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# Chestnut-sided warblers use rare song types in extreme aggressive contexts

Bruce E. Byers*

*Department of Biology, University of Massachusetts, Amherst, MA, U.S.A.*

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Songbirds of a number of species use song repertoires that contain some song types that are uttered only rarely, and are therefore unlikely to be heard by the typical listener. Singing patterns that hide song types are difficult to reconcile with putative repertoire functions that require listeners to evaluate the size or diversity of singers' repertoires. Perhaps in species with repertoires that include rarely used song types, the rare types serve a function that is required only rarely. Based on observations of chestnut-sided warblers, *Setophaga pensylvanica*, I hypothesized that in this species, rarely used song types are reserved for use in extreme aggressive contexts. I experimentally simulated such a context (a prolonged territorial intrusion by a male competitor) by presenting song playback and a taxidermic mount on chestnut-sided warbler territories. The targeted males were much more likely to use their rare song types during the simulated intrusions than during natural baseline singing. A similar but smaller effect was evident in an analysis of natural singing that compared songs associated with fighting and chasing with songs that were not. Use of rare song types by experimental subjects did not predict their likelihood of attacking the simulated intruder. If this lack of predictive value is not an experimental artefact and extends to natural interactions, it suggests that despite their association with highly aggressive contexts, rarely used song types might not represent the strongest possible signal of aggressive motivation in chestnut-sided warblers. Perhaps use of rare types instead represents the penultimate level in a graded series of aggressive signals that culminates with a signal variant that went undetected in this experiment.


In many songbird species, individuals use songs drawn from repertoires of multiple song types. A puzzling aspect of such song repertoires is that birds may utter some of the song types in their repertoires only rarely, effectively concealing a portion of the repertoire from listeners. For example, most of the song types used by a house wren, *Troglodytes aedon*, are seldom uttered, accounting for less than 1% of sampled songs (dos Santos, Llambias, & Rendall, 2016; Rendall & Kaluthota, 2013). As a result, house wrens reveal their repertoires of up to 190 song types very slowly; even birds that had been extensively sampled (more than 3000 songs recorded) over a period of weeks continued to introduce song types that had not previously been detected (Rendall & Kaluthota, 2013). Likewise, many of the song types in a rock wren's, *Salpinctes obsoletus*, repertoire of 70–100 song types are used rarely, and new types are detected even after sampling more than 1000 songs from a bird (Kroodsma, 1975). Analysis of a large sample (more than 10 000 song bouts) of northern mockingbird, *Mimus polyglottos*, songs revealed that individuals used 102–412 different song types, but 25% of types occurred only once in the sample (Derrickson, 1987, 1988). The comparably large repertoires of tropical mockingbirds, *Mimus gilvus*, are also revealed slowly; Price and Yuan (2011) found no sign of a plateau in the accumulation of types even after sampling 200–400 songs per bird. After sampling 4000 songs from four eastern bluebirds, *Sialia sialis*, over a 6-month period, Huntsman and Ritchison (2002) were still discovering previously undetected song types among the 40–80 types in their subjects' repertoires. Many of the types in a Cassin's vireo, *Vireo cassinii*, repertoire of 44–60 phrases are uttered rarely; on average the rarest type in a bird's repertoire accounts for 0.07% of sampled songs (Hedley, 2016). Song types are similarly hidden by the singing patterns of other large-repertoire species such as the nightingale, *Luscinia megarhynchos* (Kipper & Hultsch, 2006), sedge wren, *Cistothorus platensis* (Kroodsma, Liu, Goodwin, & Bedell, 1999), and bananaquit, *Coereba flaveola* (Wunderle, Cortes, & Carromero, 1992).

Repertoires that include rarely used song types seem to be a widespread, possibly universal, feature among species with large

* Correspondence: B. E. Byers, Department of Biology, 221 Morrill Science Center, 611 North Pleasant Street, Amherst, MA 01003-9297, U.S.A.
*E-mail address:* bbyers@bio.umass.edu.

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song repertoires, but they also occur in species with more modestly sized repertoires. For example, in chaffinches, *Fringilla coelebs*, which have repertoires of up to six song types, the repertoires of many birds include song types that account for less than 5% of sampled songs (Slater, 1981, 1983). Similarly, some of the song types in the repertoires (1–9 types) of great tits, *Parus major*, go undetected even in fairly large song samples, presumably because they are uttered infrequently (Franco & Slabbekoorn, 2009; Rivera-Gutierrez, Pinxten, & Eens, 2011). In rufous-and-white wrens, *Thryophilus rufalbus*, a sample of 673 songs, on average, is required to detect all of the 6–14 song types in a bird's repertoire (Mennill & Vehrencamp, 2005).

One small-repertoire species that reveals its array of song types especially slowly is the chestnut-sided warbler, *Setophaga pensylvanica*. Males of this species have repertoires that, like the repertoires of many other wood warbler species, are partitioned into two categories, dubbed first-category songs and second-category songs (Spector, 1992); in chestnut-sided warblers, songs in the two categories are historically known as accented-ending and unaccented-ending songs, respectively (Ficken & Ficken, 1962). Accented-ending songs are distinguished by a characteristic downsweep element that concludes all accented-ending song types (Fig. 1). The median size of a chestnut sided warbler song repertoire is eight song types, and repertoires can contain as many as 12 song types, but 70–95% of a typical male's singing consists of just two predominant song types (one accented-ending type and one unaccented-ending type; Byers, 1995). The remaining accented-ending and unaccented-ending song types in a repertoire are uttered only rarely.

Accented-ending songs and unaccented-ending songs are used in different contexts (Byers, 1996a; Kroodsma, Bereson, Byers, & Minear, 1989). For example, unmated males and mated males that are near a female tend to sing accented-ending songs. Males that are near a territorial border or are involved in a fight or a chase with another male tend to use unaccented-ending songs. Unaccented-ending songs are also used at dawn, when chestnut-sided warblers present a distinctive vocal performance that consists of 20–40 min of rapidly repeated utterances of a bird's predominant unaccented-ending song type, interspersed with characteristic chips.

Chestnut-sided warbler singing after dawn generally consists of bouts of varying duration that, like the distinctive dawn performance, contain a single song type. A singer typically repeats the same song type for the duration of a bout of continuous singing; bouts that include type switches are relatively uncommon. Most switches that do occur are between the predominant accented-ending type and the predominant unaccented-ending type. For example, 759 song samples (3–10 min duration) recorded from 18 birds in one breeding season (2010) contained 81 song type switches, and 67 of these involved the predominant types only (Byers, n.d.). The remaining switches involved changes between predominant and rarely used song types.

A chestnut-sided warbler may share song types with other birds in its breeding neighbourhood, but the reason for sharing differs somewhat between accented-ending and unaccented-ending songs (Byers, 1996b; Byers, Belinsky, & Bentley, 2010). Almost all accented-ending songs fall into four different song types that are found across the species' range. Thus, within a neighbourhood, accented-ending song types are likely to be shared by multiple birds simply because there are so few types. Unaccented-ending songs are far more diverse and geographically variable, with a large number of different types present even within a locality.

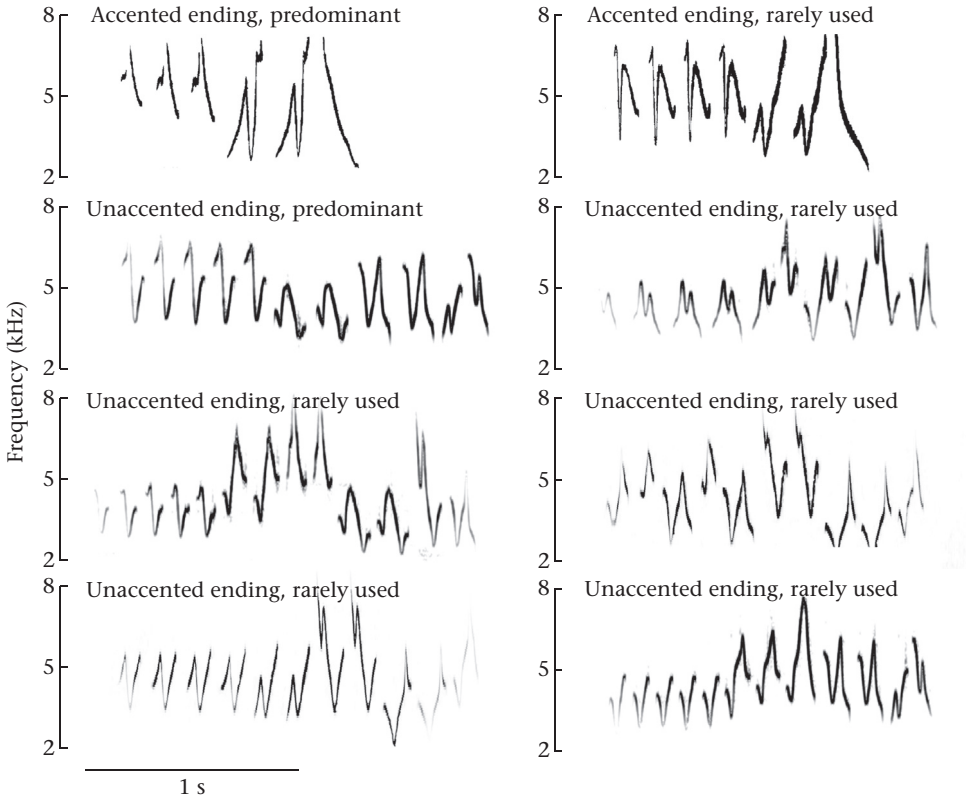


**Figure 1.** The song repertoire of a male chestnut-sided warbler. The repertoire includes two accented-ending song types (top row; distinguished by their characteristic downsweeping terminal element) and six unaccented-ending song types. One accented-ending type and one unaccented-ending type (the two types at the top of the left column) served as this male's predominant song types; together they accounted for 1384 of 1521 songs (91%) recorded from this male in 2013. The other six types in the repertoire accounted for the remaining 9% of sampled songs.