Repertoire size and song sharing among American Redstarts (*Setophaga ruticilla*) at the University of Michigan Biological Station

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Abstract
Among many passerine species, repertoire size for a given adult male is thought to directly impact fitness as a result of myriad evolutionary pressures. Recent evidence suggests, however, that the percentage of songs shared within a given males repertoire, regardless of repertoire size, may actually be responsible for the increased fitness previously thought to be influenced by repertoire size alone. Highly shared songs similar in two distant geographic regions may also function for conspecific recognition beyond mate attraction. I observed song sharing for a population of American Restarts (*Setophaga ruticilla*) located on Grapevine Point (GVP), one mile northeast of the University of Michigan Biological Station in Pellston, MI. By indentifying eight distinct song types on GVP, I documented the rate of songs shared and repertoire size for five male American Redstarts. Mean repertoire size for adult males on GVP did not differ significantly from the same mean calculated for American Redstart populations located in New Brunswick, Canada (Lemon et al. 1985). Song Type 1 was the most highly shared song on GVP and was very similar to the most shared song type (Song Type 1) in New Brunswick. These similarities support the hypothesis that highly shared song types of one population will also be highly shared among other populations. Although the specific function of these highly shared songs is unknown, evidence from other Passeriformes suggests that a high degree of song sharing implies a positive effect on individual territory tenure and subsequent fitness.

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Introduction

An investigation of geographic variation among particular species of songbirds offers an interesting perspective on song production and song learning. Many aspects of song sharing are attributable to evolutionary pressures including direct aggressive male-male interactions (Lemon 1968), mimicry of superior males (Payne 1982), the adaptation of songs to particular local environmental conditions (Baker 1975), and female attraction (Payne 1982). Song learning is impacted by these pressures as well, and the development of a complex song repertoire is thought to ultimately enhance male fitness. Evidence suggests that, with an increased probability of containing attractive syllables, larger repertoires could be highly attractive (Gil and Gahr 2002). Song sharing can also impact more specific breeding behaviors, including territory tenure and subsequent fitness. In certain passerine species, an increased rate of song sharing with other males in the local population positively influences the individual male’s ability to maintain a viable territory throughout his lifetime (Beecher et al. 2000). With an increased ability to maintain a particular territory, males with highly shared repertoires are ultimately afforded consistent mate acquisition and increased fitness (Beecher et al. 2000).

With regards to song sharing and song development, the American Redstart, Setophaga ruticilla, is a paruline warbler of considerable interest. During the first adult breeding season, males remain in their juvenile plumage, closely resembling the female with light gray on the head, gray to olive green on the back, white on the belly, and pale yellow patches on the tail, wing, and sides (Sherry and Holmes 1997). Adult males are markedly different with a glossy black plumage spotted with bright salmon orange patches on the base of the outer rectrices, the base of the remiges, and the sides of the breast; the lower underparts are white (Sherry and
Holmes 1997). These plumage differences allow for complete and accurate investigations of song sharing and song learning between age-classes.

Most individual male American Redstarts have two general song types, accented and unaccented, and there may be one to several songs of each type; second year males tend to have larger song repertoires than yearling males (Lemon et al. 1985). The purpose of this study was to investigate song complexity and repertoire size among a population of American Redstarts at the University of Michigan Biological Station. Song sharing and shared song composition were also investigated and compared with other northeast populations located in New Brunswick, Canada (Lemon et al. 1985). One may suspect, given the high degree of song sharing for a specific simple song type in New Brunswick, that highly shared songs within the current study population may be similar to those studied by Lemon et al. (1985). If one song type is found to be much more highly shared than others, as found by Lemon et al. (1985), one may further postulate that highly shared songs common in both regions might be important for conspecific recognition and unique songs used for other aspects of intra- and intersexual interactions.

Materials and Methods

Subjects and Locality

A population of American Redstarts was identified on Grapevine Point approximately one mile northwest of the University of Michigan Biological Station in Pellston, MI. The station is located along the southeast shore of Douglas Lake, into which the peninsula designated as Grapevine Point (GVP) extends north. The woody canopy at GVP is comprised of various densities of sugar maple \((Acer saccharum)\), red maple \((Acer rubrum)\), American beech \((Fagus grandifolia)\), yellow birch \((Betula alleghaniensis)\), and paper birch \((Betula papyrifera)\).
Recording on GVP

In order to account for both song variation throughout the day and habitat variation, recordings were recorded between 5:00-7:00 AM along the Grapevine Point trail using a Marantz PMD660 digital recorder with a Sennheiser unidirectional microphone mounted on a sprung handgrip. Age class of each individual was distinguished by plumage characteristics and observed at a distance of about 5-30 m using 10 × 42 binoculars. Five individuals were identified by territorial location, and each site was flagged and marked with the appropriate designation of AM (Adult Male) 1-4 or YM (Yearling Male) 1. Return visits to each territory subsequently provided multiple recordings of each individual. A fixed recording regime was not implemented, however, and some birds were recorded more than others.

Determination of Repertoire Size and Song Complexity

Since American Redstarts do not sing each song type in long strings, only a small number of samples were needed to record all commonly used songs in each individual’s repertoire (Lemon et al. 1985). Songs were analyzed using the Raven bio-acoustics software package. Each song was classified using a subjective analysis of song shape regardless of the number of syllables, as syllable number varies considerably among songs sharing the similar shape and frequency range (Lemon et al. 1985). Repertoire size was calculated for each individual as the number of novel song types identified in the first 15 uninterrupted songs in each sample as in previous work (Nicholson et al. 2007, Lemon et al. 1985). Song complexity was described by frequency range, song duration, and high and low frequencies. Song sharing was calculated as the percentage of adult males using a particular song. The data collected by Lemon et al. (1985) was then used to compare song sharing and repertoire size with other populations of American Redstarts located in New Brunswick, Canada. Due to reduced sample size and lack of
normality, a Mann-Whitney test was needed to compare mean repertoire size among adult males between my data and the data compiled by Lemon et al. (1985). A Mann-Whitney test was also used to compare means for repertoire size among yearling males. Statistical analysis was conducted using SPSS.

Results

Among the five individuals recorded, 8 distinct song types were identified (Figure 1). Song complexity characteristics varied within each song type and show considerable variation between song types as well. Each song consisted of 2 to 7 distinct phrases or notes, and all song types ranged between 2.99 and 9.35 Hz and lasted between 0.76 and 1.13 seconds (Table 1).

A Mann-Whitney test showed that the difference between the means for adult male repertoire size between the GVP and New Brunswick (Lemon et al. 1985) populations (Table 2) was not significant ($U = 40.0, P = .109$). Additionally, it should be noted that the repertoire size of the yearling male fell within the repertoire size range of yearling males recorded by Lemon et al. (1985). A Mann-Whitney test showed that the difference between the yearling male means was not significant ($U = 10.0, P = .303$), yet this comparison must be viewed as merely anecdotal considering a sample size of one.

Song sharing was shown to be variable between song types (Table 3) and this variation was directly related to the song sharing data compiled by Lemon et al. Song Type 1 was the most highly shared song type (80%), and was characterized by a repetitive trill usually followed by an accented ending. The yearling male (Bird 5) was the only bird to share the song type without the accent. This song type is similar to the most highly shared song type (Type 1,
84.6%) in Lemon’s data (Figure 2). Other song types for the GVP population were either unique (Types 6, and 8) or shared by only 20% of the population (Types 2,3,4,5, and 7).

Discussion

The emergence of eight distinct song types among the five study individuals represents variation in terms of the number of unique and shared song types consistent with other populations of American Redstarts (Lemon et al. 1985, Lemon et al. 1994, Proctor-Gray and Holmes 1981). Song complexity characteristics are also consistent with past study populations (Sherry and Holmes 1997), which leads to the conclusion that the eight song types identified characterize considerable song variation which may be further evidenced by a larger study population.

The non-significant difference between the GVP and New Brunswick populations’ means for adult male repertoire size suggests that the GVP study population shares similar song development characteristics with those found in the New Brunswick population. The mean repertoire size for yearling males fell within the range of yearling male’s repertoire sizes from the New Brunswick population. Considering other consistencies with the populations studied by Lemon et al. (1985) however, one might expect that, given a larger sample size, a trend showing smaller repertoire sizes among yearling males might have emerged in the GVP population.

Consistencies in song sharing between the New Brunswick and GVP populations raise interesting questions regarding the ecological and evolutionary function of these highly shared songs. Among several other paruline warblers, including the Blue-winged Warbler (*Vermivora pinus*), the Yellow Warbler (*Dendroica petechia*), and Chestnut-sided Warbler (*Dendroica pensylvanica*), song types can be classified into at least two different categories (Kroodsma
Most often, these categories specify each song type’s utility as either mate attraction or direct male-male interaction (Kroodsma 1981). More specific song function categorizations rely not only on song structure but also on specific behavioral cues for reliable classification. Spector (1992) classifies most wood warblers as either “performance encoded” or “form encoded” species. For form encoded species, including Black-throated Green Warblers (*Dendroica virens*), Prairie Warblers (*Dendroica discolor*), and Golden-winged Warblers (*Vermivora chrysoptera*), specific function of each song type can be assigned by merely analyzing song structure without the regard of other contextual cues (Byers 1995). As American Redstarts are performance encoded, however, song function can only be ascertained given a combined analysis of song structure and context, that is, the relative position of a given song type within a particular song bout (Byers 1995). For the current study, however, these contextual cues were not analyzed and specific song functions remain speculative. Interestingly enough, all performance encoded species generally reveal their entire repertoires in a given song bout (Byers 1995), and the data presented here can be accordingly viewed with confidence.

Pervasive sharing of Song Type 1 in New Brunswick was explained by temporal observations throughout the breeding season. Prior to the arrival of females to the breeding range, Song Type 1 was most often used, presumably to announce male presence. Later in the season, the song type was observed most often in areas where males were least in contact with one another (Lemon et al. 1985). These observations support the hypothesis that the very similar Song Type 1 from my data could be used for conspecific recognition. However, observations throughout the study are inconsistent with the specifics of Lemon et al.’s observations. Although all of the study subjects were recorded late in the breeding season, none of the males were deprived from contact with other American Redstart males. The density of American Redstarts
within the study area was high enough to practically guarantee constant neighboring contact. This discrepancy with Lemon et al.’s observations indicates that the behavioral context for song type categorization is needed to make further claim on the function of songs recorded on GVP.

Beyond specific behavioral context, song sharing may be highly influenced by the simplicity of the song type as well. Compared with all other song types, Song Type 1 has a reduced number of notes and seeming simple frequency changes. The relatively simple trill of Song Type 1 followed by an accented ending may allow for ease of copying and thus persist readily and spread quickly within a given population. Persistence of certain song types and song sharing has also been strongly linked to individual territory tenure and increased fitness. In Song Sparrows (*Melospiza melodia*), Beecher et al. (2000) showed that increased song sharing, irrespective of repertoire size, positively influenced the amount of time an individual male was able to hold a specific territory throughout his lifetime. Song Type 1, given its comparative simplicity, may provide a foundation for song sharing during initial repertoire development and thus persist after each male’s yearling breeding season.

By indentifying eight distinct song types on GVP, I documented song sharing and repertoire size even though a small sample size hindered data analysis. Mean repertoire size for both adult and yearling males on GVP did not differ significantly from the same means calculated for American Redstart populations located in New Brunswick, Canada (Lemon et al. 1985). Song Type 1 was the most highly shared song on GVP and was very similar to the most shared song type (Song Type 1) in New Brunswick. These similarities support the hypothesis that highly shared song types of one population will also be highly shared among other populations. Although the specific function of these highly shared songs can merely be
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Acknowledgments

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Literature Cited


### Song Complexity Characteristics

<table>
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<tr>
<th>Song Type</th>
<th>Low Frequency (Hz)</th>
<th>High Frequency (Hz)</th>
<th>Change in Frequency (Hz)</th>
<th>Song Duration (seconds)</th>
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<td>7795.8</td>
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**Table 1**: Mean high and low frequencies, frequency change, and duration for all song types recorded at GVP in 2009.
Table 2: Mean repertoire sizes for two populations of American Redstarts. One is located on GVP in the University of Michigan Biological Station and the other is located in New Brunswick, Canada. The number in parentheses adjacent to each value specifies the sample size.

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<tr>
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<th>Adult Males</th>
<th>Yearling Males</th>
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<tr>
<td>UMBS</td>
<td>3.25 (4)</td>
<td>3.00* (1)</td>
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<td>Lemon et al.</td>
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*Only includes one yearling male*
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<th>Song Type</th>
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*Includes both adult and yearling males

**Table 3:** The number of males using particular song types on GVP.
Figure Legends

**Figure 1:** Repertoire composition for American Redstarts on GVP. Song types are categorized using sonogram shape and song frequency characteristics. Birds 1-4 are adult males and Bird 5 is a yearling male.

**Figure 2:** Examples of most shared song type sung by male American Redstarts in New Brunswick, Canada. This song type greatly resembles song type 1 from the GVP population.
<table>
<thead>
<tr>
<th>Song Type</th>
<th>AM 1</th>
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