VOCALIZATIONS AND BILL MEASUREMENTS MAY RESOLVE SOME QUESTIONS ABOUT TAXONOMIC RELATIONSHIPS WITHIN THE FOX SPARROW COMPLEX

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ABSTRACT: The many described subspecies of the Fox Sparrow (*Passerella iliaca*) have been parsed into four groups, the Red (*iliaca* group, two or three subspecies), Sooty (*unalaschcensis* group, seven subspecies), Thick-billed (*megarhyncha* group, five subspecies) and Slate-colored (*schistacea* group, four subspecies). Intermediate populations and contact areas between these groups play a role in answering the question whether any of the groups should be considered separate species. *P. i. canescens* of the Slate-colored group shows genetic characters of both the Slate-colored and Thick-billed groups. As currently classified it comprises two disjunct populations, one breeding in the White Mountains of California and Nevada, the other in the Toiyabe Range of central Nevada. We analyzed the vocalizations and bill sizes of these two populations to see if this might shed light on their taxonomic relationships. Our analyses of song, call, and bill measurements, along with a re-examination of previously published morphologic and genetic data, suggest that the two disjunct populations currently assigned to *P. i. canescens* represent different subspecies: the central Nevada population *P. i. schistacea* (in the Slate-colored group) and the White Mountains population *P. i. megarhyncha* (in the Thick-billed group), thus eliminating *P. i. canescens* as a synonym. Our findings may have implications for any future proposals to split the Fox Sparrow groups into distinct species. If that split results in the Slate-colored and Thick-billed groups assigned to separate species, our results would include the White Mountains population in the Thick-billed species and the central Nevada population in the Slate-colored species.

Multiple sources suggest that the Fox Sparrow (*Passerella iliaca*) may comprise three or four species (Zink 1986, 1994, 2008, Byers et al. 1995, Rising 1996, Dunn and Alderfer 2017). Beadle and Rising (2003) and Wright (2019) referred to these putative species, each polytypic, as the Red Fox Sparrow (*P. iliaca*), Sooty Fox Sparrow (*P. unalaschcensis*), Slate-colored Fox Sparrow (*P. schistacea*), and Thick-billed Fox Sparrow (*P. megarhyncha*). Here, for clarity, we refer to these groups of Fox Sparrow subspecies by these English names, while using the subspecific epithet for the component subspecies. The Xeno-canto archive of bird vocalizations (www.xeno-canto.org) also catalogs Fox Sparrow recordings into four different species with these same names. Nevertheless, the North American Classification Committee of the American Ornithological Society (AOS; Chesser et al. 2022), Weckstein et al. (2002), and Clements et al. (2021) still recognize only a single Fox Sparrow species consisting of four subspecies groups.

The disagreement is based on a lack of clarity about the evolutionary history of the subspecies groups and insufficient data on their interactions in areas

of contact. For example, *P. i. altivagans* has been variously placed in both the Red and Slate-colored groups because of its mix of morphologic and genetic characteristics. Also, Zink and Kessen (1999) and Zink (2008) reported evidence of interbreeding at points of contact between the ranges of the Thick-billed and Slate-colored groups in Nevada and eastern California. Floyd et al. (2007) considered the situation at the Thick-billed/Slate-colored contact zone to be "one of the few remaining impediments to the four-way split of the Fox Sparrow." Although there may be contact between *fulva* (Thick-billed group) and *schistacea* (Slate-colored group) in southeast Oregon and northwest Nevada, the primary issues involve the population breeding in the White Mountains along the California–Nevada border. Swarth (1918) described it as *P. i. canescens*, and it has been included in the Slate-colored group (Weckstein et al. 2002). Linsdale (1936) assigned a disjunct population in central Nevada in the Toiyabe Range to *canescens*, but that population has not been studied either genetically or morphologically. Therefore, we investigated both the White Mountains and Toiyabe Range populations further, focusing on the vocal and morphological characteristics of both populations to determine to which group (Slate-colored or Thick-billed) each is best assigned. We also assessed more broadly the patterns of differences in song and call between the Thick-billed and Slate-colored groups. Although the White Mountains population shows genetic evidence of interbreeding with the Thick-billed group (Zink 1994, 2008, Zink and Weckstein 2003), these authors concluded that the degree of genetic interchange did not preclude recognition of the Slate-colored and Thick-billed groups as distinct species.

A 2003 proposal to the AOU to split the Fox Sparrow into four species was rejected on a split vote by the checklist committee (T. Chesser, J. Dunn, pers. comm.), with those voting "no" citing the need for more data from the areas of possible interbreeding among subspecies groups. Garrett et al. (2000), Zink and Weckstein (2003), Floyd et al. (2007), and Wright (2019) all suggested that studies of the vocalizations of these taxa may shed light on their taxonomic relationships and help resolve questions about populations in the contact zones. Differences in vocalizations can help reveal the extent of interaction between populations or subspecies and possibly reveal early stages of speciation (Marler and Tamura 1962, Nottebohm 1969, Baker 1975, Slabbekoorn and Smith 2002, Dingle et al. 2010, Pandolfino and Pieplow 2015). Martin (1976, 1977, 1979) published a thorough treatment of Fox Sparrow songs, but his work was restricted to locations in Utah and Idaho, all within the range of the Slate-colored group. DeCicco (2021) noted qualitative differences between the songs of Red and Sooty groups at a contact zone in Alaska, and Pieplow (2019) noted that songs of the Slate-colored group include more buzzy syllables than do those of Red or Sooty groups. However, there are no quantitative comparisons of Fox Sparrow songs by subspecies group.

Garrett et al. (2000) found the primary contact call note used by the Thick-billed group to be distinct from the call notes of the Slate-colored and Sooty groups, and equally distinct from that of the Red group (Sibley 2014, Dunn and Alderfer 2017, Pieplow 2019). Dunn and Alderfer (2017) and Heindel and Heindel (in press) also note that, in the White Mountains of California, Fox Sparrows give calls associated with the Thick-billed group, not the Slate-colored group. Because the calls of songbirds have historically

been considered innate rather than learned (Thorpe 1961), this difference may be evidence of significant divergence. Subsequent studies, however, have revealed that, in several species, certain calls may be learned or at least influenced by learning (see Marler 2004, and citations therein).

Because there are no systematic comparisons of the vocalizations of Fox Sparrows in the contact area between the Slate-colored and Thick-billed groups, we analyzed recordings of songs and calls to search for diagnostic vocal differences between them. Bill size is the primary morphologic feature distinguishing the Slate-colored and Thick-billed groups, so we also measured the bills of specimens of the Toiyabe Range and White Mountains populations and compared them to specimens of *P. i. schistacea* from northern Nevada. We also re-examined most of the published morphologic and genetic work on the Thick-billed and Slate-colored groups to see if a combination of vocal, morphologic, and genetic factors might reveal more about differences between these groups.

METHODS

From 22 to 23 June 2022 Pandolfino visited the Toiyabe Range to record Fox Sparrow songs and calls, recording vocalizations of four different individuals. For the remainder of the ranges of both the Thick-billed and Slate-colored groups we used archived recordings from Xeno-canto and the Mark Robbins/Macaulay Library (www.macaulaylibrary.org) (Figure 1). Those recordings included more than 1000 examples of full song from 121 individuals of seven subspecies and an additional 18 recordings that included only call notes. The metadata for all recordings are in Appendix 1 at https://archive.westernfieldornithologists.org/archive/V54/Pandolfino-Fox_Sparrow-WB54-2-append.pdf. To ensure that the recorded individual was a breeder at that location, we analyzed only those songs recorded from 15 May to 31 July and included at least three consecutive examples of full song from the same individual. We excluded any recordings made after broadcast of pre-recorded song. We assumed any recordings from the same location and day were from a single individual unless the recordist indicated otherwise. We analyzed recordings from the White Mountains and Toiyabe Range separately to allow comparison with the vocal characteristics of other populations of the Slate-colored and Thick-billed groups.

We analyzed recordings with Raven Pro software (KLYCCB 2022), using the selection-box tool for quantitative analyses. All analyses were conducted in a blinded fashion to avoid any possible unintentional bias,. That is, all recordings were coded so that the individual doing the analyses did not know the location of the recording. Song characters compared included average song length, average number of syllables per song, singing rate (number of songs per unit of time), percent of songs including at least one buzzy syllable, percent of songs including a terminal buzzy syllable, percent of songs including more than one buzzy syllable, and percent of songs including at least one trilled syllable. For our purposes, we defined a buzzy syllable as a continuous trace on the spectrogram with very rapid modulation of frequency. We defined a trilled syllable as a rapid series of distinct repeated notes. Figure 2 shows a representative example with two consecutive songs

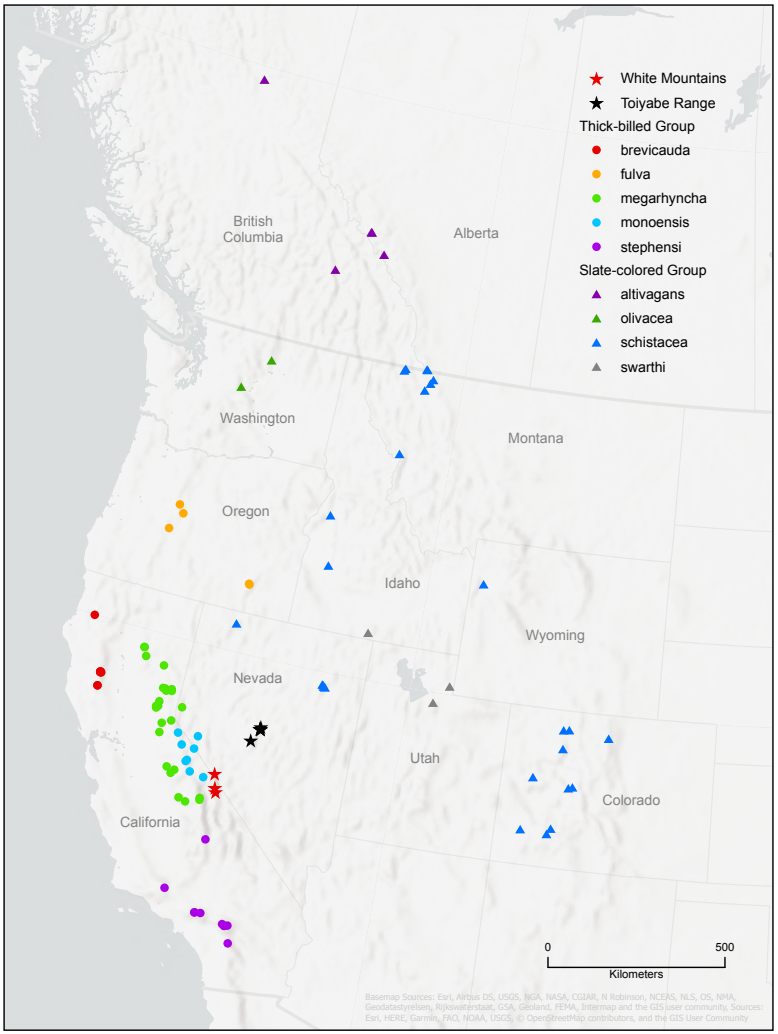

FIGURE 1. Locations of Fox Sparrow recordings used.

from an individual, the first with two buzzy syllables and the second with one buzzy syllable and one fast trill. Note that the key difference between the two is that a trill consists of discrete notes rather than a continuous modulated trace. In cases where the quality of a recording was insufficient to differentiate between a buzz and fast trill, we omitted that recording from the analysis. The possibility of a near-continuum between buzzes and very fast trills is one of the reasons such analyses should always be conducted blind.

Calls were compared qualitatively by ear and by spectrograms, also done in

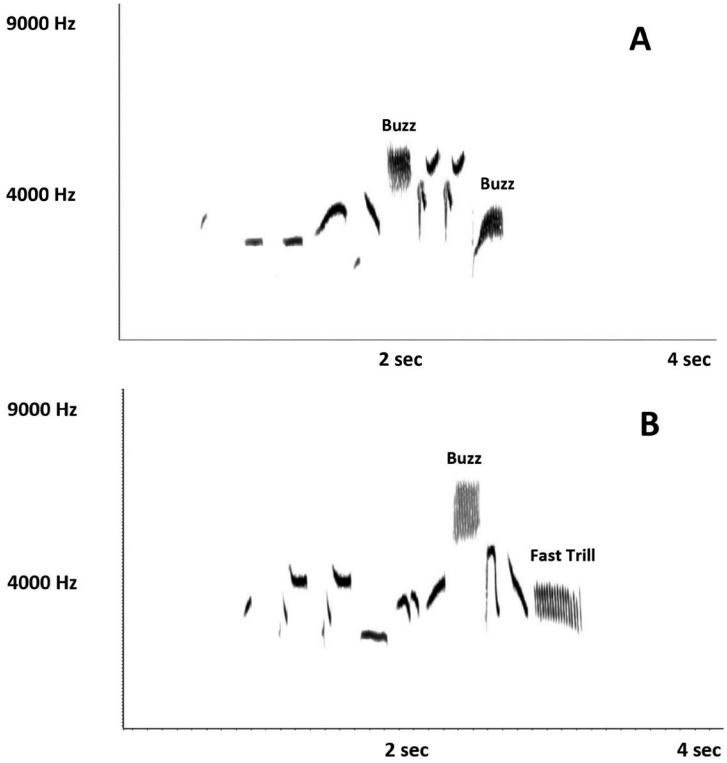

FIGURE 2. Two consecutive songs from a Fox Sparrow recorded by Randy Little 28 June 1961 in Glacier Park, Montana (xc15670). A, example of a song with two buzzy syllables; B, example of a song with one buzzy syllable and one fast trill.

a blind fashion. The difference between the typical sharp "smack" of the Slate-colored group and the metallic "tink" of the Thick-billed group is qualitatively obvious when heard. The calls can be differentiated on a spectrogram by the smeared appearance of the "tink" call, with the sound in the mid-frequencies extending up to 0.1 second after the main note. The "smack" call consists of one distinct vertical line on the spectrogram.

Pyle examined specimens in the collection at the Museum of Vertebrate Zoology at the University of California, Berkeley, from three disjunct regions (the White Mountains of eastern California and western Nevada in the west, the Toiyabe Range in central Nevada, and the Ruby Mountains in northern Nevada). Specimens of juveniles were excluded from our set. The exposed culmen was measured with a ruler scaled in millimeters from where the ridge of the culmen meets the cranial skin (often but not always the base of the feathers). Bill depth was measured with calipers perpendicularly at the anterior end of the nares ("depth at nares"). In order to compare our values with those of Swarth (1920), bill depths of specimens from the White Mountains

were also measured from the base of the exposed culmen to the angle at the rear of the mandible, to approximate Swarth's method. All measurements were taken by Pyle in a standardized manner, following Pyle (2022:8–9). Specimen catalog numbers, collection locations, dates, and measurements are tabulated in Appendix 2 at https://archive.westernfieldornithologists.org/archive/V54/Pandolfino-Fox_Sparrow-WB54-2-append.pdf.

RESULTS

Of the eight song characters measured, only the percent of songs including a buzzy syllable and the percent of songs including more than one buzzy syllable showed any promise for differentiating the Slate-colored and Thick-billed groups. Of the 272 songs (from 36 individuals) recorded in the Slate-colored range, 261 (97%) included at least one buzzy syllable, and 145 (53%) included more than one buzz. Among the 574 songs from 69 individuals of the Thick-billed group, 321 songs (53%) included at least one buzz and only 10 (less than 2%) included more than one buzzy syllable (Figure 3). A plot by subspecies of the number of songs with at least one buzz versus the number of songs with more than one buzz distinguishes the Thick-billed and Slate-colored groups well (Figure 4), with the presence of more than one buzz per song being particularly useful (Table 1). Birds of the Toiyabe Range are very similar in this respect to other Slate-colored subspecies. However, the White Mountains Fox Sparrow songs, though somewhat buzzier than other songs of the Thick-billed group, fit much better with that group than with the Slate-colored group.

We confirmed with recordings that the contact call note of the Thick-billed group (distinctly metallic "tink") is quite different and easily distinguished by visual inspection of the spectrograms and by ear from that of the Slate-colored group (sharp "smack"; six individuals). All eight individuals recorded in the White Mountains gave calls indistinguishable from those of the Thick-billed

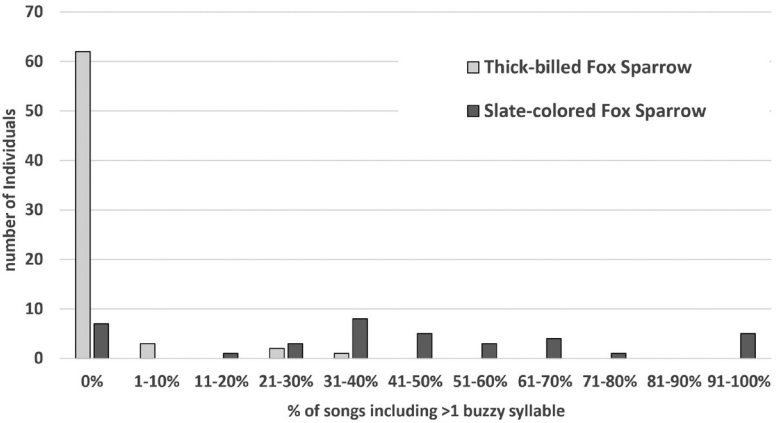

FIGURE 3. Histogram comparing the Thick-billed and Slate-colored groups of the Fox Sparrow by percent of individuals singing songs with more than one buzzy syllable.

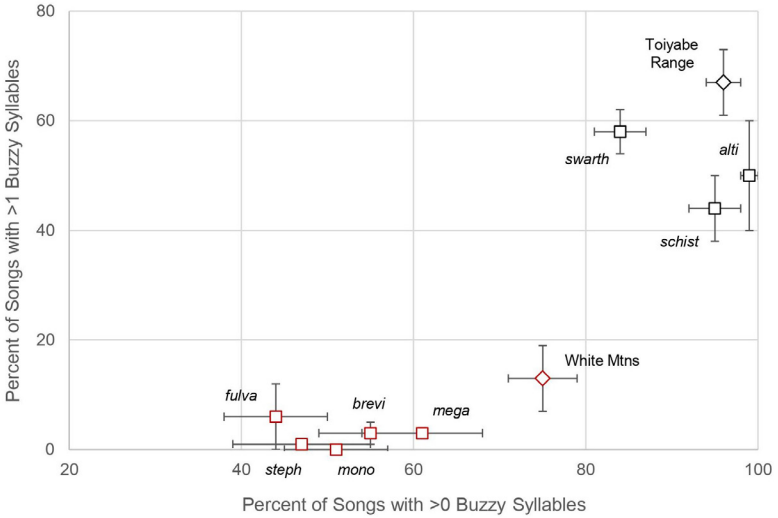

FIGURE 4. Comparison of the percent of individual Fox Sparrows singing songs containing at least one buzzy syllable (*x* axis) or more than one buzzy syllable (*y* axis) in the White Mountains (red diamond; $n = 9$) and Toiyabe Range (black diamond; $n = 7$) and by subspecies within the Thick-billed group (red squares; *brevi* = *brevicauda*, $n = 11$; *fulva*, $n = 5$; *mega* = *megarhyncha*, $n = 23$; *mono* = *monoensis*, $n = 12$; *steph* = *stephensi*, $n = 18$) and the Slate-colored group (black squares; *alti* = *altivagans*, $n = 8$; *schist* = *schistacea*, $n = 25$; *swarth* = *swarthi*, $n = 3$). Error bars represent 1 standard error.

group, whereas all six individuals recorded in the Toiyabe Range gave calls indistinguishable from those of the Slate-colored group (Figure 5).

The analysis of bill sizes of Fox Sparrows from three areas (Figure 6) showed that birds from central Nevada have bills smaller than those from the White Mountains but are similar to those of the Slate-colored group

TABLE 1 Main Vocal and Morphological Characters of Fox Sparrows from the White Mountains along the California–Nevada Border and the Toiyabe Range in Central Nevada, Compared to Reference Samples of the Slate-colored and Thick-billed Subspecies Groups

	Slate-colored	Thick-billed	White Mts.	Toiyabe Range
Song character				
n (no. individuals)	36 (272 songs)	69 (574 songs)	9 (63 songs)	7 (62 songs)
Songs with >0 buzz[a] (± SD)	96% ± 12	56% ± 35	75% ± 17	96% ± 10
Songs with >1 buzz (± SD)	51% ± 33	1% ± 6	13% ± 27[b]	76% ± 30[c]
Bill size				
n (no. individuals)	200	200	38	51
Exposed culmen (mm)	10.0–12.9[d]	11.3–16.0[d]	10.2–13.8	9.7–11.3
Depth at nares (mm)	6.2–8.4[d]	8.0–11.9[d]	6.9–9.9	6.7–8.9

[a]The term "buzz" refers to the number of buzzy syllables within a song.
[b]Seven of nine individuals included no songs with >1 buzzy syllables; range 0–75%.
[c]All seven individuals included >1 buzzy syllables in some songs; range 26–100%.
[d]Data from Pyle (2022).

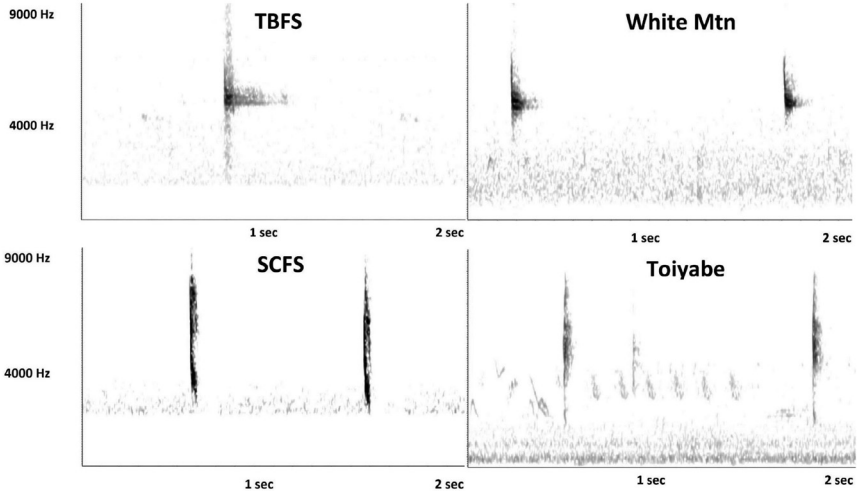

FIGURE 5. Examples of call notes. "Tink": TBFS, Thick-billed Fox Sparrow recorded by Richard Webster 5 July 1995 near Glacier Point in Yosemite National Park, California (xc125396); White Mtn, Fox Sparrow recorded by Richard Webster 3 June 1995 in Wyman Canyon, White Mountains, California (xc125411). "Smack": SCFS, Slate-colored Fox Sparrow recorded by Andrew Spencer 6 July 2007 near Stillwater Reservoir, Colorado (xc14880); Toiyabe, Fox Sparrow recorded by Pandolfino 22 June 2022 in Kingston Canyon in the Toiyabe Range, Nevada (xc734099).

from northern Nevada (Figure 7). The difference in exposed culmen was significant and the bill depth overlapped but averaged larger for the White Mountains specimens. The ranges of bill sizes for the White Mountains population fit well within those of the Thick-billed group, and the bill sizes for the Toiyabe Range birds fit well with those of the Slate-colored group (Table 1).

On the basis of proportion of buzzy syllables within songs, the Toiyabe Range Fox Sparrows sing a song typical of the Slate-colored group. In our small sample from the White Mountains, songs appear to be buzzier than typical for the Thick-billed group, but much less buzzy than typical for the Slate-colored group. The differences in our bill-size measurements of Nevada populations parallel the differences in vocalizations. By our measurements, the White Mountains birds have large bills, most comparable to the bills of the Thick-billed group. However, the central Nevada birds have bill sizes much more similar to those of the Slate-colored group of northern Nevada. Together, these characters suggest that these two disjunct populations may not be properly assigned to the same subspecies (*canescens*). Indeed, the songs, and, even more so, the call notes, suggest that the Toiyabe range birds fit well into the Slate-colored group, while the White Mountains birds fit best within the Thick-billed group.

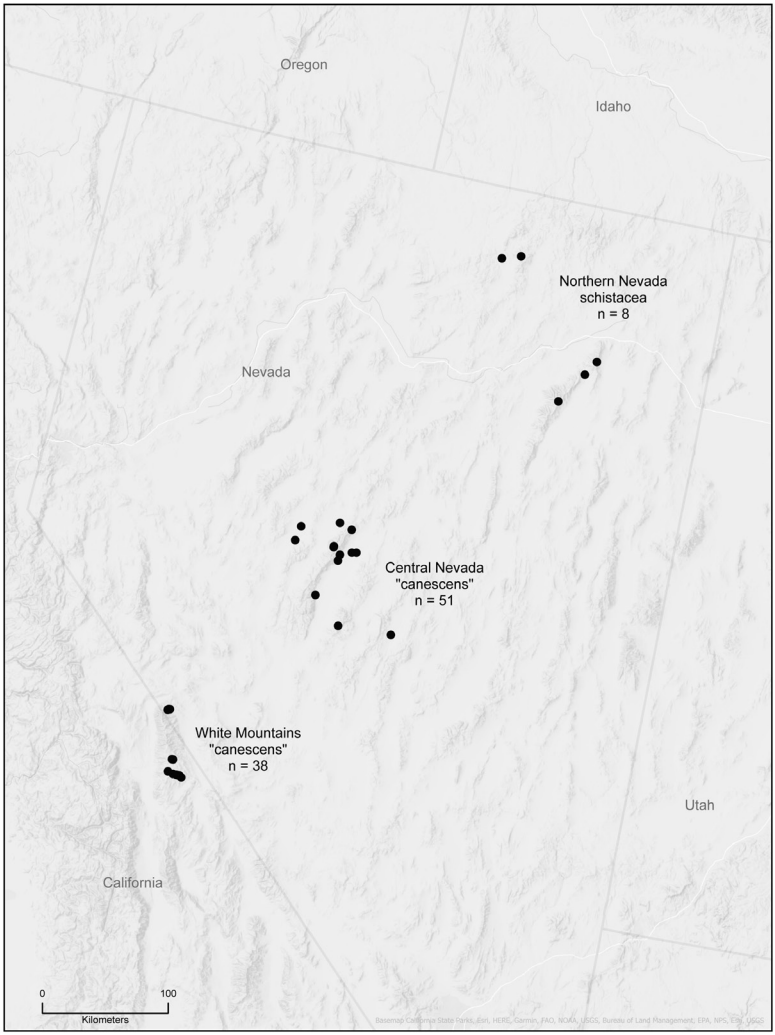

FIGURE 6. Locations and numbers of Nevada specimens compared in measurements of exposed culmen and bill depth.

DISCUSSION

It is possible that the taxonomy of the Fox Sparrow has been more thoroughly studied than that of any other North American bird species. Besides dozens of papers, three monographs (Swarth 1920, Linsdale 1928, Zink 1986) totaling a cumulative 410 pages are devoted to this issue. Yet, the number of species within this complex remains unclear enough that authors of two authoritative guides devoted to the sparrow family (Passerellidae), Beadle

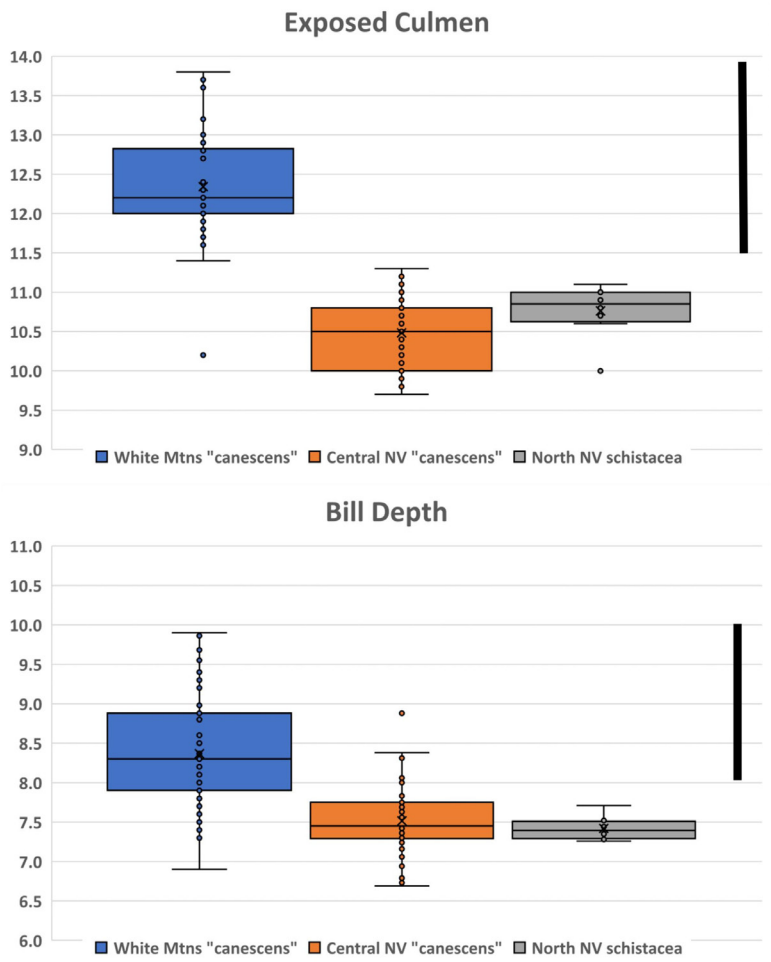

FIGURE 7. Bill measurements of specimens from three regions of Nevada: northern Nevada, *P. i. schistacea*; central Nevada, currently assigned to *P. i. canescens*; White Mountains, currently assigned to *P. i. canescens*. All measurements in millimeters. Black bars on the right represent the ranges of *P. i. megarhyncha* for these variables from Pyle (2022).

and Rising (2003) and Wright (2019), chose to split the Fox Sparrow groups into four species prior to any decision by the AOS. One primary area of controversy centers on the birds breeding in the White Mountains of California and Nevada (Zink and Kessen 1999, Floyd et al. 2007, Zink 2008). On the basis of specimens from that area Swarth (1918) described the subspecies *canescens*, then Linsdale (1936) concluded that the Fox Sparrows of central-eastern Nevada (the Toquima, Toiyabe, and Monitor ranges, east into White

Pine County) were also *canescens*, even though more than 160 km of inappropriate breeding habitat separates the White Mountains from the closest of those mountain ranges (Figure 1). This subspecies was placed within the Slate-colored group (American Ornithologists' Union 1998), despite the White Mountains population being closer to the ranges of two subspecies of the Thick-billed group, *monoensis* on the east slope of the Sierra Nevada near Mono Lake and *megarhyncha* elsewhere in the Sierra Nevada (Figure 1).

Zink (1994) and Zink and Weckstein (2003) found genetic evidence of introgression between the Fox Sparrows of the Thick-billed group and *canescens* of the White Mountains, which has been cited as evidence against splitting the Fox Sparrow complex into four species (Floyd et al. 2007). To date, the genetics of the *canescens* Fox Sparrows in central-eastern Nevada has not been studied.

Our analyses of vocalizations of Fox Sparrows of both the White Mountains and Toiyabe Range showed that those populations differ distinctly in both the primary contact call and song. The songs of the Toiyabe Range birds match well with those of the Slate-colored group, while the White Mountains Fox Sparrows sing most like the Thick-billed group. The pattern of difference in the contact call is the same. Interestingly, Linsdale (1938), in his monograph on the ecology of the Toiyabe Range area, mentioned a comment by Alden Miller (who accompanied Linsdale on his collecting trip to that area) that the call notes of the Fox Sparrow in that range sounded different from the ones he heard in the Sierra Nevada of California (in the Thick-billed range). And our bill-size measurements also showed better alignment of the White Mountains birds with the Thick-billed group and the Toiyabe Range birds with the Slate-colored group.

Our results prompted us to re-examine the published morphologic and genetic data on *canescens*. The data on morphology of Swarth (1918, 1920) and Linsdale (1928) were based solely on the White Mountains population, as was the morphologic and genetic work of Zink (1986, 1994, 2008) and Zink and Weckstein (2003). Behle and Selander (1951), in their description of *swarthi* (in the Slate-colored group) from Idaho and Utah, included some measurements of specimens from both disjunct populations assigned to *canescens*, but it is unclear what proportion of those specimens were from which population. Below we review some of these findings with regard to physical measurements and genetics.

Morphology

Swarth (1920) found that the wing, tail, and tarsus measurements of the White Mountains Fox Sparrows overlapped broadly with both those of *schistacea* of the Slate-colored group and other subspecies now considered in the Thick-billed group (*fulva*, *megarhyncha*, *brevicauda*, *monoensis*, and *stephensi*). Compared to birds of the Thick-billed group, Swarth's measurements showed that the White Mountains birds tended to be slightly smaller in most measures, however, and significantly smaller in exposed culmen, bill depth, and bill width. His measurements of bill length (exposed culmen) and bill depth were similar to those of the Slate-colored group (subspecies *schistacea*).

Swarth's (1920) values for bill depth for the various Fox Sparrow taxa are consistently larger than those of Pyle (2022). For example, values for the

Thick-billed from Pyle (2022) range from 8.0 to 11.9 mm, whereas Swarth's range from 10.5 to 15.5 mm. Values for the Slate-colored in Pyle (2022) range from 6.2 to 8.4 mm, Swarth's from 8.8 to 10.2 mm. As noted above, Swarth's method of measuring bill depth (from the base of the exposed culmen to the angle at the rear of the mandible) differs from Pyle's for depth at nares. Pyle also measured the bill depth of the White Mountains specimens by Swarth's method and found a range of values from 8.6 to10.8 mm, compared to the range of 6.9 to 9.9 mm in depth at nares. Of the specimens currently in the collection at the Museum of Vertebrate Zoology, only 12 were collected early enough (27 July to 18 August 1917) to have been included in Swarth's set of six. Of those 12 specimens, five were juveniles. Thus, in addition to a difference in method, it may be that Swarth's sample included one or more juvenile birds, which tend to have smaller bills.

Linsdale (1928) compared skeletal features (skull, mandibular rami, sternum, pelvis, tibiotarsus, humerus, radius, ulna, and furcula) in some detail and found broad overlap between the Fox Sparrows of the White Mountains and other Thick-billed subspecies. Measurements of the sternum, pelvis, and furcula were very similar; other measures tended toward the low end range of the various Thick-billed subspecies pooled but were very similar to those of subspecies *fulva*.

Zink (1986) examined specimens from California and Oregon, within the ranges of the Thick-billed subspecies *fulva*, *brevicauda*, *megarhyncha*, *monoensis*, and *stephensi*, and two sites in northern Nevada in the range of the Slate-colored subspecies *schistacea*. He included in his analysis specimens from the White Mountains but none from central-eastern Nevada. His morphology data were presented in a series of phenograms showing relationships among the samples based on measurements of the wing, tail, bill, tarsus, and toe as well as a set of skeletal measurements similar to those of Linsdale (1928). The results showed the White Mountains specimens more closely allied with other Thick-billed subspecies (in particular, *fulva*) than with *schistacea*. A phenogram based on external characteristics of males showed the White Mountains specimens nested with those from a site in central Oregon (range of *fulva*), within a larger set that included specimens from an eastern Oregon site (*fulva*) and those from the two northern Nevada sites (*schistacea*). A similar phenogram for females placed the White Mountains birds with those from northeastern California (*fulva*) and within a large set including a number of northern and central Sierra Nevada sites (all either *megarhyncha* or *monoensis* of the Thick-billed group). Phenograms based on skeletal data from males produced relationships for the White Mountains specimens essentially identical to those from external characters. Phenograms based on females' skeletons placed the White Mountains birds with those from northeastern California in the ranges of both *fulva* and *megarhyncha*.

Genetics

Zink (1986) also used protein electrophoresis to investigate genetic relationships among the same set of specimens used in his morphological analyses, but those data showed no evidence of relatedness among geographic neighbor populations. Zink (1994) and Zink and Weckstein (2003) used mitochondrial DNA to analyze relationships within the Fox Sparrow

complex, finding that, among the four subspecies groups, the Sooty and Slate-colored represented sister lineages. Zink (1994) found a mix of Slate-colored and Thick-billed haplotypes in specimens collected in eastern Oregon and California where the ranges of those two groups approach each other. Specimens from the White Mountains also showed a mix of haplotypes, those associated with the Thick-billed group outnumbering those associated with the Slate-colored group by a ratio of 7:4. Note that Figure 5 in Zink (1994) is mislabeled with the White Mountains abbreviation, WM, assigned correctly to site 11 and incorrectly to site 4. Site 4 should be designated RB, for the Ruby Mountains in the range of the Slate-colored group. Zink (1994) concluded that the data supported four separate phylogenetic and perhaps biological species. Data from microsatellite DNA (Zink 2008) also revealed a mix of the Thick-billed and Slate-colored Fox Sparrows. Interestingly, these data placed the White Mountains Fox Sparrows sampled in the Nevada portion of the range within a clade occupied exclusively by subspecies of the Thick-billed, rather than the Slate-colored group, while samples from the California areas of the range nested within a clade including a mix of locations associated with the Slate-colored, Thick-billed, and Red Fox Sparrow groups (see Figure 2 in Zink and Weckstein 2003).

Conclusions

Our data on songs, calls, and bill size suggest that the two disjunct populations (White Mountains of eastern California and Toiyabe Range of central Nevada) now assigned to *canescens* may not belong in the same subspecies, or even in the same subspecies group. The songs and calls of the Toiyabe Range birds fit perfectly with those of the Slate-colored group, while the White Mountains birds' songs and calls are more similar to those of the Thick-billed group. The bill sizes of these populations also support these relationships.

A review of morphological and genetic data suggests that the White Mountains population nests more naturally within the Thick-billed group than the Slate-colored group. The phenograms of Zink (1986) combining a broad set of physical traits generally nested the White Mountains birds within the Thick-billed rather than the Slate-colored group. While showing clear introgression between the Slate-colored and Thick-billed groups, DNA of the White Mountains birds, particularly their mitochondrial DNA, revealed a greater influence of the Thick-billed than of the Slate-colored genotype. Zink and Kessen (1999), in reviewing the status of this taxonomic puzzle, showed an interesting figure tracing both DNA and morphological data for various western Fox Sparrow populations. That figure showed the White Mountains Fox Sparrows notably distinct from Slate-colored populations in northern Nevada in terms of both morphology and genetics, and intermediate between two Thick-billed populations from eastern Oregon and Mono County, California (of subspecies *fulva* and *monoensis*).

Therefore, with regard to the Fox Sparrows currently assigned to *canescens*, we suggest:

1. The White Mountains Fox Sparrow population should be considered a member of the Thick-billed group. Bill size, call, and song clearly align better with that group, and the degree of DNA introgression from the Slate-colored group is similar to that observed for other subspecies within the Thick-billed

group (especially *fulva* and *monoensis*). The range and characteristics of this population suggest it fits best subsumed into the subspecies *megarhyncha*. The distribution of song and exposed culmen values shown in Figures 4 and 7 confirm that the White Mountains population fits within *megarhyncha* by the 75% rule proposed by Patten and Unitt (2002). While it is beyond the scope of this study, the same is likely the case for *fulva* and *monoensis*, as suggested by Pyle (2022) and Unitt (2004).

2. Fox Sparrows in the Toiyabe and other mountain ranges of central-eastern Nevada should be subsumed within subspecies *schistacea* of the Slate-colored group as their vocalizations and bill size are indistinguishable from those of other nearby populations of this subspecies.

These conclusions may affect decisions about splitting the Fox Sparrow complex into distinct species. The taxonomic realignment we suggest changes the issue regarding the White Mountains birds from one involving introgression between populations of two different putative species into a confident classification of these birds within one putative species.

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