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COMPARISON OF VOCALIZATIONS OF FOUR U.S. SUBSPECIES OF THE WHITE-BREASTED NUTHATCH

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ABSTRACT: There are distinct regional differences among the vocalizations of the White-breasted Nuthatch (*Sitta carolinensis*), but only one subspecies (*S. c. carolinensis*) has been the subject of published vocal analyses. We used recordings made throughout the ranges of four U.S. subspecies to compare their vocalizations qualitatively and quantitatively, finding that these vocalizations may be categorized in three groups, eastern (*S. c. carolinensis*), interior west (*S. c. nelsoni* and *S. c. tenuissima*), and Pacific (*S. c. aculeata*). All four subspecies sing a simple song consisting of an evenly spaced series of overslurred notes. The rate of this song varies from <5 notes/sec to >12 notes/sec. The pitch of these songs increases from east to west, being lowest in *S. c. carolinensis* and highest in *S. c. aculeata*. *Sitta c. aculeata* also has an additional song unique to that taxon consisting of a series of sharply slurred, evenly spaced notes that fall, then rise, and then fall in pitch. Both *S. c. carolinensis* and *S. c. aculeata* frequently give a simple call note that is very distinctly and rapidly modulated; it is significantly higher in pitch in *S. c. aculeata* than in *S. c. carolinensis*. Neither interior subspecies makes a similar call. Both interior subspecies commonly give two calls absent from the repertoires of *S. c. carolinensis* and *S. c. aculeata*, one consisting of tightly paired notes given at a constant pace, the other a very rapid, unevenly spaced series of single notes given in short bursts. We found no diagnostic differences between the two interior subspecies in either song or calls.

Although as many as six subspecies of the White-breasted Nuthatch (*Sitta carolinensis*) have been described within the United States, only four of them occupy substantial geographic ranges: roughly, *S. c. carolinensis* in the East and the Great Plains, *S. c. nelsoni* in the central and southern Rocky Mountains and eastern Great Basin, *S. c. tenuissima* in the high and eastern Sierra Nevada, eastern Cascades, and western Great Basin, and *S. c. aculeata* west of the Sierra Nevada and the Cascades (Hawbecker 1948, Spellman and Klicka 2007, Grubb and Pravosudov 2008). Phillips (1986) recognized also *S. c. cookei* in northeastern North America (synonymized with *S. c. carolinensis* by Wood 1992) and *S. c. oberholseri* found in the Chisos Mountains of western Texas. Four or five additional subspecies occur in Mexico.

Except for the pale back of *S. c. carolinensis*, plumage and structural differences among the subspecies are subtle, with significant overlap in most variables (Pyle 1997, Mlodinow 2014), making consistent visual field identification difficult. Genetic analyses suggest that each of the four widespread subspecies represents a distinct clade, and that the White-breasted Nuthatch may comprise three or four biological species (Spellman and Klicka 2007, Walstrom et al. 2011).

It is well-known that the vocalizations of White-breasted Nuthatches differ regionally (Dunn and Blom 1987, J. L. Dunn in Gaines 1988, Sibley 2000, 2014, Mlodinow 2014), falling into three regional groups: an eastern group corresponding to *S. c. carolinensis*, an interior west group corresponding to *S. c. nelsoni* and *S. c. tenuissima*, and a Pacific group corresponding to *S. c. aculeata*. However, the only detailed published analysis of White-breasted Nuthatch vocalizations (Richison 1983) was restricted to one site in Minnesota and therefore included only the eastern subspecies (*S. c. carolinensis*). Most other publications that have addressed the vocalizations of this species have likewise been restricted to the eastern subspecies (Tyler 1916, Kilham 1972, 1981, Harrap and Quinn 1996, Elliot 2005). Thus the vocalizations of the other White-breasted Nuthatch subspecies have not been analyzed in detail.

Differences in vocalizations can both represent and reinforce barriers to gene flow, serving as a mechanism for assortative mating and thus promoting speciation (Newton 2003). Therefore, an analysis of the White-breasted Nuthatch's vocalizations may help clarify its taxonomy. We analyzed recordings from throughout the ranges of these four subspecies and compared vocalizations both qualitatively and quantitatively to better understand the variation in their vocalizations, to determine which, if any, vocalizations can be used

Figure 1. Locations of analyzed recordings of calls and songs of the White-breasted Nuthatch.

to identify these taxa in the field, and to compare variation in vocalizations to previously described morphologic and genetic variation among these taxa.

METHODS

Figure 1 shows the locations of all recordings used in our analyses. These recordings included those available from the archives of the Cornell Laboratory of Ornithology's Macaulay Library (macaulaylibrary.org/), recordings available at www.xeno-canto.org/, our own recordings, and recordings obtained from other recordists (all recordists noted in the Acknowledgments). We selected recordings from locations within the range of each subspecies consistent with published morphometric data, avoiding locations where the ranges of subspecies may be in contact.

We selected recordings of quality sufficient for quantitative analysis. For each recording, we measured four variables: note duration, note rate (number of notes per second), number of notes in a continuous series of notes, and difference in frequency between successive partials (pitch). The partials are the multiple tones that make up a single nasal sound; on the spectrogram, they appear as individual traces arranged in a vertical stack. We used frequency difference between partials rather than fundamental frequency as a proxy for pitch because the purported fundamental frequencies in White-breasted Nuthatch vocalizations are frequently faint or absent. In complex sounds consisting of a stack of partials in harmonic series, the frequency difference between partials is equal to the frequency of the fundamental, and the human ear hears the pitch of the fundamental even if one or more of the lowest partials, including the fundamental, are filtered out (Fastl and Zwicker 2007). Thus a listener hears these sounds at the frequency of the difference between the partials, not at the frequency of the strongest partial on the spectrogram.

It is possible that White-breasted Nuthatch vocalizations are not harmonic series (i.e., that the difference in frequency between partials is not equal to the frequency of the fundamental). At least in the similarly structured sounds of the Black-capped Chickadee (*Poecile atricapillus*), the stack of partials on the spectrogram can actually represent a set of heterodyne frequencies (frequencies produced by the combination of two different frequencies) generated by the acoustic coupling of the two sides of the syrinx, rather than a harmonic series with a true fundamental frequency (Nowicki and Capranica 1986). In sounds of this type, the pitch the human ear perceives does not always match the frequency difference between partials (Fastl and Zwicker 2007), but the discrepancy is likely to be small in most cases.

For all measurements we used the selection boxes in Raven Pro (www.birds.cornell.edu/brp/raven/RavenOverview.html) applied to spectrograms of the vocalizations. For the time variables (duration of notes and rate of delivery), we averaged measurements from at least four consecutive series of calls or songs for each individual. We defined frequency as the difference between the loudest partial (darkest on the spectrogram) and the partial just above it at the temporal midpoint of the note. For this variable, we averaged at least ten different measurements from at least five consecutive songs or calls for each individual.

To assess the significance of differences between measures of vocalizations in comparisons of more than two subspecies, we used Mann–Whitney *U*-tests and applied Bonferroni adjustments (Dytham 2003).

Terminology

A bewildering variety of names has been used to describe White-breasted Nuthatch vocalizations. For example, the single nasal call of *S. c. carolinensis* has been variously described as a *quank* (Tyler 1916, Richison 1983), *kun* or *kaan* (Kilham 1981), *yank* (Dunn et al. 1983, Elliot 2005, Sibley 2014), and *yenk* or *renk* (Sibley 2000). The corresponding single call of *S. c. aculeata* has been described as *wheer* (Dunn and Alderfer 2011) or as *eeern* or *beeerf* (Sibley 2000) Also, the common contact calls often given by foraging pairs (a vocalization not analyzed here) have been termed *hits* (Tyler 1916, Richison 1983), *tucks* (Richison 1983), and *inks* (Elliot 2005, Sibley 2014). For the purposes of this analysis, we use the terms below for each of the vocalizations studied:

Overslur. We use this term to describe a sound that rises and then falls in pitch (Pieplow 2007).

Quanks. We use this general term for the notes in each of the calls analyzed as it suggests the very nasal quality of all these notes.

Modulated quanks. These comprise the single overslurred notes given by *S. c. carolinensis* and *aculeata*, both of which show a distinct pattern of frequency modulation within the note.

Disyllabic quanks. These comprise the tightly paired notes given by *S. c. nelsoni* and *tenuissima*, *yidi yidi yidi* in Sibley (2000, 2014), *yida* in Dunn and Alderfer (2011). These paired notes may be given singly or in a continuous, evenly paced series.

Rapid quanks. We use this term for the very rapid bursts of notes given by *S. c. nelsoni* and *tenuissima* (*yidididid* in Sibley 2014).

Simple song. By this we mean the evenly paced series of overslurred notes, all on one pitch, given by all four taxa.

Tooey song. This refers to the evenly spaced series of notes given by *S. c. aculeata*, each note of which drops, then rises, then falls again in pitch (*tuey tuey tuey* in Sibley 2014).

RESULTS

Each of the four subspecies of White-breasted Nuthatch we analyzed gives a simple song consisting of an evenly spaced series of overslurred notes, all on the same pitch (Figure 2). *S. c. aculeata* also gives a *tooey* song consisting of an evenly spaced series of distinctly slurred notes, with each note first falling, then rising, and then falling again in pitch (Figure 3). It sings this *tooey* song much more often than it does the simple version. On the basis of over 100 observations in California and Oregon, we heard the *tooey* song approximately ten times as often as the simple song (simple song heard in 10 of 109 song observations).

The rate at which the notes of the simple song are delivered varies from less than 5/sec to over 12/sec, and in none of the subspecies we compared did we find a distinct division between slow and fast versions (Figure 4). There

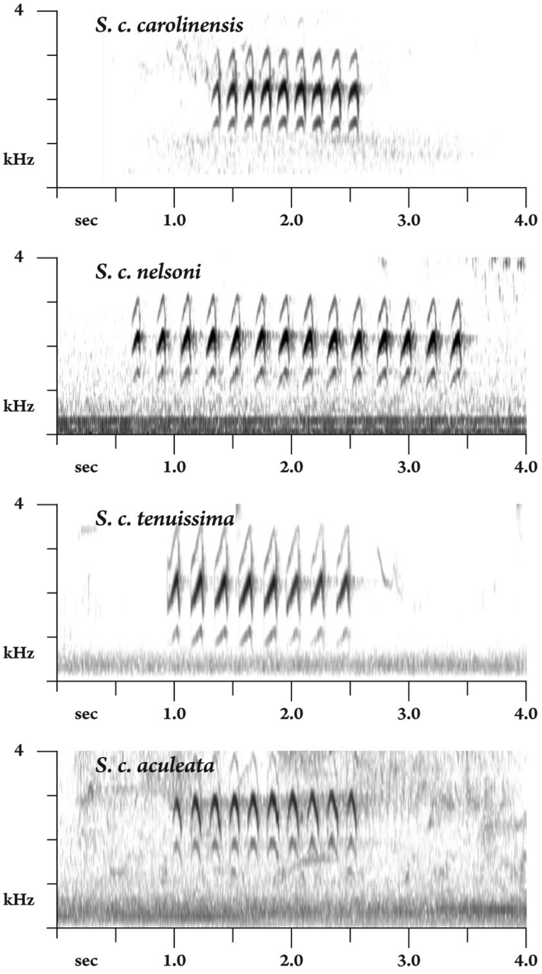

Figure 2. Spectrograms of the simple songs of four subspecies of the White-breasted Nuthatch. *S. c. carolinensis*: recorded 11 February 2012 in Platte County, Nebraska by N. Pieplow (recording not used in the analysis). *S. c. nelsoni*: recorded 22 June 2007 south of Estes Park, Larimer County, Colorado, by N. Pieplow. *S. c. tenuissima*: recorded 21 Apr 2015 in Lava Beds National Monument, Siskiyou County, California, by E. Pandolfino. *S. c. aculeata*: recorded 9 April 2015 near Red Bluff, Tehama County, California by E. Pandolfino. Examples of these songs can be heard at www.westernfieldornithologists.org/W-B_Nuthatch/.

were no significant differences in song rate (number of notes per second) or in the number of notes in a song among these taxa (Table 1). We noted that, within a given bout of singing, the rate remained remarkably constant from song to song. On average, the variation in rate of note delivery between

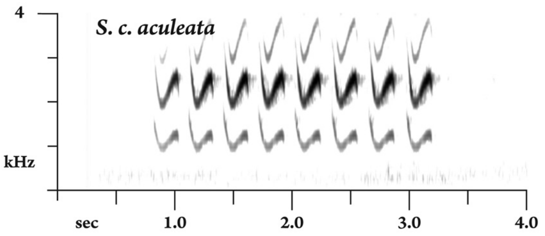

Figure 3. Spectrogram of the *tooey* song of *S. c. aculeata* recorded 17 February 2015 in southeastern Sacramento County, California by E. Pandolfino. Examples of this song can be heard at www.westernfieldornithologists.org/W-B_Nuthatch/.

the fastest and slowest rate within a set of successive simple songs from an individual was less than 0.2 notes/sec (0.16, 0.19, 0.17, and 0.15 notes/sec for *S. c. carolinensis*, *nelsoni*, *tenuissima*, and *aculeata*, respectively).

The pitch of the simple song increased from east to west with the songs of *S. c. carolinensis* being the lowest and those of *S. c. aculeata* the highest (Figure 5; Table 1). The songs of *S. c. carolinensis* differed significantly in pitch from those of the other three taxa. The songs of *S. c. nelsoni* and *tenuissima* were not significantly different in pitch, nor were the songs of *S. c. tenuissima* and *aculeata*. The observed range of frequencies for each subspecies pair overlapped except for *S. c. carolinensis* vs. *S. c. aculeata*.

S. c. carolinensis and *aculeata* both give an overslurred, rapidly modulated *quank* note (Figure 6) that may be delivered singly, in pairs, or in short series. We found no analogous note in any recording of the other subspecies. This note averaged higher in pitch (Figure 7) in *S. c. aculeata* than in *S. c. carolinensis*. The difference in pitch for this note was highly significant ($P < 0.0001$), with no overlap in range (487–588 Hz for *carolinensis* vs. 863–1036 Hz for *aculeata*).

Both of the interior subspecies (*S. c. nelsoni* and *tenuissima*) give two types of calls that we did not observe in any recording of the other two subspecies. Disyllabic *quanks* consist of tightly paired notes (Figure 8), the note

Table 1 Comparison of Pitch, Song Rate, and Number of Notes of the Simple Song of Four Subspecies of the White-breasted Nuthatch

	carolinensis	*nelsoni*	*tenuissima*	*aculeata*[a]
n	24	24	14	10
Mean pitch[b]	673 ± 97	788 ± 126	892 ± 147	1039 ± 128
Range	504–904	604–1136	758–1200	917–1266
Mean rate[c]	8 ± 2	8 ± 2	7 ± 2	6 ± 2
Range	5–11	5–12	4–10	4–10
Mean notes[d]	12 ± 4	10 ± 3	10 ± 4	9 ± 4
Range	7–22	6–17	5–20	4–16

[a] Simple song only; does not include *tooey* songs.

[b] Hertz, plus or minus standard deviation.

[c] Notes per second, plus or minus standard deviation.

[d] Number of notes per song, plus or minus standard deviation.

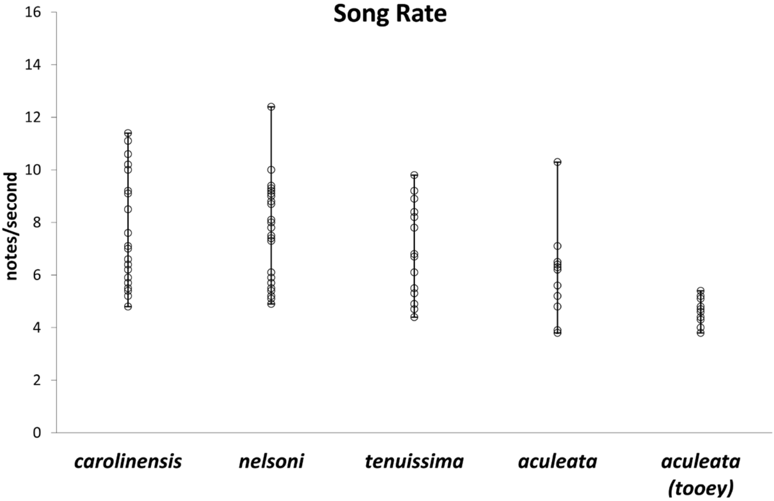

Figure 4. Distribution of song rates (notes/second) for the simple songs of *Sitta c. carolinensis*, *nelsoni*, *tenuissima*, and *aculeata*.

pairs usually given in an evenly spaced series. However, disyllabic *quank* note pairs may also be given singly or in groups of two. These tightly paired notes produce a "rough edge" to the vocalization that can be easily distinguished by the human ear in the field. Rapid *quanks* are given in short, uneven, and very rapid bursts of notes (Figure 9). Between *nelsoni* and *tenuissima*, the rate of delivery of the notes in these calls did not differ significantly (Table 2). However, the pitches showed significant differences, with the calls of *S. c.*

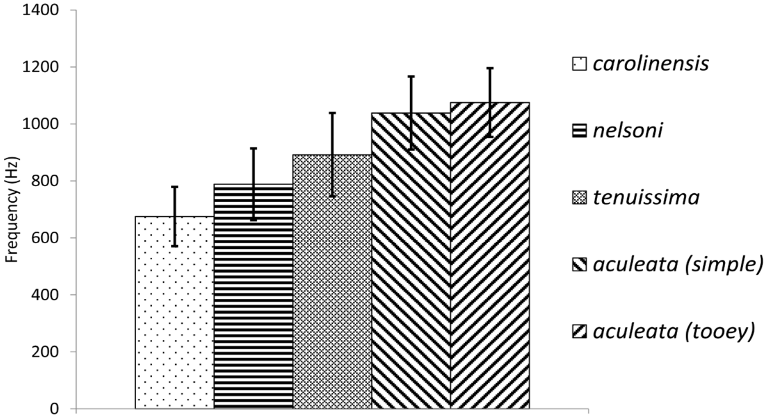

Figure 5. Comparison of the pitch (difference between partials) of songs of *Sitta c. carolinensis*, *nelsoni*, *tenuissima*, and *aculeata*. Error bars represent one standard deviation.

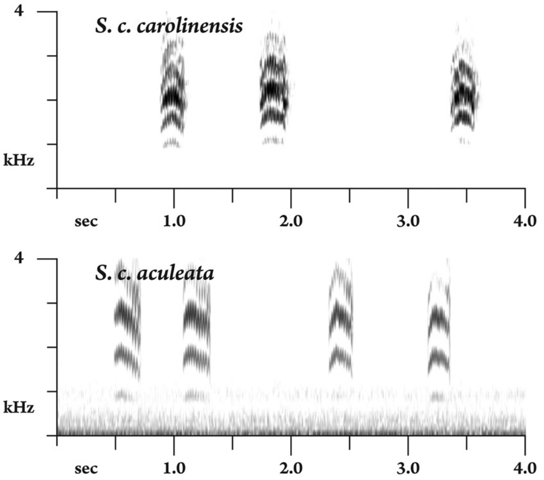

Figure 6. Spectrograms of modulated quank calls of *S. c. carolinensis* (recorded 20 September 2009 in Manistee County, Michigan, by N. Pieplow; recording not used in the analysis) and *S. c. aculeata* (recorded 18 December 2014 in eastern Placer County, California, by E. Pandolfino). Examples of these calls can be heard at www.westernfieldornithologists.org/W-B_Nuthatch/.

nelsoni lower in pitch than those of *S. c. tenuissima* (Table 2). However, the difference in pitch is probably too small to be reliably distinguished by ear in the field by most observers, and the observed ranges of pitch of both disyllabic *quanks* and rapid *quanks* overlapped considerably (Table 2).

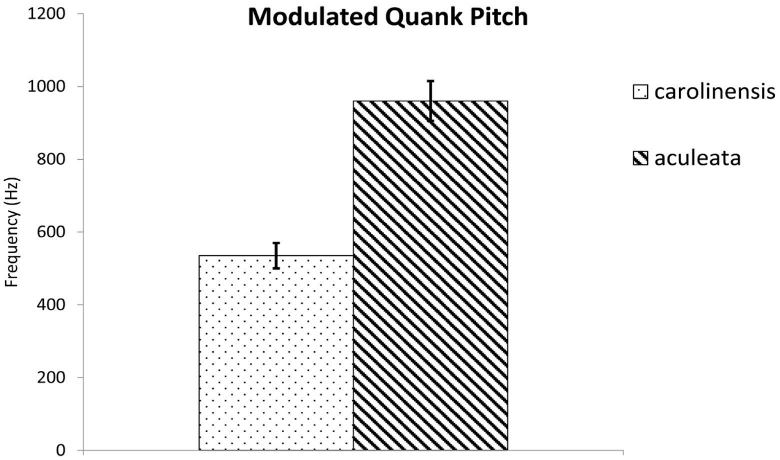

Figure 7. Comparison of the pitch (difference between partials) of modulated quank calls of *S. c. carolinensis* and *S. c. aculeata*. Error bars represent standard deviation.

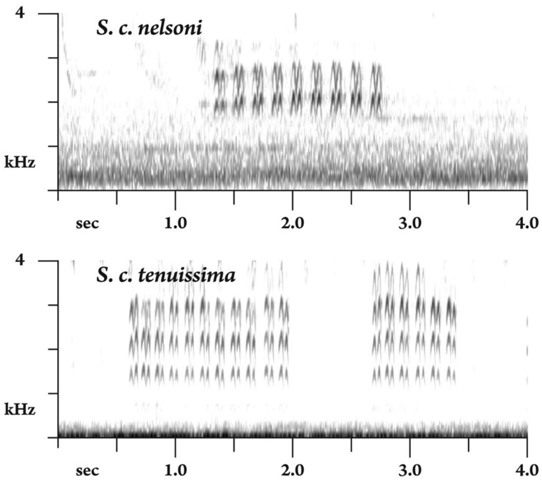

Figure 8. Spectrograms of disyllabic quank calls of *S. c. nelsoni* (recorded 3 September 2008 in Mesa County, Colorado, by N. Pieplow) and *S. c. tenuissima* (recorded 22 January 2015 at Juanita Lake, Siskiyou County, California, by E. Pandolfino). Examples of these calls can be heard at www.westernfieldornithologists.org/W-B_Nuthatch/.

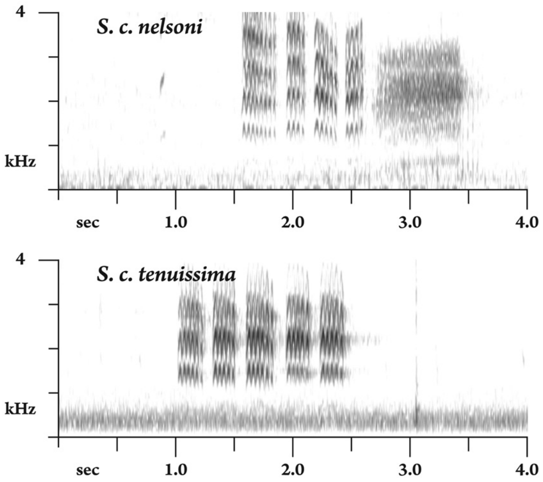

Figure 9. Spectrograms of rapid quank calls of *S. c. nelsoni* (recorded 9 March 2008 at Mesa Lakes Lodge, Mesa County, Colorado, by N. Pieplow) and *S. c. tenuissima* (recorded 19 April 2015 in Union County, Oregon, by E. Pandolfino). Note call of Clark's Nutcracker (*Nucifraga columbiana*) just after rapid quank in recording of *S. c. nelsoni*. Examples of these calls can be heard at www.westernfieldornithologists.org/W-B_Nuthatch/.

Table 2 Comparison of Pitch and Rate for Disyllabic and Rapid Quanks of *Sitta c. nelsoni* and *tenuissima*

	nelsoni	*tenuissima*	*P*
Disyllabic quank			
n	12	13	
Mean pitch[a]	705 ± 50	816 ± 51	0.0003
Range	633–803	760–929	
Mean rate[b]	6.7 ± 1.1	7.1 ± 1.0	0.3
Range	5.2-9.1	5.5-8.9	
Rapid quank			
n	14	18	
Mean pitch[a]	701 ± 83	889 ± 86	0.0003
Range	620–908	750–1068	
Mean rate[b]	20 ± 4	19 ± 3	0.6
Range	11–25	13–25	

[a] Hertz, plus or minus standard deviation.

[b] Notes per second, plus or minus standard deviation.

DISCUSSION

Our results indicate that, from qualitative and quantitative analyses of vocalizations, these four subspecies of the White-breasted Nuthatch fall into three distinct vocalization groups. *S. c. carolinensis* and *aculeata* share qualitatively similar calls (modulated *quanks*) and song; however, both these vocalizations are delivered at significantly different pitches with no overlap in frequency. In addition, *S. c. aculeata* gives a *tooey* song unique to this subspecies. The two interior subspecies, *S. c. nelsoni* and *tenuissima*, both give call types (disyllabic *quanks* and rapid *quanks*) that were not observed in the other two subspecies. Although the pitches of the calls and songs of these two interior subspecies differ slightly, the ranges of frequency of all those vocalizations overlap.

Field Identification

Except when the pale back of *S. c. carolinensis* can be assessed, especially in contrast with the black on the tertials, it can be difficult or impossible to distinguish these four taxa visually in the field. On the basis of our analyses, *S. c. aculeata* can be confidently identified if one hears the more common *tooey* song, as no other subspecies sings a similar song. In addition, both *S. c. aculeata* and *S. c. carolinensis* can be distinguished by their modulated *quank* calls, which differ strongly from any vocalizations of *S. c. tenuissima* or *S. c. nelsoni*, and which differ from one another in pitch, with no overlap. Disyllabic *quanks* or rapid *quanks* should allow one to confidently identify a nuthatch as either *S. c. nelsoni* or *tenuissima*. The similarity of these calls and the overlap of frequencies suggest that differentiating between these two interior subspecies by call may be impossible in the field. Even if recordings are obtained, only calls outside of the range of overlap in frequency may be useful for identification. Likewise, overlapping frequencies of the simple songs of all four subspecies renders that song generally useless for identification for all except *S. c. carolinensis* vs. *aculeata*.

Taxonomic Implications

Our analyses of differences in vocalizations suggest three distinct taxonomic groups within the U.S., an eastern group consisting of *S. c. carolinensis*, an interior group including both *S. c. nelsoni* and *tenuissima*, and a Pacific group including *S. c. aculeata*. Because few recordings of White-breasted Nuthatches are available from Mexico, we were unable to analyze vocalizations of those taxa statistically. Qualitatively, however, *S. c. alexandrae* in the Sierra San Pedro Mártir of northern Baja California fits with *S. c. aculeata* on the basis of recordings of modulated *quanks* (www.xeno-canto.org/72055, recordist R. E. Webster) in the same frequency range as those of *S. c. aculeata*. Conversely, *S. c. lagunae* in the Sierra de la Laguna of southern Baja California fits into the interior group on the basis of recordings of disyllabic *quanks* (www.xeno-canto.org/72055, recordist R. E. Webster; macaulaylibrary.org/audio/161719, recordist M. J. Iliff; N. Pieplow recordings). Disyllabic and rapid *quanks* have likewise been recorded throughout the range of the interior Mexican subspecies *S. c. mexicana* (www.xeno-canto.org/229762, recordist Peter Boesman; www.xeno-canto.org/67052, recordist Daniel Lane), and *S. c. oberholseri* (www.xeno-canto.org/229763, recordist Peter Boesman).

Our analysis of vocalizations is consistent with both structural and plumage characters of these subspecies, which also suggest three groups with *S. c. nelsoni* and *tenuissima* more similar to each other than to *aculeata* and *carolinensis* (Hawbecker 1948, Pyle 1997, Sibley 2000). Genetic studies suggested that each of these four may be a distinct clade (Spellman and Klicka 2007, Walstrom et al. 2011). However, Hawbecker (1948) identified specimens from central southern Nevada that appeared to be intergrades between *S. c. nelsoni* and *tenuissima*, and Spellman and Klicka (2007) found mixed haplotypes between these two taxa in the same region. These genetic analyses confirmed those two interior subspecies as sister taxa more closely related to each other than to the other two U.S. subspecies. Spellman and Klicka (2007) grouped *S. c. mexicana* and *lagunae* with *S. c. nelsoni*, which also aligns well with the qualitative similarity of vocalizations we noted above.

Slow vs. Fast Song

Tyler (1916), Kilham (1981), Richison (1983), and Elliott (2005) studied vocalizations of *S. c. carolinensis* over extended periods at locations in Massachusetts, New Hampshire, Minnesota, and Ohio, respectively. Each author described both a slow song and fast song, with the fast song generally given at approximately twice the rate of the slow song. Tyler (1916) and Elliott (2005) reported never hearing songs of intermediate cadence from any individuals. But we found no clear distinction between slow and fast songs in recordings made throughout the ranges of any of the four subspecies we analyzed. It may be that a given individual sings stereotyped slow or fast songs, as Ghalambor and Martin (1999) suggested for the Red-breasted Nuthatch (*Sitta canadensis*), but that variation between individuals and across the range of each subspecies produces the relatively continuous set of song rates we observed (Figure 4).

There are no studies similar to the ones cited above for any of the other subspecies of the White-breasted Nuthatch. However, we have noted two examples of *S. c. tenuissima* switching from a slow song to a fast song, in each case approximately doubling the cadence. One example in which an individual bird switches from slow to fast song, apparently in response to songs and calls from a distant White-breasted Nuthatch, can be heard at www.xeno-canto.org/239350. Kilham (1981) observed fast song only in agonistic encounters, while Richison (1983) and Elliott (2005) observed this song type in a variety of contexts.

It is possible that the distinction between *tooey* and simple songs in *S. c. aculeata* corresponds to the distinction between slow and fast song in other subspecies, but more study is needed.

Further Study

We made no attempt to characterize the function or context of White-breasted Nuthatch vocalizations, including by season. Studies similar to those of Richison (1983) and Elliott (2005) for the other subspecies are needed for the roles of vocalizations such as the disyllabic and rapid *quanks* of the interior subspecies to be understood. Such studies could also test the hypothesis that individual White-breasted Nuthatches sing two stereotyped songs at different rates, as well as investigating the function of those two songs, and the function of the *tooey* song in *S. c. aculeata*.

The possibility of vocal learning in North American nuthatches requires investigation. Strong circumstantial evidence from patterns of individual and regional variation indicates that song may be learned in the European Nuthatch (*Sitta europaea*; e.g., White 2012), and it is possible that song, at least, is learned in the White-breasted Nuthatch as well.

We did not perform any playback experiments in the field to test how and whether White-breasted Nuthatches differentiate between the sounds of their own subspecies and those of other subspecies. Such experiments could help clarify whether vocal differences between groups contribute to reproductive isolation. Detailed studies of the contact zones between these subspecies could help to determine the extent of reproductive isolation and gene flow, if any, between these groups, and to provide a more conclusive answer to the question of species boundaries in this complex.

ACKNOWLEDGMENTS

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