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Repertoire structure, song sharing, reproductive success, and territory tenure in a population of Canada Warblers (*Cardellina canadensis*) in central New Hampshire

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Draft

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Abstract

Sexual selection for larger repertoires and the social advantages of sharing songs with territorial neighbours are two forces which may drive the evolution of complex song repertoires in songbirds. To evaluate the influence of these two selective pressures on repertoire evolution in a species with a complex repertoire, we examined repertoire structure, song sharing, reproductive success, and territory tenure in a Canada Warbler (*Cardellina canadensis* (L., 1766)) population in New Hampshire. Over two breeding seasons, we recorded 63 singing males, classified their song repertoires, quantified male song sharing, and determined male reproductive success and territory tenure. Male Canada Warblers had complex repertoires averaging 12 phrases (particular sequences of song elements) and 55 variants (songs composed of particular sequences of phrases). Song sharing decreased significantly with distance between territories, all of which were <1.75 km apart. Network analysis revealed clusters of male neighbours with high variant sharing, which was significantly associated with longer territory tenure. Overall pairing and fledging success were high, but were not related to repertoire size or song sharing. Our results suggest that song sharing aids in male territory acquisition and defence, and that females may therefore select mates based on their ability to retain a high-quality territory.

Key words: Canada Warbler, *Cardellina canadensis*, song repertoires, song sharing, reproductive success, territory tenure.

Introduction

Many bird species attract mates and defend territories using only one type of song, while others have repertoires of multiple songs (Catchpole and Slater 2008). Two hypotheses seek to explain repertoire evolution in the context of sexual selection (reviewed in Beecher and Brenowitz 2005). The repertoire size hypothesis states that female choice drives increased repertoire size, and is supported by evidence that males with larger repertoires have higher lifetime reproductive success (e.g., McGregor et al. 1981; Buchanan and Catchpole 1997; Reid et al. 2005). The song sharing hypothesis states that males who share more songs with neighbours (males who share a territory boundary) are more successful at defending territories against those neighbours (e.g., Beecher et al. 2000b). However, there is conflicting support for and against the repertoire size hypothesis among studies conducted on different populations of the same species (reviewed in Byers and Kroodsma 2009). In their review, Byers and Kroodsma (2009) found that field studies showed less support for the repertoire size hypothesis than did lab studies, and that opposing results were obtained for 8 of 12 species with multiple studies. Furthermore, the two hypotheses may not be mutually exclusive, as female birds of some species prefer locally-shared songs (O’Loghlen and Rothstein 1995; O’Loghlen and Beecher 1999; Hernandez et al. 2009) or prefer males who are dominant in countersinging interactions (Mennill et al. 2002).

Several studies on male reproductive success and song attributes have shown support for the repertoire size hypothesis (reviewed in Byers and Kroodsma 2009). A 20-year study of a resident Song Sparrow (*Melospiza melodia* (Wilson, A, 1810)) population found that males with larger repertoires had higher lifetime reproductive success (Reid et al. 2005). In field studies on the Sedge Warbler (*Acrocephalus schoenobaenus* (L., 1758)), males with larger syllable

repertoire sizes paired earlier than males with smaller syllable repertoires (Catchpole 1980; Buchanan and Catchpole 1997). However, male territory size was also correlated with pairing date in the latter study (Buchanan and Catchpole 1997), and older, more experienced males in this species have larger repertoires (Nicholson et al. 2007). Indeed, stronger support found for the repertoire size hypothesis in lab studies than in field studies suggests that females in natural situations may select mates based on attributes other than a large repertoire (Byers and Kroodsma 2009).

Song sharing between neighbours is prevalent in many songbird species, such that repertoire similarity decreases as distance between territories increases (e.g., Hill et al. 1999; Foote et al. 2007; Koetz et al. 2007; Rivera-Gutierrez et al. 2010). Song sharing may increase reproductive success (Payne et al. 1988) and length of territory tenure (Beecher et al. 2000*b*), by allowing males to engage in aggressive intrasexual encounters using shared songs (Krebs et al. 1981; Beecher et al. 2000*a*; Vehrencamp 2001). Shared songs permit song matching between males, an aggressive signal, during territorial countersinging (Beecher et al. 2000*a*; Vehrencamp 2001; Vehrencamp et al. 2014). Indigo Bunting (*Passerina cyanea* (L., 1766)) males in their first breeding season who shared older neighbours' songs had higher pairing success than non-sharers (Payne et al. 1988). Male Song Sparrows who shared more songs with neighbours had longer territory tenure (number of years defending a given territory) in a population with high overall sharing (Beecher et al. 2000*b*), but not in a population with low sharing (Hughes et al. 2007). Evidence that older male Song Sparrows preferentially sing the most commonly shared songs within a song neighbourhood (a cluster of males on adjacent territories with similar songs) suggests that use of shared songs is related to breeding experience and may facilitate longer territory tenure (Lapierre et al. 2011).

In the Oscine suborder of passerines, song sharing arises from song learning, which occurs primarily in a bird's first year, but may continue throughout life in some species and populations (Catchpole and Slater 2008). Species who learn songs range from closed-ended learners, where song learning ends after the first year of life, to open-ended learners, where new songs can be learned throughout life (reviewed in Beecher and Brenowitz 2005). Each male may learn more songs than he eventually uses in his repertoire and subsequently drop songs that are not shared (McGregor and Krebs 1989; Nelson 2000; Nordby et al. 2007). For example, Great Tits *Parus major* L., 1758 modify their repertoires by adding and dropping songs according to frequency of use among other members of the population (McGregor and Krebs 1989).

The Family Parulidae (North American wood-warblers) is a well-studied oscine group in which males of many species share songs with territorial neighbours (Lemon et al. 1994; Byers 1996; Beebe 2002; Janes and Ryker 2006). Some parulids continue to modify their repertoires after their first year (reviewed in Spector 1992). For example, male American Redstarts (*Setophaga ruticilla* (L., 1758)) add and delete serial mode songs, used primarily in male-male interactions, from their repertoires between their first and second breeding seasons depending on whether these song types are also used by neighbouring males (Lemon et al. 1994). Canada Warbler (*Cardellina canadensis* (L., 1766)) males have complex repertoires of multiple song types used differentially by social context (Demko et al. 2013). This species is therefore ideal for evaluating the repertoire size and song sharing hypotheses in the context of male territory tenure and reproductive success.

The objective of this study was to test the repertoire size and song sharing hypotheses by quantifying song repertoire composition and relating patterns of song sharing to duration of

territory tenure and reproductive success among males in a dense breeding population of Canada Warblers. If females prefer males with larger repertoires or more shared songs, we predict that male repertoire size or song sharing will be positively correlated with reproductive success. If use of shared songs is advantageous in territory acquisition and retention by males, we predict that: (1) neighbouring males will share more songs than non-neighbours; (2) males with higher sharing will enjoy longer territory tenure; and (3) first-year males will modify their repertoires to share more songs with older neighbours. Our results will help to elucidate whether intra- or intersexual selective pressures act to shape and maintain complex repertoires in Canada Warblers and other oscine species.

Materials and methods

Study site and subjects

We recorded territorial male Canada Warbler songs from May to July 2010 and 2011 in Canaan, New Hampshire, USA (43°40'N, 72°03'W), at two study plots. The north plot was in the Bear Pond Natural Area, a mixed upland forest, and the south plot was in the Canaan Town Forest, a red maple (*Acer rubrum* L.) swamp; the two plots are <450 m apart and separated by Bear Pond. The average adult male return rate (52%), pairing success (91%), and fledging success (75%) have been high in this population since a study of the species' breeding ecology began in 2003 (Hallworth et al. 2008).

We captured male Canada Warblers using mist-nets and playback, uniquely colour-banded them, and aged them as first-year breeders (second-year or SY) or older males (after-second-year or ASY) according to plumage characteristics (Rappole 1983; Pyle 1997). We

visited territorial males every 2-7 days to monitor their breeding status, and confirmed fledging by observing an adult carrying food or seeing at least one fledgling in the territory (Hallworth et al. 2008). We obtained 20-60 min continuous recordings of focal males from the start of the dawn chorus at approximately 0330-0345 h EST until morning vocal activity waned at approximately 1030 h EST. We recorded at a sample rate of 48 kHz with a Marantz Professional PMD661 digital recorder, Sennheiser ME62/K6 microphone, and SME PR-1000 parabola. All procedures involving animals were approved by the Dalhousie University Committee on Laboratory Animals (Protocol Number 10-017).

Song structure and repertoire size

We viewed spectrograms using Raven Pro 1.3 software (www.birds.cornell.edu/raven), and classified vocalizations using a coding system that allowed comparisons within and among males. *Elements*, or discrete units on spectrograms (e.g., Byers 1995), were classified by shape, frequency range, and duration, and were of two types: *song elements* and *calls* (Fig. 1). Song elements were the smallest units comprising songs, while calls were shorter duration (<0.06 s) and larger frequency bandwidth (>4.5 kHz) vocalizations. A *phrase* was a particular sequence of song elements, and a *variant* was a particular sequence of one or more phrases, typically preceded by one or more calls (Demko et al. 2013).

The total number of songs recorded from each male in a given year ranged from 149-1239 (mean $\pm$ SD = 549 ± 268). To verify that we had sampled repertoires thoroughly, we produced a cumulative plot of the number of new variants observed by the total number of songs recorded from a given male (Gil and Slater 2000). We plotted one continuous bout of dawn song from each male ($n = 36$) for which we had dawn recordings. A continuous song bout was defined

as a song sequence with between-song pauses of ≤ 30 s (Wiley et al. 1994). Since the number of new variants observed for most birds began to level off around 20-30 songs (Fig. 2), a sample of ≥ 149 songs recorded per male was considered sufficient for song sharing analyses.

For 11 males with dawn recordings in both 2010 and 2011, we found that each male used all of his common variants (i.e., those representing $>5\%$ of the total number of variants recorded per year) in both years. Therefore, we are confident that males used all of their common variants during a full 30-45 min dawn bout. We separated song sharing analyses by year to account for between-season shifts in territory size, location, and occupancy. We combined data from both years for reproductive success analyses, but included each male in only one randomly-selected year if recordings from both years were available.

To evaluate whether the number of recorded songs influenced repertoire size estimates, we used Pearson's correlations to test for associations between both phrase and variant repertoire sizes and the total number of songs recorded. To evaluate whether among-male repertoire sizes remained stable between years, we used paired *t*-tests. We used unequal variance *t*-tests to test for differences in repertoire size between failed and successful breeders.

Song sharing

To quantify the relationship between song sharing and distance between territories, we compared phrase and variant sharing between all pairwise comparisons of studied males. For phrase sharing, we calculated pairwise Jaccard's similarity coefficients, with a correction for differences in repertoire size (MacDougall-Shackleton et al. 2009) to minimize the effect of among-male variation in repertoire size. Phrases were shared if $\geq 50\%$ of elements had the same

shape and order. For any two males, A and B, the adjusted Jaccard's similarity coefficient, S_j (adj), is calculated as:

$$(1) \quad S_j(\text{adj}) = c / ((a+b+c)-d)$$

where a is the number of phrases in A's repertoire, but not in B's; b is the number of phrases in B's repertoire, but not in A's; c is the number of phrases common to A and B; and d is the difference between the phrase repertoire size of A and B.

For variant sharing, we calculated the frequency of use of each variant as a proportion of total songs recorded from each male. This information was used to calculate pairwise Bray-Curtis similarity coefficients, which weight each variant based on the frequency of occurrence, such that the importance of rare variants is not overemphasized (Clarke and Warwick 2001).

We produced minimum convex polygon territory maps in ArcGIS 10 software (ESRI, Redlands, CA) from GPS points of each male's singing locations (mean $\pm$ SD: 21 ± 10 , range 3-49). We calculated the median centre of each male's singing area using the Median Center tool under Spatial Statistics Tools-Measuring Geographic Distributions in ArcToolbox. The median centre reduces the weight of outlier points compared to the mean centre. We then calculated pairwise distances between median centres with the Point Distance tool under Analysis Tools-Proximity in ArcToolbox. Territories defended by males in this study were <1.75 km apart.

To test for associations between distance between territories and both phrase and variant sharing, we ran Mantel tests on the pairwise sharing values (converted to dissimilarity values to produce a distance measure) and territory distance matrices (e.g., Hill et al. 1999; Akçay et al. 2014). We conducted this analysis for all males with both (1) a sample of ≥ 149 recorded songs and (2) available territory locations, as described above (2010: $n = 22$; 2011: $n = 33$). We used

R packages ‘vegan’ to produce distance matrices and ‘ade4’ to perform Mantel tests. To compare song sharing between neighbours (males who share a territory boundary) and non-neighbours, we used Wilcoxon signed-rank tests with the mean sharing coefficients among neighbours and non-neighbours for each male (2010: $n = 22$; 2011: $n = 33$). Data were combined for both plots since the shortest distance between the north and south plot boundary was less than the greatest distance between male territory boundaries within the larger north plot.

To assess whether distinct song neighbourhoods were present, we used a network analysis method, Newman’s eigenvector, on the Bray-Curtis similarity matrices in program SOCPROG. This method calculates an eigenvalue for each male and an optimal modularity (fit) of the arrangement. The modularity algorithm determines whether there are fewer connections (i.e., shared songs) between males than expected randomly. Eigenvalues and modularity range from 0 for no association to 1 for a strong association. Eigenvalues near 0 indicate uncertainty in the group membership of a given male; a modularity of >0.3 indicates strong community structure (Newman 2006). Newman’s method is objective because it does not rely on an arbitrary cut-off value to assign clusters and does not require *a priori* assignment of the number of clusters. We included 63 males with ≥ 30 available recorded songs in this analysis (2010: $n = 41$; 2011: $n = 50$); 28 of these males were recorded in both years.

To assess the relationship between song sharing and years of territory tenure, we used Spearman’s rank correlations because data were not normally distributed. We compared both mean and maximum phrase and variant sharing coefficients of each male to the number of years present at the site by the end of the 2011 season. Mean sharing was the average sharing coefficient of a given male with all other males, and maximum sharing was the highest sharing coefficient of that male with any other male. High mean sharing indicates that a male shares

more songs with many males in the population, while high maximum sharing indicates that a male shares more songs with at least one other male. We used Wilcoxon signed-rank tests to determine whether mean and maximum repertoire sharing differed between successful and failed breeders.

Repertoire modification

We compared within- and between-year phrase use among a sub-sample of two SYs and eight ASYs to determine whether phrase addition and deletion varies by age class. For this comparison, we used only males with at least two available dawn recordings, which provided an exhaustive phrase repertoire sample. Except for Newman's method, we performed all statistical analyses using R 2.15.2 (www.R-project.org).

Results

Repertoire size

Phrase and variant repertoire sizes varied among male Canada Warblers, while within-male repertoire size and composition were largely consistent between years. Among the subset of males used in both years of the song sharing analysis ($n = 44$), 72 phrases were recombined to produce 1677 unique variants. Repertoire sizes ranged from 7-16 phrases (mean $\pm$ SD: 12 ± 2) and 11-134 variants (55 ± 27). Males recorded in both 2010 and 2011 ($n = 11$) did not change the size of their phrase (t -test: $t = 1.46$, $df = 10$, $P = 0.176$) or variant ($t = 0.11$, $df = 10$, $P = 0.914$) repertoires significantly between years. Two males who were new arrivals in 2010 used fewer phrases in 2011 than 2010, while the other nine did not change their phrase repertoires between years (Table 1).

The number of variants observed per male increased with the total number of songs recorded, although most variants were rare (i.e., represented <1% of the total number of variants recorded per year for a given male). As such, there were significant positive correlations between the percentage of rare variants observed and both variant repertoire size (Pearson correlation: $r_{42} = 0.77$, $P < 0.0001$) and total number of songs recorded ($r_{42} = 0.44$, $P = 0.003$). Variant repertoire size was highly positively correlated with both phrase repertoire size ($r_{42} = 0.62$, $P < 0.0001$) and the total number of songs recorded ($r_{42} = 0.42$, $P = 0.005$) yet phrase repertoire size and number of songs recorded per male were not significantly correlated ($r_{42} = 0.02$, $P = 0.891$).

During this study, overall fledging success of all males at the site was 58% (22 of 38 males) in 2010 and 81% (38 of 47 males) in 2011. Fledging success was not related to repertoire size in either year, although it was lower in 2010 (44%; 8 of 18 males) than in 2011 (80%; 24 of 30 males). We found no significant difference between fledging success and either phrase (t -test: 2010, $t = 1.33$, $df = 11.62$, $P = 0.208$; 2011, $t = 0.22$, $df = 11.54$, $P = 0.833$) or variant repertoire size (2010, $t = 0.99$, $df = 14.86$, $P = 0.336$; 2011, $t = 0.21$, $df = 7.62$, $P = 0.834$). Pairing success was high, 95% (20 of 21 males) in 2010 and 94% (30 of 32 males) in 2011, so the small sample size of unpaired males precluded a statistical comparison.

Song sharing

Both phrase and variant sharing among males decreased significantly with distance between territory centres. Phrase repertoire dissimilarity and distance between territories were significantly positively correlated in both 2010 (Mantel test: $r = 0.52$, $P = 0.001$) and 2011 ($r = 0.39$, $P = 0.001$; Fig. 3). Variant repertoire dissimilarity and distance between territories were

also significantly correlated in 2010 (Mantel test: $r = 0.51$, $P = 0.001$) and 2011 ($r = 0.36$, $P = 0.001$; Fig. 3).

Neighbouring males shared more of their repertoires than did non-neighbours in both years. This was the case for both phrase (Wilcoxon signed-rank test; 2010: $W = 159$, $P = 0.0005$; 2011: $W = 541$, $P < 0.0001$) and variant repertoires (2010: $W = 170$, $P < 0.0001$; 2011: $W = 531$, $P < 0.0001$).

Newman's method identified six clusters based on song similarity (song neighbourhoods) of 2-15 males in 2010 (modularity = 0.478; Fig. 4A), and seven clusters of 2-19 males in 2011 (modularity = 0.401; Fig. 4B). Two clusters in 2011 ('grey shaded' and 'thin black border') included males from both study plots, while the rest were exclusive to one plot (Fig. 4B). Two clusters ('dotted border' and 'striped') had the same membership in both years. In both of these clusters, males had highly similar repertoires, indicated by high eigenvalues. Six males present in both years (5, 12, 18, 48, 68, and 74) were assigned to a different cluster in each year.

Neighbouring males were grouped together between years even if the overall group composition changed, suggesting little within-male repertoire turnover between years. For example, males 5, 12, 48, 68, and 74 belonged to the same neighbourhood in both years: the 'dotted fill' neighbourhood in 2010 (Fig. 4A), and the 'light grey border' neighbourhood in 2011 (Fig. 4B). Some neighbourhoods were maintained between years when males on peripheral territories in 2010 moved to more central vacant territories in 2011, where they shared songs with more neighbours (e.g., male 6 in south plot and males 7 and 10 in north plot; Fig. 4).

Males with longer territory tenure shared a significantly greater proportion of variants, but not phrases, with other males at the site. There was a positive relationship between both mean and maximum variant sharing and number of years on territory at the site (mean: $\rho = 0.37$,

$P = 0.017$, Fig. 5A; max: $\rho = 0.32$, $P = 0.036$, Fig. 5B). However, neither mean nor maximum phrase sharing were significantly associated with years of territory tenure (mean: $\rho = 0.005$, $P = 0.976$; max: $\rho = 0.20$, $P = 0.211$).

Fledging success did not differ consistently overall with either mean or maximum repertoire sharing among males. Successful breeders had significantly higher maximum variant sharing (Wilcoxon signed-rank test: $W = 17$, $P = 0.045$) than failed breeders in 2010, but not in 2011 ($W = 57.5$, $P = 0.468$). Mean variant, mean phrase, and maximum phrase sharing were not significantly different between successful and failed breeders in either year ($P > 0.05$).

Repertoire modification

Within-year phrase turnover was observed in the two SY males examined (Table 1). SY-6 and SY-14 both dropped and added phrases within a year. In contrast, only ASY-4 changed his within-year phrase repertoire content. During his first year at the site, ASY-4 dropped two phrases which were not used by other males at the site (Table 1).

Between-year phrase turnover occurred in two males: one SY and one ASY. In 2011, SY-6 dropped one of the phrases added in 2010. ASY-35's phrase repertoire did not change during 2010, but he added one phrase and dropped two from 2010 to 2011 (Table 1). The dropped phrases were used by his neighbours 59 and 72, who did not return to the site in 2011.

Repertoire composition shifts involved modification of individual elements. For instance, in 2010, SY-6 gradually altered one of his songs (Fig. 6A-D) to more closely match the element structure and frequency range of the equivalent song used by two ASY male neighbours, 17 (Fig. 6E) and 75 (Fig. 6F). When all three males returned to the site in 2011, male 6 had retained his modified song (Fig. 6G).

Discussion

Our results provide support for the song sharing hypothesis but not for the repertoire hypothesis. Male Canada Warblers have complex repertoires which appear to remain largely stable over time in number of song elements, phrases, and variants. Song sharing decreased significantly with distance between territories, and neighbouring males in our study population shared much of their variant repertoires such that distinct song neighbourhoods were apparent. Males who shared more songs with their neighbours tended to have longer territory tenure, but neither repertoire size nor song sharing was significantly related to annual male pairing or fledging success.

The overall stability of repertoire size between years for male Canada Warblers has also been documented in other oscine passerine species. In longitudinal studies of Great Tits (McGregor and Krebs 1989) and American Redstarts (Lemon et al. 1994), repertoire size did not change overall with male age, although repertoire size increases or modifications were most frequent between the first and second breeding seasons. Although male Sedge Warblers increased their repertoire size with age, their within-year repertoire sizes did not vary despite considerable song turnover (Nicholson et al. 2007). Since male Canada Warblers live up to nine years (L. Reitsma unpubl. data), a longer duration study would be useful to explore similar effects on repertoire size and composition.

No relationship was found between fledging success and either repertoire size or degree of song sharing. This suggests that other factors, such as local breeding experience and territory quality, may have influenced the reproductive success of male Canada Warblers in our study population. Experienced breeders predominated at both study plots, as evidenced by male high site fidelity, pairing success, and fledging success (Hallworth et al. 2008; this study). Local

breeding experience correlates with higher reproductive success in other bird populations; for example, philopatric male Great Reed Warblers (*Acrocephalus arundinaceus* (L., 1758)) had higher lifetime reproductive success than immigrants, irrespective of age (Bensch et al. 1998). In Collared Flycatchers (*Ficedula albicollis* (Temminck, 1815)), philopatric males selected and defended higher-quality nest boxes and thus had higher mating success than recent immigrants (Pärt 1994). Females may therefore assess mate quality based on cues such as territory size (Buchanan and Catchpole 1997) and presence of superior nest sites (Pärt 1994). The abundance of suitable Canada Warbler nest sites in the study area potentially contributed to the high overall reproductive success in this population, and nest success may also be influenced by female experience, since females select nest sites and build the nests (Goodnow and Reitsma 2011).

Although many non-neighbours shared parts of songs (phrases), whole songs (variants) were typically shared only among neighbours. A similar spatial pattern of whole-song sharing with neighbours has been described in other bird populations with low male turnover between years, owing to year-round residency or high levels of breeding site fidelity (e.g., Hughes et al. 1998; Beecher et al. 2000b; Trillo and Vehrencamp 2005). Although migratory, Canada Warblers showed high male return rates at the study site (Hallworth et al. 2008), which may have promoted long-term use of shared songs among neighbouring males in the population. In addition, the higher inter-annual male return rate during this study at the north plot (88%) compared to the south plot (58%) may have further facilitated development and persistence of song neighbourhoods at the north plot.

Song neighbourhoods in this population appear to result, at least in part, from longer territory tenure of males with shared variant repertoires. The higher variant sharing among male Canada Warblers with longer territory tenure is consistent with patterns observed in other

songbird populations (e.g., Beecher et al. 2000*b*). Age is a related variable often used in song sharing studies (e.g., Cosens and Sealy 1986; Nicholson et al. 2007), although we used tenure because exact age was unknown for 13 males first captured as ASYs. In Song Sparrows, older males preferentially sing the most shared songs in their neighbourhood (Lapierre et al. 2011), which may permit increased aggression towards and dominance over territorial neighbours (Beecher et al. 2000*b*). Our field observations and unpublished recordings are consistent with these ideas: males with phrases and variants differing from locally common songs attempted to establish territories in mid-May 2010, but were displaced when the previous year's territory holders returned in late May. In 2011, unbanded males prospecting at the site with songs audibly distinct from local songs were unable to establish territories (A. Demko unpubl. data).

Our results also suggest that Canada Warbler song neighbourhoods may persist through repertoire modification by newly-established SY males or dropping of unshared phrases by ASY males. Both patterns are well-described in other oscine species (e.g., Payne and Payne 1993; Lemon et al. 1994; Nordby et al. 2007; Kiefer et al. 2010), and appear to occur in response to social influences from neighbours. For example, SY male Indigo Buntings typically copied a neighbouring ASY male to more closely match the local songs (Payne and Payne 1993). In one population of American Redstarts, over 40% of ASY males added or deleted songs between seasons based on whether or not neighbours sang them (Lemon et al. 1994). Although we documented repertoire modification in both SYs and two of eight ASYs analyzed, a larger sample size and long-term data set would strengthen evidence for this behaviour.

The patterns of phrase turnover and element modification we observed in our population suggest that phrases, elements, or both may be the fundamental units of song learning in Canada Warblers. A 19-year longitudinal analysis of element and song type turnover in a population of

Chestnut-sided Warblers *Setophaga pensylvanica* (L., 1766) demonstrated that cultural evolution of song occurred through rearrangement of song elements by new males to produce novel song types (Byers et al. 2010). Among the more variable unaccented song types, 25% of elements present in year 1 were still present in year 19, yet over two-thirds (68%) of new songs contained both old and new elements (Byers et al. 2010). A long-term study of song in a population spanning at least ten years (e.g., Payne and Payne 1993; Lemon et al. 1994; Byers et al. 2010) would be necessary to assess whether song learning occurs through similar mechanisms in Canada Warblers.

In conclusion, results of our study suggest that song sharing between neighbours may drive repertoire complexity in Canada Warblers. Phrase repertoire size remained stable between years despite addition and loss of individual phrases. Neither phrase nor variant repertoire size was correlated with reproductive success, contrary to the repertoire hypothesis, although high pairing and fledging rates in the population may be responsible for the lack of correlation. High song sharing between neighbours, higher sharing with longer duration of territory tenure, and copying of shared songs by first-year breeding males support the song sharing hypothesis. Studies of female mate choice by song in Canada Warblers across a gradient of reproductive performance (e.g., whether females prefer local or shared songs versus large or complex repertoires in males with a greater range of pairing and fledging success) would be necessary to definitively test the relationship between song and fitness. Interactive playback studies to examine how song matching or varying patterns of song delivery are used in male-male interactions (e.g., Vehrencamp et al. 2014) could further test the song sharing hypothesis in Canada Warblers and other songbird species with complex repertoires.

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Tables

Table 1. Within- and between-year phrase repertoire modification in SY and ASY male Canada Warblers (*Cardellina canadensis*).

Bird ID	Phrases added in 2010	Phrases dropped in 2010	Phrases added in 2011	Phrases dropped in 2011	Maximum phrase repertoire ¹	Number of recordings analyzed
SY-6	2	2	0	1	12	4
SY-14 ²	5	2	-	-	14	4
ASY-4	0	2	0	0	9	3
ASY-11	0	0	0	0	12	4
ASY-18	0	0	0	0	11	3
ASY-23	0	0	0	0	11	3
ASY-35	0	0	1	2	12	3
ASY-40 ³	-	-	0	0	8	2
ASY-52	0	0	0	0	16	3
ASY-75	0	0	0	0	11	2

¹The maximum number of phrases observed within a single recording of a given male.

²Male did not return to site in 2011.

³No dawn recordings available in 2010.

Figure captions

Fig. 1. Spectrograms demonstrating within-male song complexity in Canada Warblers (*Cardellina canadensis*). Three variants from male 18's repertoire show song elements and phrases (in brackets); phrases occurring in more than one variant are enclosed in boxes.

Fig. 2. Cumulative plot of the number of new variants produced by male Canada Warblers (*Cardellina canadensis*) with total number of songs recorded. Each line represents a continuous dawn song sequence from one male ($n = 36$).

Fig. 3. Phrase and variant repertoire similarity decreased with distance between territory centres of male Canada Warblers (*Cardellina canadensis*) in 2010 ($n = 22$) and 2011 ($n = 33$); each point represents a pairwise comparison of two males.

Fig. 4. Map of male Canada Warbler (*Cardellina canadensis*) territories in (A) 2010 ($n = 41$) and (B) 2011 ($n = 50$) labelled by song neighbourhood. Each border pattern represents a given song neighbourhood. Individual males are indicated by unique numbers. North plot territories are at top of figure; south plot territories are at bottom. Territory numbers with no border indicate males with insufficient song data (<30 songs recorded) to include in the analysis.

Fig. 5. Significant positive relationship between (A) mean and (B) maximum variant sharing and years of territory tenure in male Canada Warblers (*Cardellina canadensis*).

Fig. 6. Element modification over time in a song recorded from SY-6, a male Canada Warbler (*Cardellina canadensis*), on (A) 25 May 2010; (B) 31 May 2010; (C) 14 June 2010; (D) 30 June 2010; and (E) 3 June 2011. This song closely matched the equivalent song in two ASY

neighbours: (F) male 17, recorded on 9 July 2010 and (G) male 75, recorded on 27 May 2010.

The reference line at 5 kHz reveals the rising frequency of SY-6's song over time.

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