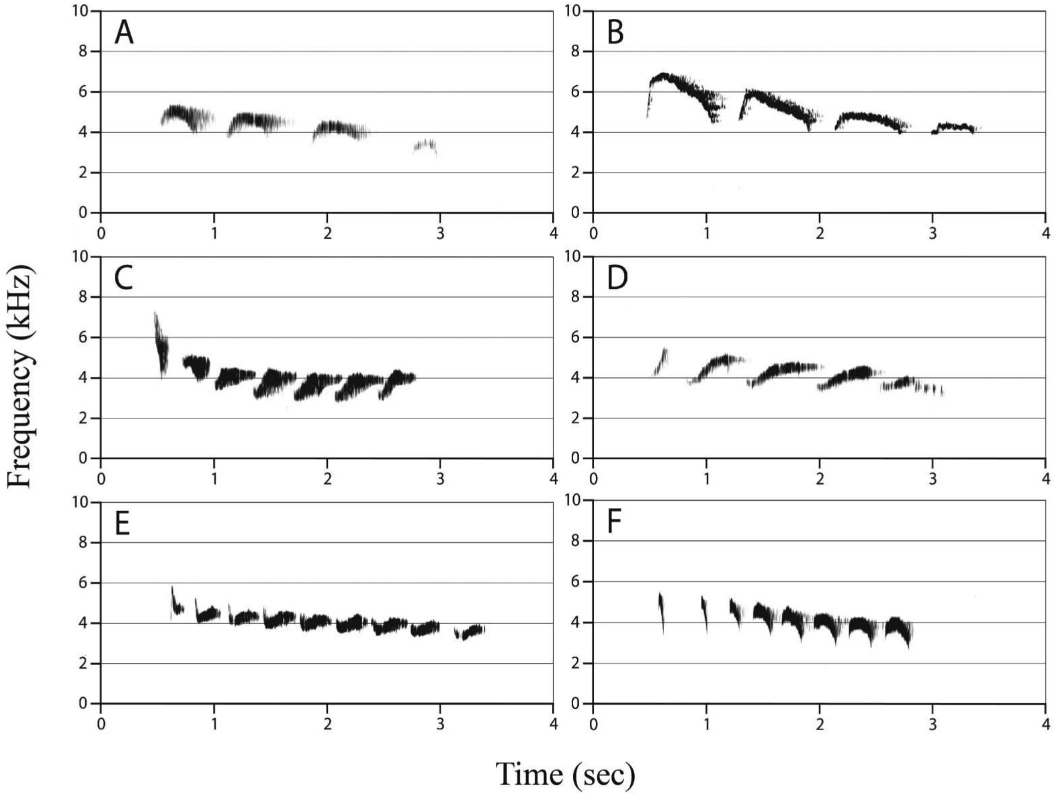

FIG. 3. Primary songs of principal vocal groups recovered in this analyses. (A) *S. m. mexicanus*, Francisco Morazan, Honduras (XC185348); (B) *S. m. pullus,* Cocle, Panama (XC3301); (C) *S. m. obscurior*, Ecuador (84_Esm07); (D) *S. m. andinus*, Lara, Venezuela (XC41899); (E) *S. m. macconnelli*, Cayenne, French Guiana (XC64999); (F) *S. rufigularis*, Mato Grosso, Brazil (XC39469).

Kruskal-Wallis tests of each variable confirmed that multiple populations were present within the complex (all $P < 0.05$). Pairwise comparisons of populations confirmed the distinctiveness of *S. m. pullus* from all other populations except for *S. m. mexicanus* and *S. m. bahiae*. The second most distinctive population recovered was *S. m. obscurior*, which was only inseparable from *S. m. mexicanus*. A complete breakdown of pairwise comparisons can be found in Appendix 2.

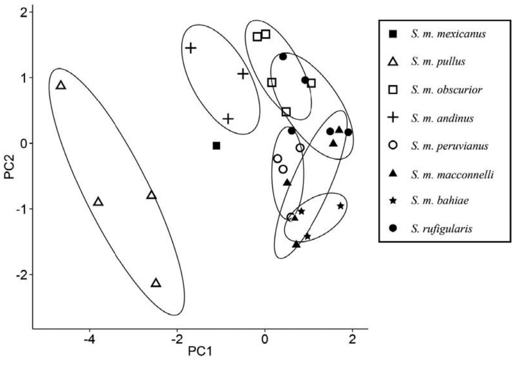

FIG. 4. PCA scores of *Sclerurus mexicanus* subspecies and *S. rufigularis* songs. Taxa are ordered based on range from north to south.

PCA of songs revealed a similar breakdown of populations, strongly separating *S. m. pullus* from other populations (PC1 with 63.4% explained variation and PC2 with 21.0%). The song of *S. m. mexicanus* appeared fairly distinct from all other populations. Two non-overlapping South American vocal groups were revealed within *S. mexicanus*: 1) *obscurior* and *andinus*; and 2) *peruvianus*, *macconnelli*, and *bahiae*. A PCA excluding song pace yielded the same groups (PC1 with 62.3% explained variation and PC2 with 26.5%; Fig. 4); however, songs of the nominate and *S. m. andinus* appear more similar,

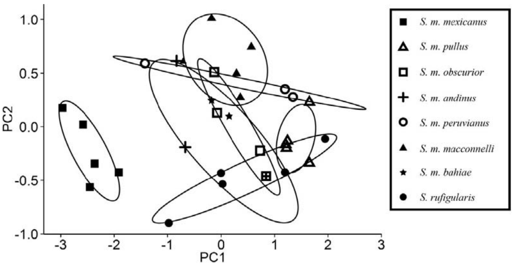

FIG. 5. Call notes of *Sclerurus mexicanus* subspecies and *S. rufigularis* in PCA space. Taxa are ordered based on range from north to south.

while those of *S. m. obscurior* become discrete from *S. m. andinus*. The songs of the close relative *S. rufigularis*, whose range overlaps most of the Amazonian populations of *S. mexicanus*, appear almost intermediate between South American vocal groups.

An initial DFA of all *S. mexicanus* populations against *S. rufigularis* (Proposal 1) assigned all individuals to the same population, implying that *S. rufigularis* is not an effective outgroup for *S. mexicanus* as a single species. A test of Proposal 2 recovered the distinctiveness of *S. m. mexicanus* from South American populations, but failed to properly assign *S. rufigularis* (error = 7.14%, LD1 = 99.41, LD2 = 0.01). Further separating the groups into four species (Proposal 3) possessed less support, with an error of 10.71% (LD1 = 72.05, LD2 = 26.00). The only population that was completely assigned to a correct group was *S. m. obscurior*. Dividing *S. mexicanus* from *S. pullus* (Proposal 4) produced the most accurate results with an error of 0.04% (LD1 = 78.25, LD2 = 19.62). *S. m. mexicanus*, *S. m. pullus*, *S. m. obscurior*, *S. m. macconnelli*, and *S. rufigularis* were all assigned to groups with 100% accuracy. Expanding to the liberal Proposal 5 failed to support the separation of *S. peruvianus* from *S. macconnelli* and resulted in only *S. m. mexicanus*, *S. m. pullus*, and *S. rufigularis* being correctly assigned to groups (error = 14.30%, LD1 = 72.01, LD2 = 25.59). In every DFA, one recording of *S. m. andinus* was erroneously assigned to *S. m. obscurior*.

Calls.—Calls of all populations of *S. mexicanus* are extremely similar differing subtly in their quality and their pitch. As such, the primary focus was on the actual measurements of call vocalizations. Calls of *S. mexicanus* and *S. rufigularis* clearly form multiple groups with regard to maximum frequency ($X^2 = 20.00$, d.f. = 7, $P = 0.006$) and frequency range ($X^2 = 21.17$, d.f. = 7, $P = 0.004$). The most distinctive group was *S. m. mexicanus*, which was significantly different with respect to both variables from every other population ($P < 0.05$) except for *S. m. peruvianus*, with which it overlapped in frequency range ($W = 3$, $P = 0.25$), and *S. m. bahiae*, which overlapped in both variables (both $W = 10$, $P = 0.095$). The second most distinctive group, *S. m. pullus*, exhibited overlap with *S. m. peruvianus* and *S. m. macconnelli* with respect to maximum frequency and *S. m. bahiae* and *S. rufigularis* in both variables ($P > 0.05$), but was significantly different in all other comparisons ($P < 0.05$; Appendix 2). An exploration in PCA space confirmed the distinctiveness of *S. m. mexicanus* and highlighted its distance in vocal space from *S. m. pullus* (PC1 with 89.6% explained variation and PC2 with 10.4%; Fig. 5).

DFAs of the proposed splits were repeated for call data and similarly failed to support the separation of *S. rufigularis* from the *S. mexicanus* complex. All proposals revealed extensive overlap between the calls of *S. m. obscurior*, *S. m. andinus*, *S. m. peruvianus*, *S. m. macconnelli*, and *S. m. rufigularis*. The most well supported proposal was Proposal 4, with *S. m. mexicanus*, *S. m. pullus*, and *S. m. macconnelli* predicted with 100% accuracy (error = 24.24%, LD1 = 73.51, LD2 = 26.49).

DISCUSSION

The breaks in vocal structure we found largely parallel the topology presented by d'Horta et al. (2013), but overall patterns of vocal similarity are shrouded by conserved characters. The nominate *S. m. mexicanus* and *S. m. pullus*, distantly related to South American taxa, genetically are supported as divergent by vocal data. We recovered two distinct groups between *S. m. mexicanus* and *S. m. pullus* with regard to both calls and songs. Within South America, the most distinctive populations were found to be *S. m. obscurior* and *S. m. andinus*, both of which are supported by phylogenetic analyses (d'Horta et al. 2013). Our inability to discern *S. m. macconnelli* from *S. m. peruvianus* is potentially an artifact of the young age of the clades and undefined range boundaries. Regrettably, no genetic data has yet been analyzed from *S. m. bahiae*, but it appears to be part of the *macconnelli/peruvianus* group. *S. rufigularis*, which is broadly sympatric with *S. m. peruvianus* and *S. m. macconnelli*, was found to be an ineffective outgroup and was only recovered as a distinct population when multiple groups of equal distinctiveness were allowed within *S. mexicanus*. Despite being embedded in the vocal space of *S. mexicanus*, *S. rufigularis* is morphologically distinct and recognized as a syntopic sister species to *S. mexicanus* sensu lato (Remsen 2003, d'Horta et al. 2013, Clements et al. 2014).

Differentiating Vocalizations.—It is immediately evident that vocalization traits are split between two different groups: the slower singing Central American populations and the faster South American populations. All analyses of calls highlight the distinctiveness of *S. m. mexicanus*, and all song characters show the uniqueness of *S. m. pullus*. DFAs successfully recovered this break with respect to song, but erroneously assigned *S. rufigularis* to the South American clade of *S. mexicanus*. Few pairwise metrics were capable of separating *S. rufigularis* from *S. m. macconnelli* or *S. m. bahiae*, and the species overlapped broadly in PCA space with *S. m. obscurior* and *S. m. macconnelli*. Similarly, broad-scale DFAs were incapable of recovering *S. rufigularis* as a distinct group from *S. mexicanus* with respect to both calls and songs.

Within South American *S. mexicanus* populations, there is a large amount of vocal overlap. The most distinctive populations were *S. m. andinus* and *S. m. obscurior*, which were placed in unique groups using PCA analyses that disregarded pace, yet still overlapped extensively with regards to pairwise tests. Understanding qualitative differences is therefore imperative for augmenting the conserved quantitative traits of *Sclerurus* vocalizations. One of the most obvious qualitative traits within songs is an introductory call note at the start of a song bout. This note immediately precedes normal songs and is reminiscent of birds' typical calls. This introductory call was not present in *S. m. mexicanus*, *S. m. pullus*, or *S. m. andinus* and may be useful in identifying individuals in regions where *S. m. pullus* or *S. m. andinus* come into contact with *S. m. obscurior*. The importance and variability of these calls requires more study, as their delivery varied among and within individuals in a population and may be an example of individual variation within suboscine vocalizations (Moseley and Wiley 2013). Similarly, ending trills were present in *S. m. pullus, S. m. andinus*, *S. m. peruvianus*, *S. m. bahiae*, and *S. m. macconnelli* and also varied by individual. It could not be determined whether these birds were agitated or if the trills were a normal part of the song repertoire for the population.

The similarity in song quality between populations is possibly due to the retention of ancestral song characters or conservatism of vocal characters within *Sclerurus*. Calls show an extreme degree of conservatism in vocal space, with South American populations (including *S. rufigularis*) being indistinguishable. Even the songs of distantly related taxa are congruent enough to elicit responses from other populations (e.g., *S. m. mexicanus* frequently respond to *S. m. andinus* tapes in southern Mexico [M. Retter, pers. comm.]). Other similar sounding species groups that are not significantly different vocally may also be allo- or parapatric species-level taxa that have separated ecologically and are not locally sympatric (McCormack et al. 2009, Wooten and Gibbs 2012).

Within some areas of the range of *S. mexicanus*, particularly in regions of potential local sympatry between populations, subspecies are often misidentified. This problem is most evident in the western foothills of the Andes, where intermediate recordings have been identified by recordists as either *S. m. obscurior* or *S. m. andinus*, particularly at mid elevations. Recordings of agitated individuals vary considerably from the natural vocalizations of a population and further confound proper identification; for instance, one *S. m. andinus* recording (BSA 31061) after playback is most similar to *S. m. obscurior* recordings in vocal space. This raises questions of whether birds that are not giving natural songs can be properly identified in the field and highlights the need for more recordings of each population.

Delineating Distinct Species Groups.—Potential confusion in identifying *Sclerurus* individuals by voice is not restricted to *S. mexicanus* sensu lato but inclusive of its sister taxon, *S. rufigularis*. Genetic data revealed *S. rufigularis* to be embedded within the *S. mexicanus* complex (d'Horta et al. 2013), and we found a parallel result in vocal space. Many similar vocalizations within *S. mexicanus* (and *S. rufigularis*) occur between allopatric groups, reinforcing the hypothesis that potential local parapatry may help drive song divergence (Jang and Gerhardt 2006). Within this complex, differences between valid, recognized species (i.e., *S. rufigularis* and *S. mexicanus*) are equal to those differences seen between populations within *S. mexicanus*. Even in the syntopic case of *S. rufigularis* and *S. m. macconnelli*, the data do not show a complete separation in vocal space, yet two distinct morphotypes exist in near complete sympatry (Remsen 2003, Kirschel et al. 2009).

CONCLUSION

The phylogenetic data gathered by d'Horta et al. (2013) supports the recognition of several species in the *S. mexicanus* group and, at minimum, warrants the recognition of three species (*S. mexicanus* north of the Darién, *S. obscurior* south of the Darién, and *S. rufigularis*). From a phylogenetic and a vocal perspective, considering all populations of *S. mexicanus* to be the same species also requires subsuming *S. rufigularis* as a morphologically distinct syntopic subspecies. The best supported proposal using vocal data recognizes four species within *S. mexicanus* sensu lato as distinctive as the outgroup, with strong support for a fifth group. Furthermore, these data indicate that these groups are largely identifiable if recorded. We therefore recommend recognizing five different species within *S. mexicanus* sensu lato: *S. mexicanus* (Tawny-throated Leaftosser, Sclater 1856); *S. pullus* (Isthmian Leaftosser, Bangs 1902); *S. obscurior* (Dusky Leaftosser, Hartert 1901); *S. andinus* (Andean Leaftosser, Chapman 1914); and *S. macconnelli* (Guianan Leaftosser, Chubb 1919), containing the subspecies *S. m. peruvianus*, *S. m. macconnelli*, and *S. m. bahiae*.

These five groups are monophyletic, possess consistent phenotypic differences, and can be recreated using vocal data. This proposal parallels d'Horta et al. (2013), with the exceptions of a lack of recognition for *S. m. peruvianus* from *S. m. macconnelli* and the separation of *S. m. pullus* from *S. m. mexicanus*. While the latter is corroborated by the phylogenetic species concept (de Queiroz 2007), the former is a conservative recommendation based on a lack of confidence in vocal distinctiveness of the Amazonian taxa. The inability to clearly separate vocalizations of *S. mexicanus* sensu lato from *S. rufigularis* further highlights the conserved nature of vocalizations within furnariids and the use of recordings to assist in resolving phylogenies.

Future research in the genus *Sclerurus* should focus on obtaining recordings from throughout the genus's range, assessing species' status and distributions, and gathering genetic material from contact zones. These studies should be broadly inclusive of the entire superspecies and investigate vocal differences not only between *Sclerurus mexicanus* sensu lato populations, but within Sclerurinae as a whole. A more robust dataset of natural vocalizations is required to address the vocal repertoire of these populations and to ascertain their distributions. Many zones of potential sympatry have been identified, and studying the interactions of populations within these areas is necessary for fully understanding mechanisms separating these species.

ACKNOWLEDGMENTS

We thank the numerous recordists who sent us their recordings, the Macaulay Library and the Banco de Sonidos Animales for a loan of available recordings, and other recordists who made their recordings available through anthologies and internet collections. We thank M. J. Anderson, J. V. Remsen Jr., and M. B. Robbins for their advice regarding the study of this complex, M. J. Retter and A. J. Spencer for information about singing in wild birds, and J. S. Soberón and G. Seeholzer for assistance with R. We thank two anonymous reviewers for their help in improving this manuscript. We also thank Louisiana State University, the University of Kansas, Tulane University, and our current institutions for their support.

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APPENDIX 1. Recordings used in this analysis. S and C refer to Song and Call, respectively. Collections are annotated as follows: AV# = Avian Vocalizations Center, BSA = Banco de Sonidos Animales, ML = Macaulay Library, and XC = Xeno-Canto.

Subspecies	Catalog number	Type	Recordist	Country	Long.	Lat.
S. m. mexicanus	XC185348	S	O. Komar	Honduras	−87.1	14.2
	XC233029	C	N. Komar	Guatemala	−90.2	15.2
	ML127232	C	C. A. Marantz	Mexico		
	ML90073	C	J. Sterling	Mexico		
	XC96752	C	M. Grosselet	Mexico	−92.7	15.6
	XC96751	C	M. Grosselet	Mexico	−92.7	15.6
S. m. pullus	ML54228	S	M. B. Robbins	Panama	−82.3	8.7
	80-Ross-pullus	S	D. L. Ross, Jr.	Costa Rica		
	AV#18535	S	P. C. Rasmussen	Costa Rica	−83.6	9.8
	XC166448	S	M. Nelson	Costa Rica	−83.6	9.8
	ML25800	C	T. A. Parker, III	Panama		
	ML25823	C	T. A. Parker, III	Panama		
	ML54228	C	M. B. Robbins	Panama	−82.3	8.7
	Ross-Call	C	D. L. Ross, Jr.	Costa Rica		
	XC3301	C	D. Bradley	Panama	−80.7	8.4
S. m. obscurior	Ahlman_Song_Tape	S	R. Ahlman	Ecuador	−78.8	0.0
	SW_Canade so	S	S. Woods	Ecuador	−79.3	0.5
	84_ESM_obscurior	S	N. Krabbe and J. Nilsson	Ecuador		
	SW_3 Canade	S	S. Woods	Ecuador	−79.3	0.5
	XC229409	S	P. Boesman	Ecuador	−78.5	0.8
	Ahlman_Call_Tape	C	R. Ahlman	Ecuador	−78.8	0.0
	84_Esm20_obscurior	C	N. Krabbe and J. Nilsson	Ecuador		
	SW_2 Canade	C	S. Woods	Ecuador	−79.3	0.5
	S_Canade so	C	S. Woods	Ecuador	−79.3	0.5
S. m. andinus	2325VZLA	S	P. Boesman	Venezuela		
	29351148 andinus	S	P. Boesman	Venezuela		
	XC41899	S	J. G. Leon	Venezuela	−69.6	9.7
	BSA31061	S	A. M. Cuervo	Colombia		
	BSA10954	C	F. G. Stiles	Colombia	−77.1	1.1
	BSA31057	C	A. M. Cuervo	Colombia		
	0935-1149_andinus	C	P. Boesman	Venezuela		

APPENDIX 1. Continued.

Subspecies	Catalog number	Type	Recordist	Country	Long.	Lat.
	BSA10955	C	F. G. Stiles	Colombia	−77.1	1.1
S. m. peruvianus	Tawny-throatedLeaftosser2011-8-13-4	S	A. Spencer	Ecuador	−78.6	−4.3
	XC2870	S/C	A. B. Hennessey	Bolivia	−67.1	−15.1
	Tawny-throatedLeaftosser2011-8-13-2	S	A. Spencer	Ecuador	−78.6	−4.3
	265-01_peruvianus	S/C	D. Michael	Ecuador		
	265-04_peruvianus	C	N. Krabbe	Ecuador		
S. m. macconnelli	XC64999	S	A. Renaudier	French Guiana	−53.1	3.0
	XC84105	S	A. Lees	Brazil	−48.1	−3.7
	XC44172	S	A. Renaudier	French Guiana		
	XC15882	S	B. Davis	Brazil	−56.0	−9.2
	XC229407	S	P. Boesman	Brazil	−50.5	−6.0
	ML48094	C	P. R. Isler	Brazil		
	XC65001	C	A. Renaudier	French Guiana	−53.1	3.0
	XC59223	C	A. Renaudier	French Guiana	−52.5	4.5
	XC39467-8	C	A. Spencer	Brazil	−55.9	−9.6
	XC119565	C	G. Leite	Brazil	−57.1	−5.6
S. m. bahiae	XC80470	S	J. Minns	Brazil	−45.2	−23.5
	1032 Macarani	S	C. Albano	Brazil	−40.5	−15.8
	XC87367	S	R. D. Rosa	Brazil		
	1032 Itubera	C	C. Albano	Brazil		
	XC80469	C	J. Minns	Brazil	−45.2	−23.5
S. rufigularis	XC114285	S	J. King	French Guiana	−53.2	3.6
	XC39469	S	A. Spencer	Brazil	−55.9	−9.6
	XC6728	S	N. Athanas	Ecuador	−76.5	−0.5
	XC77036	S	T. Brooks	Ecuador	−76.4	−0.7
	XC94210	S	D. F. Lane	Ecuador	−76.5	−0.5
	XC119581	C	G. Leite	Brazil	−56.1	−5.3
	XC128667	C	A. Renaudier	French Guiana	−52.5	4.6
	XC147216	C	J. Engel	Brazil	−46.8	−3.8
	XC147431	C	G. Leite	Brazil	−57.0	−5.5
	XC74175	C	J. Tobias and N. Seddon	Bolivia	−65.6	−10.5

APPENDIX 2. Significance of *P* values in pairwise Wilcoxon rank sum tests. Values indicated with an asterisk were not fully quantified as they contained equal values (an artifact of scale within the analysis program). Subspecies are indicated by the first three letters of their specific epithet (e.g., *mex-ruf* = *S. m. mexicanus* – *S. rufigularis*).

	Songs					Calls	
Pairs	Length (sec)	Pace (notes*sec^{-1})	Max. freq. (Hz)	Freq. range (Hz)	1st Note length (sec)	Max. freq. (Hz)	Freq. range (Hz)
mex-pul	0.40	0.40	0.40	0.80	0.40	0.008	0.008
mex-obs	0.33	0.33	1.00	0.67	0.33	0.016	0.016
mex-and	1.00	0.67	0.50	1.00	0.50	0.016	0.016
mex-per	0.80	0.40	0.80	0.40	0.40	0.036	0.25
mex-mac	1.00	0.40	0.33	0.33	0.33	0.008	0.008
mex-bah	0.50	0.50	0.50	0.50	0.50	0.095	0.095
mex-ruf	0.33	0.33	0.67	0.33	0.235*	0.008	0.008
pul-obs	0.016	0.016	0.016	0.11	0.016	0.016	0.016
pul-and	0.057	0.13	0.11	0.86	0.057	0.016	0.016
pul-per	0.029	0.029	0.029	0.029	0.029	1.00	0.036
pul-mac	0.11	0.029	0.016	0.016	0.016	0.095	0.008
pul-bah	0.11	0.057	0.057	0.057	0.057	0.095	0.095
pul-ruf	0.016	0.016	0.016	0.032	0.019*	0.095	0.55
obs-and	0.071	0.095	0.25	0.071	0.036	0.20	0.89
obs-per	0.016	0.29	0.29	0.016	0.56	0.63	0.86
obs-mac	0.056	0.19	0.056	0.008	1.00	0.19	0.41
obs-bah	0.036	0.036	0.071	0.036	0.036	0.53	0.80
obs-ruf	0.22	0.008	0.095	0.31	0.012*	0.73	0.41
and-per	0.63	0.13	0.057	0.057	0.057	0.40	0.63
and-mac	0.79	0.27	0.036	0.036	0.036	0.063	0.73
and-bah	0.10	1.00	0.10	0.10	0.10	1.00	1.00
and-ruf	0.25	0.57	0.074	0.056	0.036*	1.00	0.41
per-mac	1.00	0.029	0.29	0.063	0.91	0.57	0.57
per-bah	0.11	0.057	0.40	0.057	0.057	0.80	0.80
per-ruf	0.032	0.016	0.73	0.56	0.020*	0.79	0.79
mac-bah	0.39	0.29	0.79	0.39	0.14	0.38	0.86
mac-ruf	0.31	0.064	0.69	0.056	0.036*	0.79	0.79
bah-ruf	0.036	0.25	1.00	0.14	0.76*	0.86	0.19