TEMPORAL AND INDIVIDUAL SONG VARIATION IN THE CANADA WARBLER (*CARDELLINA CANADENSIS*)

by

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DEPARTMENT OF BIOLOGY

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled “TEMPORAL AND INDIVIDUAL SONG VARIATION IN THE CANADA WARBLER (*CARDELLINA CANADENSIS*)” by Alana Demko in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

Song repertoire structure, organization, and use were studied in 68 male Canada Warblers (*Cardellina canadensis*) in a breeding population in New Hampshire in 2010-2011. On average, males had complex repertoires of 12 phrases and 55 variants. Repertoire sharing was negatively related to distance between territories, and positively related to longer territory tenure, evidence that males learn songs from neighbours. Males used two singing modes: (I) slow, regular delivery of less variable songs, and (II) fast, intermittent delivery of more variable songs interspersed with chips. Males used Mode I when unpaired and when near females, and Mode II at dawn and during territory disputes, a pattern similar to other warbler species with two song categories. Detectability (whether a male sang) differed little between 1-, 3-, 5-, and 10-min count intervals. Song output and detectability were highest at dawn and in unpaired males, and lowest in paired males late in the season.

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CHAPTER 1: INTRODUCTION

1.1 THE CANADA WARBLER

The Canada Warbler (*Cardellina canadensis*) is a small migratory songbird in the Family Parulidae (North American wood-warblers) whose population has declined sharply over the past 50 years (Savignac 2008). The species breeds from May-August in Canada's boreal forest from northeastern British Columbia to the Atlantic Provinces, and in the Great Lakes region, the northeastern US, and the southern Appalachian Mountains (Savignac 2008). It winters mainly in mid-elevation (1,000-2,100 m) cloud forests on the eastern slope of the Andes in Colombia, Ecuador, Peru, and Venezuela (Reitsma et al. 2010). Breeding Bird Survey (BBS) data suggest an overall population size of 1.4 million individuals in 2004 (Rich et al. 2004), but also a 4.5% per year range-wide decline from 1968-2007, and a 5.4% per year decline from 1997-2007 (Savignac 2008). The Canada Warbler is therefore a species of international conservation concern, listed as Threatened under Canada's Species at Risk Act (SARA) in 2010, and as a Partners in Flight Continental Watch List species (Rich et al. 2004). Potential threats to the species include deforestation and development on both the breeding and wintering grounds (Savignac 2008).

Recent studies in the northeastern US have described Canada Warbler breeding ecology and identified habitat of high regional conservation priority (Lambert and Faccio 2005, Hallworth et al. 2008a,b; Reitsma et al. 2008, Chace et al. 2009, Goodnow and Reitsma 2011). The species' breeding habitat requirements include a complex understory shrub layer, varied topography, and nearby standing water (Reitsma et al. 2010). In Vermont and New Hampshire, Canada Warblers occur in high densities in wet mixed forest with low canopy height, emergent perch trees, and high shrub and fern cover (Hallworth et al. 2008a, Chace et al. 2009). In western Canada, they occupy deciduous forests with steep slopes, often near water; in the southern Appalachians, they are most common at higher elevations, up to 2,200 m (Reitsma et al. 2010). Forest gaps, where dense ground cover and fallen logs provide suitable nesting and foraging substrate, are another key feature of Canada Warbler habitat (Faccio 2003, Chace et al. 2009). Females lay 4-5 eggs in well-concealed nests on or near the ground, in areas with high understory stem density (Reitsma et al. 2010, Goodnow and Reitsma 2011).

Vocal behaviour is one aspect of Canada Warbler breeding ecology that remains unstudied. Only male Canada Warblers sing, and reportedly have repertoires of complex and variable songs (Lemon et al. 1983, Reitsma et al. 2010). Little is known, however, about either intra-individual variation in repertoire structure and organization, or inter-individual communication, such as use of specific songs based on social context. Also unknown is whether male Canada Warblers vary their song output according to breeding status, temporal factors, or number of conspecific neighbours.

1.2 REPERTOIRES AND SONG SHARING

The repertoire and song sharing hypotheses both aim to explain the structure and function of songbird vocal repertoires (Beecher and Brenowitz 2005). The two hypotheses make different predictions but are not necessarily mutually-exclusive. The repertoire hypothesis states that a larger repertoire size is selected for, mainly through female preference. It predicts that males with larger repertoires will have higher reproductive success (e.g., McGregor et al. 1981). The song sharing hypothesis claims that a high proportion of shared songs, rather than a large repertoire per se, is selected for, mainly because it may be beneficial in male-male competition. It predicts that males sharing a high proportion of songs with neighbours will have longer territory tenure (e.g., Beecher et al. 2000a). Many warbler species use shared songs, and territorial males may modify or copy their neighbours' songs (e.g., Lemon et al. 1994, Byers 1996, Beebee 2002). In Chapter 2 (Repertoire Structure and Song Sharing in a Population of Canada Warblers in Central New Hampshire), I describe Canada Warbler song structure and repertoire composition, examine variation in relation to reproductive success, and quantify song sharing among males in a breeding population in New Hampshire.

1.3 SINGING MODES

Two singing systems have been documented among different members of the Family Parulidae (Spector 1992). In the first, males have one multi-purpose song type (e.g., Ovenbirds *Seiurus aurocapilla*: Lein 1981; Kentucky Warblers *Geothlypis formosa*: Tsipoura and Morton 1988). In the second, males use one or more songs in their repertoire (first category) for long-distance broadcast singing, and use the remainder (second category) at dawn and during close interactions with conspecific males (e.g., Chestnut-sided Warblers *Setophaga pensylvanica*: Kroodsma et al. 1989, Byers 1995). In some species, modes of song delivery also differ between the two categories, with second category songs delivered at a faster rate and with more immediate variety than first category songs (e.g., American Redstarts *Setophaga ruticilla*: Lemon et al. 1985, 1994; Hooded Warblers *S. citrina*: Wiley et al. 1994).

According to the revised parulid phylogeny (Lovette et al. 2010, Chesser et al. 2011), all species within a genus use the same singing system; however, *Cardellina* may be an exception. Wilson's Warblers (*Cardellina pusilla*) apparently have only one song type per male (Ammon and Gilbert 1999), but no quantitative vocal analysis is available for this species or other *Cardellina*. Whether Canada Warblers divide their repertoires into two categories or singing modes and use them in different contexts has not been studied (Reitsma et al. 2010). In Chapter 3 (Use of Two Singing Modes in Different Social Contexts in the Canada Warbler), I assess whether male Canada Warblers use more than one song category or singing mode, and if so, whether category or mode use varies according to social context and time of day.

1.4 DETECTABILITY

Territorial male birds do not always sing owing to many factors (e.g., time of day, breeding status), and are therefore not always detected and recorded by observers on aural point counts (Anderson 2001). Other studies have reported that paired males are approximately half as detectable as unpaired males because of reduced vocal output (e.g., Best and Petersen 1982, Wilson and Bart 1985, Gibbs and Wenny 1993, Staicer et al. 2006). The lower detectability of paired birds may reduce estimates of a given species' abundance at sites with high pairing success. Thus, high-quality breeding sites could be overlooked for conservation efforts in favour of low-quality sites with a higher proportion of more vocal unpaired males.

Males of many species also have different peak periods of diel vocal activity depending on pairing status (e.g., Hayes et al. 1986, Bolsinger 2000) or conspecific density (e.g., Liu 2004, Sexton et al. 2007). Anecdotal evidence suggests that Canada Warbler song output is greatly reduced in paired males compared to unpaired males, and may be highest at dawn during the nesting period (Reitsma et al. 2010). In Chapter 4 (Breeding Status and Temporal Effects on Detectability of Territorial Male Canada Warblers), I test whether detectability differed with breeding status, time of day, time of season, number of neighbours, and length of survey period.

CHAPTER 2: REPERTOIRE STRUCTURE AND SONG SHARING IN A POPULATION OF CANADA WARBLERS IN CENTRAL NEW HAMPSHIRE

2.1 INTRODUCTION

Many bird species attract mates or defend territories using only one type of song, while others have repertoires of multiple songs. The repertoire and song sharing hypotheses both address repertoire development in the context of sexual selection (reviewed in Beecher and Brenowitz 2005). The repertoire hypothesis suggests 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, Reid et al. 2005). The song sharing hypothesis states that males who share more songs with neighbours are more successful at defending or retaining territories (Beecher et al. 2000a). These two hypotheses may not be mutually exclusive, as female birds of some species prefer familiar local songs (O'Loghlen and Beecher 1999, O'Loghlen and Rothstein 1995, Hernandez et al. 2009) or males who are dominant in countersinging interactions (e.g., Mennill et al. 2002).

Song sharing between neighbours is prevalent in many songbird species, and repertoire similarity between individuals typically decreases with increased distance between territories (e.g., Hill et al. 1999, Foote and Barber 2007, Koetz et al. 2007, Rivera-Gutierrez et al. 2010). Dialects occur when most individuals within one geographic area share the same song (e.g., Puget Sound White-crowned Sparrows *Zonotrichia leucophrys pugetensis*; Nelson 2000). Song neighbourhoods (clusters of males with similar song repertoires) develop when song sharing is highest among immediate neighbours, such as in Song Sparrows (*Melospiza melodia*; Hughes et al. 1998) and Great Tits (*Parus major*; McGregor and Krebs 1989).

Song sharing arises from song learning, which usually occurs in a male's first year, but may continue throughout life in some species and populations. Species who learn songs are either closed-ended learners (song learning ends after the first year of life) or open-ended learners (new songs can be learned throughout life; 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, a process called 'selective attrition' (Nelson 2000, Nordby et al. 2007). Similarly, Great Tits modify their repertoires by adding and dropping songs according to their frequency of use within the population (McGregor and Krebs 1989).

The degree of song sharing varies both within and among species, and is dependent on factors such as migratory status and site fidelity. For example, male Song Sparrows resident in Washington share full song types, while fully or partially migratory males in Pennsylvania share only portions of songs (Hughes et al. 1998). Migratory Song Sparrow populations with high male return rates also exhibit full song type sharing, suggesting that site fidelity may contribute to song continuity within a population (Foote and Barber 2007).

Song sharing may increase lifetime reproductive success (Payne 1982) and length of territory tenure (Beecher et al. 2000a), by allowing males to engage in aggressive intrasexual encounters using shared songs (Krebs et al. 1981, Beecher et al. 2000b). Indigo Bunting (*Passerina cyanea*) males in their first breeding season who shared older neighbours' songs had higher pairing, nesting, and fledging success than non-sharers (Payne 1982). Longer territory tenure for male Song Sparrows who shared more songs with neighbours was observed in a population with high overall sharing (Beecher et al. 2000a), but not in a population with low sharing (Hughes et al. 2007). Shared songs permit song matching during territorial countersinging interactions: more aggressive 'type matching' (reply with same song) early in the season when establishing boundaries, and less aggressive 'repertoire matching' (reply with shared non-matching song) later in the season (Beecher et al. 2000b). Conversely, use of unshared songs may aid in individual recognition (Nordby et al. 2007) and signal conflict de-escalation (Beecher and Campbell 2005). Recent work showing that older males preferentially sing the most commonly shared songs within a neighbourhood suggests that use of shared songs is related to breeding experience and may facilitate longer territory tenure (Lapierre et al. 2011).

Many species of the Family Parulidae (North American wood-warblers) exhibit song neighbourhoods (Lemon et al. 1994, Byers 1996, Beebee 2002) or dialects (Janes and Ryker 2006) of shared songs. Canada Warblers are reported to have complex songs, with very little repetition of notes within songs compared to other warbler species (Lemon et al. 1983), yet repertoires have not been quantified or song sharing documented (Reitsma et al. 2010). Some parulids continue to modify their repertoires after their first year (reviewed in Spector 1992). For example, the American Redstart's repertoire of serial songs, used in male-male encounters, is modified chiefly between the first and second breeding seasons through addition and deletion of songs (Lemon et al. 1994).

The purpose of this study was to describe Canada Warbler song structure and repertoire composition, and to quantify song sharing patterns in a population of breeding Canada Warblers in central New Hampshire. This information will be useful in assessing which selective pressures (e.g., female mate choice, male competition for territories) are acting upon development and maintenance of complex repertoires in this species.

2.2 METHODS

2.2.1 Study Site and Subjects

I recorded 66 territorial male Canada Warblers from May-July 2010 and 2011 in the Canaan Town Forest (40 ha) and Bear Pond Natural Area (363 ha), near Canaan, NH, USA (43°40'N, 72°03'W). The study site contained two plots, which were separated by Bear Pond and were 450 m apart at the closest extent. The upper plot is a regenerating mixed upland forest harvested in 1985, and the lower plot is a Red Maple (*Acer rubrum*) swamp. An intensive study of Canada Warbler breeding ecology had been underway at these two study plots since 2003. High average adult male return rate (52%), pairing success (91%), and fledging success (75%) are characteristic of this population (Hallworth et al. 2008a).

Males were captured using mist-nets and song playback, and uniquely colour-banded to allow visual identification in the field; females were colour-banded opportunistically. Males were aged as first-year breeders (second-year or SY) or older males (after-second-year or ASY) according to plumage characteristics (Rappole 1983, Pyle 1997). Territorial males were monitored every 2-7 days post-arrival to assess pairing status and nesting activity; GPS points of their locations were marked to produce territory maps. Successful fledging was confirmed by either observing an adult feeding at least one fledgling or delivering food to multiple locations (Hallworth et al. 2008a). Egg-laying, hatching, and fledging dates were only available for all males in 2010, when intensive nest-searching and monitoring was part of a concurrent study.

I recorded singing males daily (weather permitting) during the period of peak vocal activity, from the start of the dawn chorus at approx. 0430-0445 EDT (40 min before sunrise) to approx. 1130 EDT (6 h after sunrise). Sunrise times at the site ranged from 0506 EDT (11-20 June) to 0529 EDT (10 May). I recorded entire dawn bouts for one male each day. Following the dawn chorus, I obtained 20-30 min continuous recordings of focal males approximately once weekly; I varied the order of subsequent visits to minimize temporal effects. I made recordings at a sample rate of 48 kHz using a Marantz Professional PMD661 digital recorder, Sennheiser ME62/K6 microphone, and SME PR-1000 parabola.

2.2.2 Song Structure

I viewed spectrograms using Raven Pro 1.3 software (www.birds.cornell.edu/raven), with default settings adjusted for contrast and brightness as necessary. I classified all recorded vocalizations using a coding system that enabled me to describe intra-individual complexity, yet allowed inter-individual comparison (Appendices A-B). *Elements* were discrete units on spectrograms (e.g., Byers 1995), and were of two types: *song elements* and *calls* (Appendix A contains the full catalogue). Song elements were the smallest units comprising songs; they were first coded by lower-case letters based on shape, then coded by numbers within each shape class based on frequency range and duration (Fig. 2.1). Calls were classified by upper-case letters for shape, frequency range, and duration. Chips were calls of shorter duration (<0.06 s) and wider frequency range (>4.5 kHz) used either alone or with song elements. Two calls never used with song elements were identified: a high-pitched call at 6-8 kHz ('E'), and a buzzy call at 2.5-5.5 kHz ('α'; Appendix A). A *phrase* was a unique sequence of 1-7 song elements (Appendix B); phrases with missing introductory or final elements were denoted as *partial phrases*. A *song variant* (hereafter referred to as *variant*) was a unique sequence of one or more phrases nearly always preceded by one or more chips. Only one male in the study population did not reliably use ≥1 chip immediately before songs during regular daytime singing. Chips used within a sequence of song elements were considered to be part of a variant; chips preceding a variant were not (Fig. 2.1).

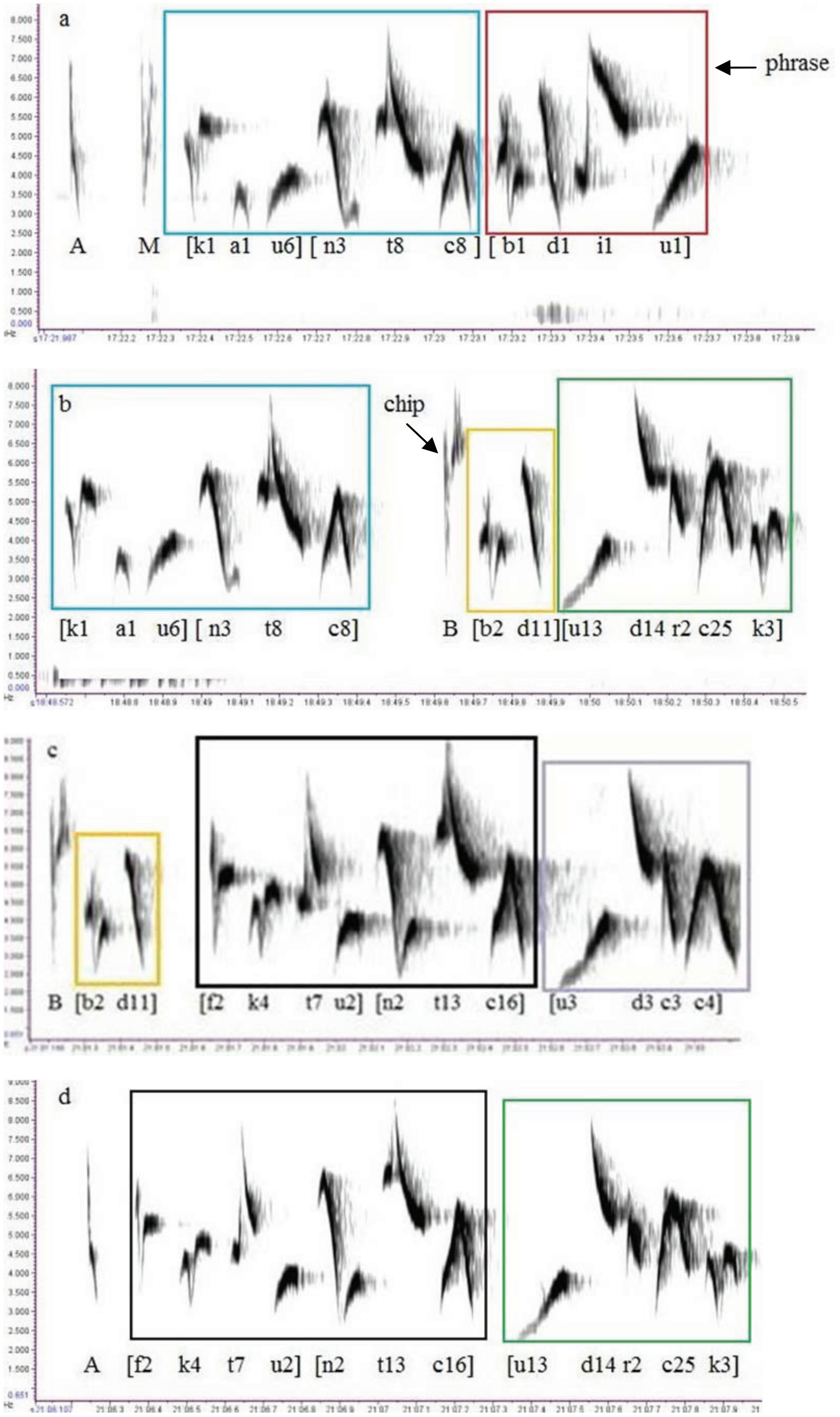

Figure 2.1 Spectrograms of four variants (a-d) from Canada Warbler male 18's repertoire showing coded elements and phrases. Phrases shared between variants are enclosed in boxes.

Within individuals, a *song type* was the most commonly used variant of those with the same phrase sequence, including partial phrases. Song types were difficult to assign objectively, since many variants contained the same phrases or partial phrases, and were thus not discrete ‘types’. Owing to high song type variability among individuals, all variants recorded from each male were included in song sharing analyses.

2.2.3 Samples Used

I included 44 males for which I had Mode II recordings (see Chapter 3): either dawn recordings, or daytime recordings sung at a high rate with many variants (2010: n = 22; 2011: n = 33); eleven males had available Mode II recordings in both years. The total number of songs recorded from each individual in a given year ranged from 149-1239 (mean ± SD = 549 ± 268). In 10 males for which I had dawn recordings in 2010 and 2011, I recorded all variants representing >5% of total variants in both years. Thus, all commonly used variants were likely used during a full 30-45 min dawn bout. I separated most song sharing analyses by year to account for between-season shifts in territory size, location, and occupancy. For repertoire size analyses and comparisons of song sharing with years of territory tenure, I included each male in only one year (i.e. the 11 males from both years were included in 2011 only).

I produced a cumulative plot comparing the number of new variants observed to the total number of songs recorded (Gil and Slater 2000). I plotted one continuous dawn song bout each from each male (n = 36) for which I had dawn recordings. Since the number of new variants observed began to level off around 20-30 songs (Fig. 2.2), a sample of ≥149 songs recorded per male was likely sufficient for song sharing analyses.

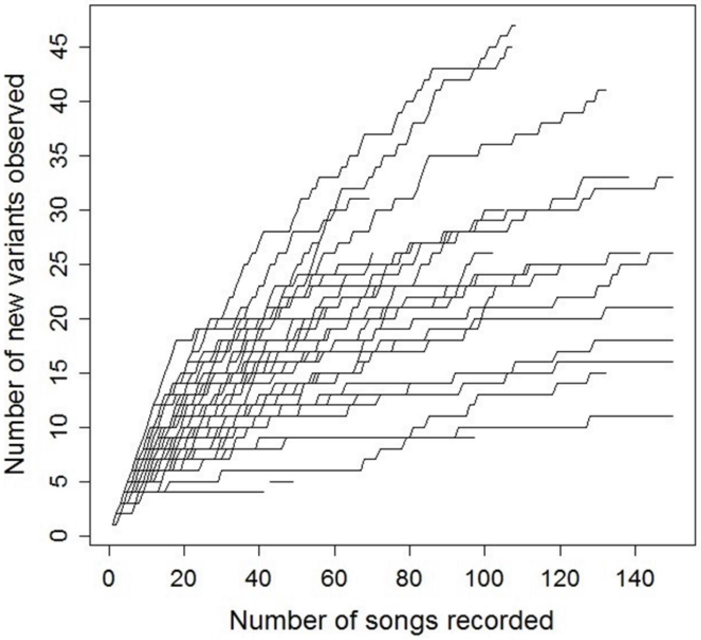

Figure 2.2 Cumulative plot of number of new variants observed with total number of songs recorded. Each line represents a continuous dawn song sequence from an individual male (n=36).

2.2.4 Repertoire Size

To determine whether estimates of repertoire size are influenced by the number of songs in a recorded sample, I used Pearson's correlations to test for associations between the repertoire size of phrases and variants and the total number of songs recorded. To assess whether individual repertoire size remained stable between years, I used paired t-tests to determine if phrase (parts of song) and variant (whole song) repertoire size differed for males recorded in both years. I also tested for correlations between repertoire size and fledging success. Overall fledging success at the site was 57.9% (22/38 males) in 2010 and 80.9% (38/47 males) in 2011. Male pairing success was 91.8% (45/49 males) in 2010 and 90.6% (48/53 males) in 2011, so the sample size of unpaired males was too small to test for effects of pairing status.

2.2.5 Song Sharing

To assess the relationship between song sharing and distance between territories, I compared phrase and variant repertoire sharing between each pair of males at the study site. For phrase repertoire sharing, I calculated pairwise Jaccard's similarity coefficients, with a correction for differences in repertoire size (MacDougall-Shackleton et al. 2009). For two males, A and B, S_j (adjusted) = $c/((a+b+c)-d)$, where:

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

By using corrected song sharing coefficients, I minimized the effect of inter-individual variation in repertoire size on the song sharing analysis. Although not statistically significant, the Pearson correlation between phrase repertoire size and uncorrected song sharing coefficients was higher (2010: $r_{20} = 0.40$, $P = 0.062$; 2011: $r_{31} = 0.25$, $P = 0.156$) than the correlation between phrase repertoire size and corrected sharing coefficients (2010: $r_{20} = 0.06$, $P = 0.782$; 2011: $r_{31} = 0.16$, $P = 0.386$). Phrases were considered 'shared' if they shared ≥50% of elements by number, shape, and order.

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

I produced minimum convex polygon territory maps in ArcGIS 10 software (ESRI, Redlands, CA) using GPS locations where each male sang (mean ± SD: 21±10, range 3-49). I 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. I then calculated pairwise distances between median centres with the Point Distance tool under Analysis Tools-Proximity in ArcToolbox.

For both phrase and variant sharing, I ran Mantel tests on the pairwise sharing coefficient and territory distance matrices to test for an association between vocal sharing and distance (e.g., Hill et al. 1999). Linear regressions on sharing coefficients and territory distance assessed the direction and strength of this association for phrase sharing; I log transformed 2011 data to achieve normality. I used Spearman's rank correlations to relate variant sharing with territory distance, since data transformations failed to improve normality. Wilcoxon signed-rank tests determined whether song sharing differed between neighbours (males sharing a territory boundary) and non-neighbours (males not sharing a territory boundary). A territory boundary was a location where two males interacted vocally or physically. Data were combined for both sites for this analysis, since the distance between the upper and lower plots was less than the distance between males within the upper plot.

To assess the relationship between song sharing and years of territory tenure, I used Spearman's rank correlations because data were not normally distributed. I compared both mean and maximum phrase and variant sharing coefficients of each male to the number of years present at the site. 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. I used Wilcoxon signed-rank tests to determine whether mean and maximum repertoire sharing differed between successful and failed breeders.

Within- and between-season phrase use of a sub-sample of 11 males–SYs (n=3), new ASYs (first year at site; n=3), and old ASYs (≥2 years at site; n=5)–was examined to determine whether phrase addition and deletion is more pronounced in new arrivals. I used only males for which I had ≥2 dawn recordings (i.e. complete or near-complete phrase repertoire was recorded), either within or between years, to compare phrase turnover.

To assess whether distinct song neighbourhoods (spatially clustered groups of males with similar repertoires) were present in the study population, I used a cluster analysis, Newman's eigenvector method, on the Bray-Curtis similarity matrices in program SOCPROG**.** This method calculates an eigenvalue for each individual and an optimal modularity of the arrangement. The range of both eigenvalues and modularity is 0 (no association) to 1 (strong association). Eigenvalues near 0 indicate uncertainty in group membership of a given individual; a modularity of > 0.3 indicates strong community structure. The modularity algorithm determines whether there are fewer connections (i.e. shared songs) between individuals than expected if randomly distributed (Newman 2006). Newman’s method is more objective than hierarchical cluster analysis, which has no standard cut-off value to assign clusters and ends by clustering all individuals together. I included all males with ≥30 recorded songs in this analysis (2010: 41 males; 2011: 50 males); 28 males were included in both years. I performed all statistical analyses except for Newman’s method using R 2.9.2 (www.R-project.org).

2.3 RESULTS

2.3.1 Repertoire Size

I identified 153 different song elements, 34 chips, and 2 calls among all 66 male Canada Warblers recorded at the study site (Appendix A). Males combined song elements to produce 72 phrases, and many song elements were used in multiple phrases (Appendix B). Among the subset of males used in both years of song sharing analyses (n = 44), phrases were recombined to produce 1677 unique variants.

Male Canada Warbler phrase and variant repertoire sizes showed inter-individual variation, although within-individual repertoire size and composition was consistent between years. Canada Warbler males had repertoires of 7-16 phrases (mean ± SD: 12 ± 2) and 11-134 variants (55 ± 27). The 11 males recorded in both 2010 and 2011 did not change their phrase repertoire size ($t = 1.46$, df = 10, $P = 0.176$) or variant repertoire size ($t = 0.11$, df = 10, $P = 0.914$) significantly between years. Two of the males who were new arrivals in 2010 used fewer phrases in 2011 than 2010; the remaining nine did not change their phrase repertoire composition between years.

Male Canada Warblers with larger phrase repertoires tended to have larger variant repertoires. The number of variants observed per male increased with total number of songs recorded, although most variants were rare (i.e., comprised <1% of the total sample). Phrase and variant repertoire sizes were highly positively correlated (Pearson correlation: $r_{42} = 0.62$, $P < 0.0001$). Number of variants was significantly correlated with total number of songs recorded ($r_{42} = 0.42$, $P = 0.005$). Phrase repertoire size and number of songs recorded per male were not significantly correlated, however ($r_{42} = 0.02$, $P = 0.891$). Significant positive correlations between the percentage of rare variants (<1% each of total songs) and both variant number ($r_{42} = 0.77$, $P < 0.0001$; Fig. 2.3) and total songs recorded ($r_{42} = 0.44$, $P = 0.003$; Fig. 2.3) appear to result in more variants observed with more recorded songs.

Fledging success was lower in 2010 (44.4%; 8/18 males) than in 2011 (80.0%; 24/30), but was not related to repertoire size in either year. No significant difference was found between fledging success and either phrase repertoire size (2010, $t = 1.33$, df = 11.62, $P = 0.208$; 2011, $t = 0.22$, df = 11.54, $P = 0.833$) or variant repertoire size (t-test: 2010, $t = 0.99$, df = 14.86, $P = 0.336$; 2011, $t = 0.21$, df = 7.62, $P = 0.834$). Pairing success was 95.2% (20/21) in 2010 and 93.8% (30/32) in 2011; a small sample size of unpaired males precluded statistical analysis. See Appendix C for summary statistics.

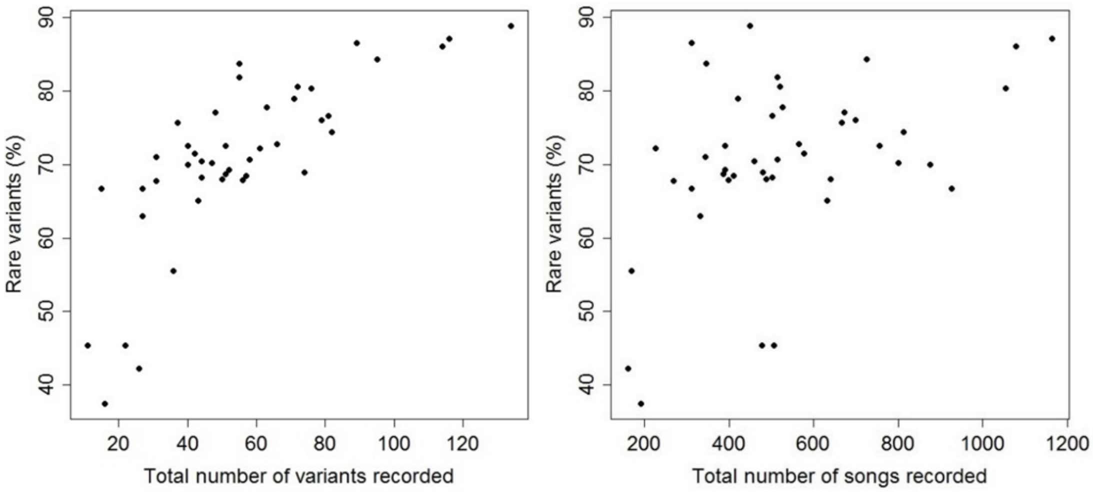

Figure 2.3 Percentage of rare variants (<1% of songs recorded) increased with total number of variants recorded (left) and total songs recorded (right; n=44).

2.3.2 Song Sharing and Distance Between Males

The degree of song sharing decreased with distance between territories for both phrase and variant repertoires of male Canada Warblers in the study population. Phrase repertoire similarity and distance were significantly associated in both years (Mantel test: $P = 0.001$ for each year). Sharing decreased significantly with distance between territories in both 2010 (linear regression: $r^2 = 0.26$, $df = 229$, $P < 0.0001$) and 2011 ($r^2 = 0.16$, $df = 526$, $P < 0.0001$; Fig. 2.4).

Variant repertoire similarity and distance were significantly associated in both years (Mantel test: $P = 0.001$ for each year). Sharing was negatively correlated with distance between territories in both 2010 (Spearman rank correlation $\rho = -0.52$, $P < 0.0001$) and 2011 ($\rho = -0.36$, $P < 0.0001$; Fig. 2.5).

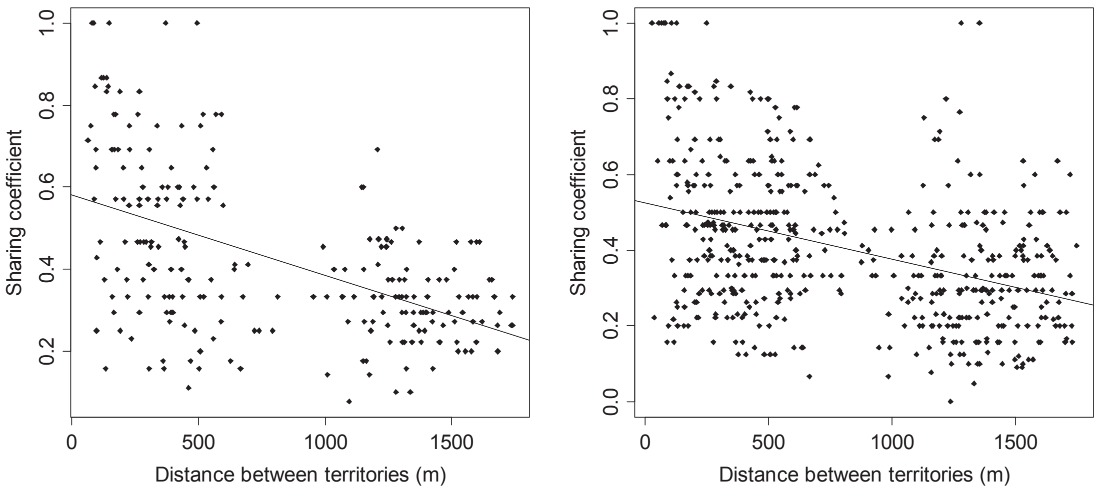

Figure 2.4 Decrease in phrase repertoire similarity with distance in 2010 (left) and 2011 (right). Points represent pairwise comparisons of males. Males in same plot were 29-1065 m apart, while those in different plots were 920-1749 m apart.

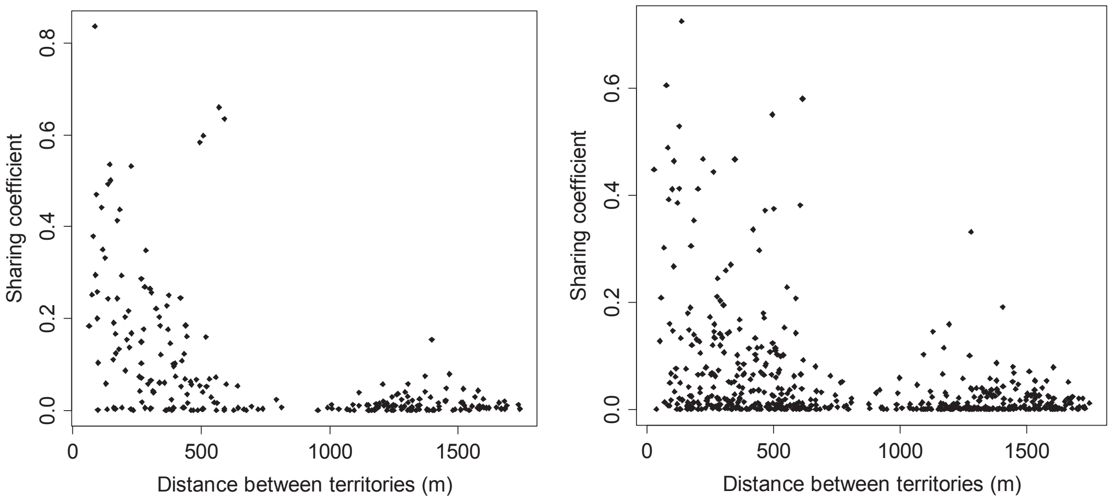

Figure 2.5 Decrease in variant repertoire similarity with distance in 2010 (left) and 2011 (right). Points represent pairwise comparisons of males. Males in same plot were 29-1065 m apart, while those in different plots were 920-1749 m apart.

2.3.3 Song Sharing with Neighbours

Males shared a higher proportion of their repertoires with territorial neighbours than with 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: $W = 531$, $P < 0.0001$).

2.3.4 Song Sharing and Territory Tenure

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 present at the site (mean: $\rho = 0.37$, $P = 0.017$; max: $\rho = 0.32$, $P = 0.036$; Fig. 2.6). Neither mean nor maximum phrase sharing were significantly associated with years of territory tenure (mean: $\rho = 0.005$, $P = 0.976$; max: $\rho = 0.20$, $P = 0.211$).

2.3.5 Song Sharing and Fledging Success

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

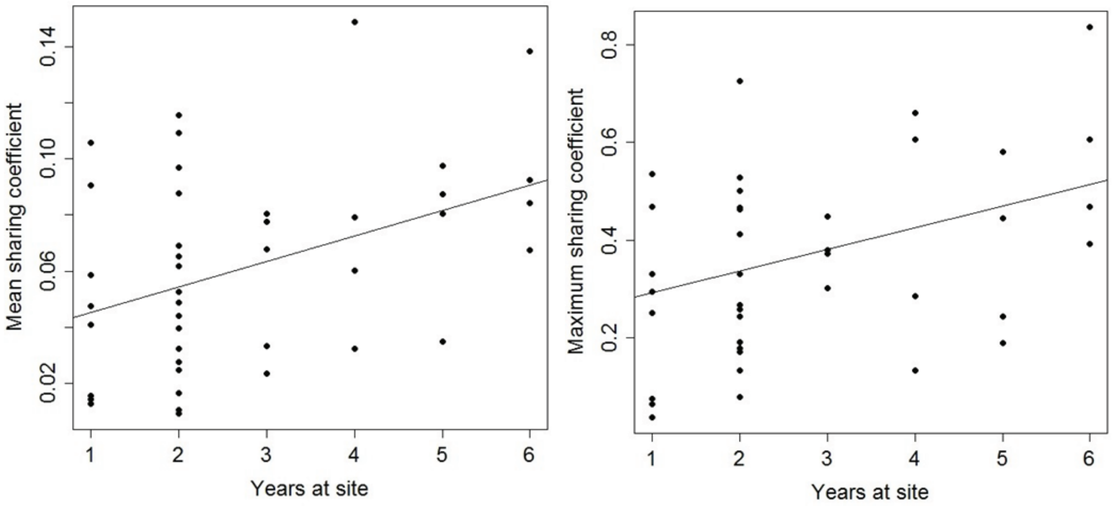

Figure 2.6 Significant positive relationship between mean (left) and maximum (right) variant sharing and years at site.

2.3.6 Within-season Repertoire Changes

Within-season phrase turnover was observed in two SY males, but not in seven ASY males with recordings that enabled comparison of phrase repertoires within a season (Table 2.1). SY-6 and SY-14 both dropped and added phrases within a breeding season. Only one ASY showed within-season changes in his phrase repertoire content. During his first breeding season at the site, ASY-4 dropped two phrases that were not used by any other males at the study site. Small sample sizes precluded statistical comparison of the SY and ASYdata.

2.3.7 Between-season Repertoire Changes

Between-season phrase turnover occurred in both SYs and one of seven ASYs (Table 2.2). In 2011, SY-6 dropped one of the phrases added in 2010 (Table 2.1). ASY-35's phrase repertoire did not change during 2010 (Table 2.1), but he added one phrase and dropped two from 2010 to 2011 (Table 2.2). Among his neighbours, the dropped phrases were used only by birds 59 and 72, who did not return to the site in 2011.

Table 2.1 Within-season phrase repertoire change in SY and ASY males.

Bird	Male category[1]	Year	Phrases added	Phrases dropped	Maximum phrase repertoire[2]	Number of recordings
SY-6	new	2010	2	2	12	3
SY-14	new	2010	5	2	14	4
ASY-4	new	2010	0	2	9	2
ASY-35	new	2010	0	0	12	2
ASY-11	old	2010	0	0	12	3
ASY-18	old	2010	0	0	11	2
ASY-23	old	2010	0	0	11	2
ASY-52	old	2010	0	0	16	3
ASY-75	old	2011	0	0	11	4

[1] 'New': male's first year at site; 'old': male at site for ≥2 years.

[2] The maximum number of phrases in a single recording of that individual.

Table 2.2 Between-season phrase repertoire change in SY and ASY males.

Bird	Male category[1]	Phrases added	Phrases dropped	Maximum phrase repertoire[2]	Number of recordings
SY-6	new	0	1	12	4
SY-9	new	2	1	14	2
ASY-4	new	0	0	9	3
ASY-35	new	1	2	12	3
ASY-40	new	0	0	8	2
ASY-11	old	0	0	12	4
ASY-18	old	0	0	11	3
ASY-23	old	0	0	11	3
ASY-75	old	0	0	11	5

[1] Refers to status in 2010 (see Table 2.1).

[2] The maximum number of phrases in a single recording of a given individual.

2.3.8 Element Modification

Minor modification of individual elements may allow repertoire alteration in SY male Canada Warblers, but a small sample size precluded detailed analysis. One example is that of SY male 6, and his two ASY neighbours, 17 and 75. SY 6 modified individual elements over the 2010 breeding season (Fig. 2.7a-d) to more closely match element structure and frequency range of a song shared with male 17 (Fig. 2.7e) and male 75 (Fig. 2.7f). All three birds returned to the site in 2011, and male 6 retained his modified song (Fig. 2.7g).

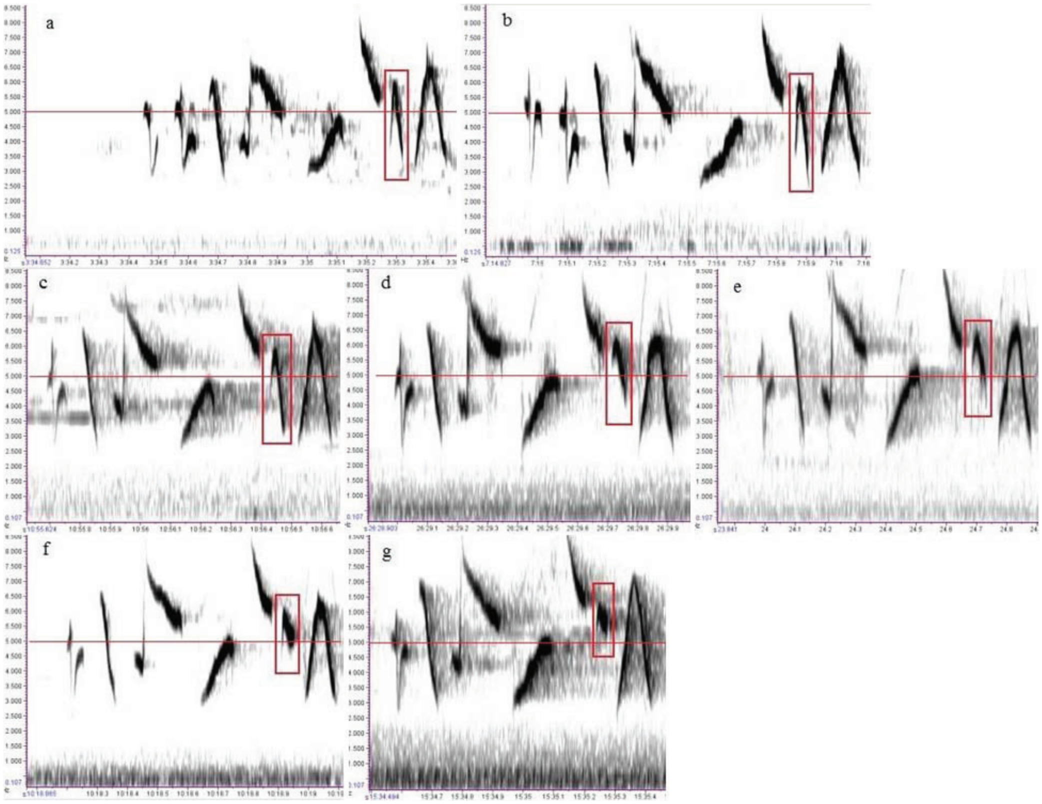

Figure 2.7 Shared songs recorded from SY male 6 on (a) 25 May 2010, (b) 31 May 2010, (c) 14 June 2010, (d) 30 June 2010, and (e) 3 June 2011. Same song recorded from neighbours (f) male 17 on 9 July 2010 and (g) male 75 on 27 May 2010. Reference line at 5 kHz highlights rising pitch of SY-6's song over time.

2.3.9 Cluster Analysis and Song Neighbourhoods

Newman's eigenvector method revealed six song-based clusters, or 'neighbourhoods', of 2-15 individuals in 2010 (modularity = 0.478; Fig. 2.8), and seven neighbourhoods of 2-19 individuals in 2011 (modularity = 0.401; Fig. 2.9). Two neighbourhoods in 2011 (grey shaded and thin black border) included males from both plots, while the remainder were exclusive to one study plot (Fig. 2.9). Two neighbourhoods (dotted border and striped: Figs. 2.8-2.9) had the same membership in both years. Males in both of these clusters also showed high repertoire similarity, indicated by high eigenvalues (Appendix D). Six males present in both years (5, 12, 18, 48, 68, and 74) were assigned to a different cluster in each year. In general, smaller clusters had higher repertoire similarity among members than did larger clusters (Appendix D).

Neighbouring males were grouped together between seasons by Newman's method even if the overall group composition varied, suggesting little repertoire turnover within individuals between years. For example, males 5, 12, 48, 68, and 74 were part of the dotted neighbourhood in 2010 (Fig. 2.8), and all were assigned to the grey border neighbourhood in 2011 (Fig. 2.9). Some neighbourhoods were maintained when males on peripheral territories in 2010 moved to vacant territories in 2011, where they shared songs with more neighbours (e.g., male 6 in lower, males 7 and 10 in upper; Figs. 2.8-2.9). The arrival or departure of individual members from the study site, and more thorough sampling coverage of peripheral areas in 2011, accounted for other shifts in neighbourhood composition.

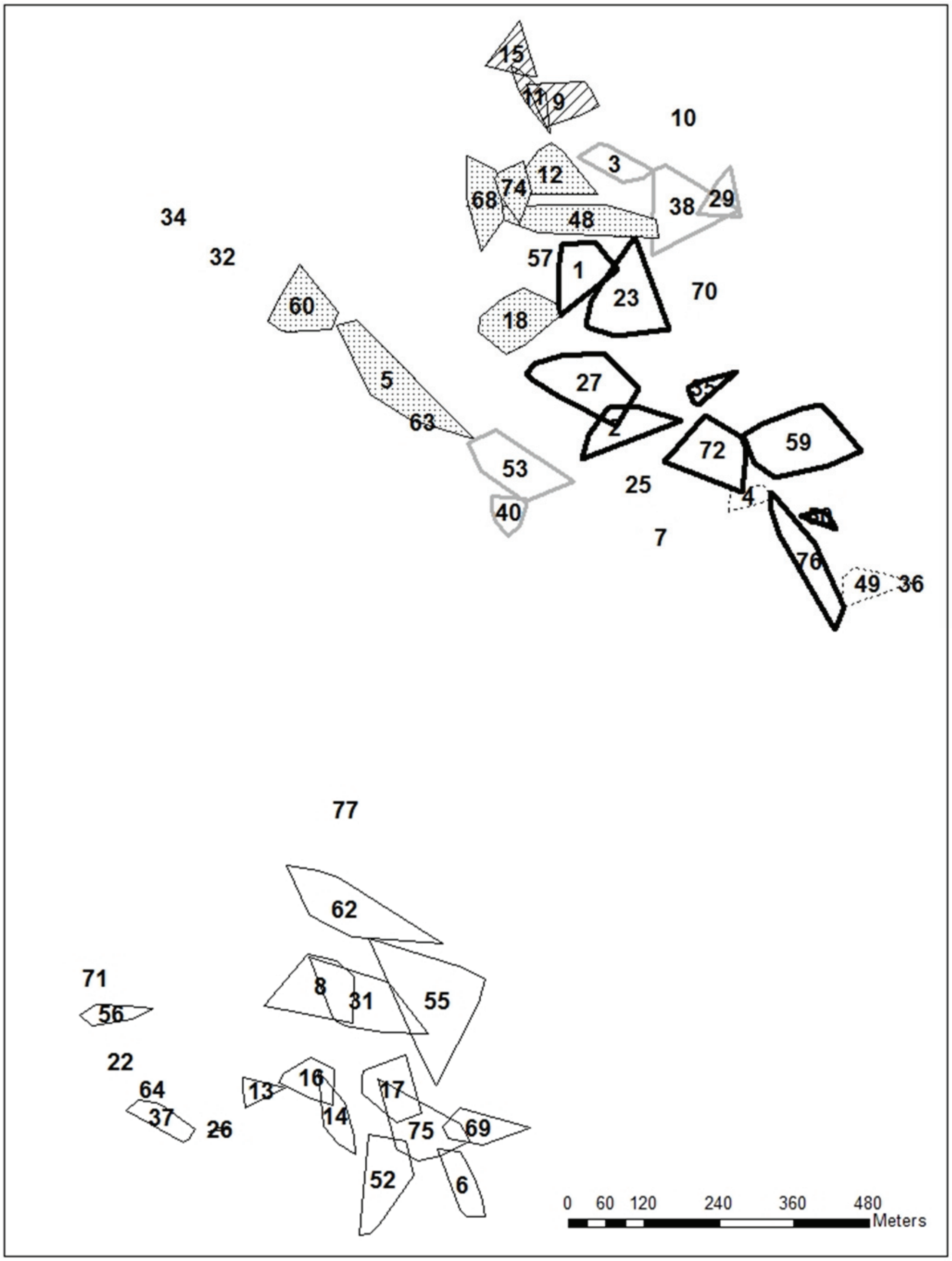

Figure 2.8 Canada Warbler territories in 2010 labelled by song neighbourhood. Upper plot territories are at top of figure; lower plot territories are at bottom. Territory numbers with no border indicate males with insufficient song data (<30 songs) to include in the analysis.

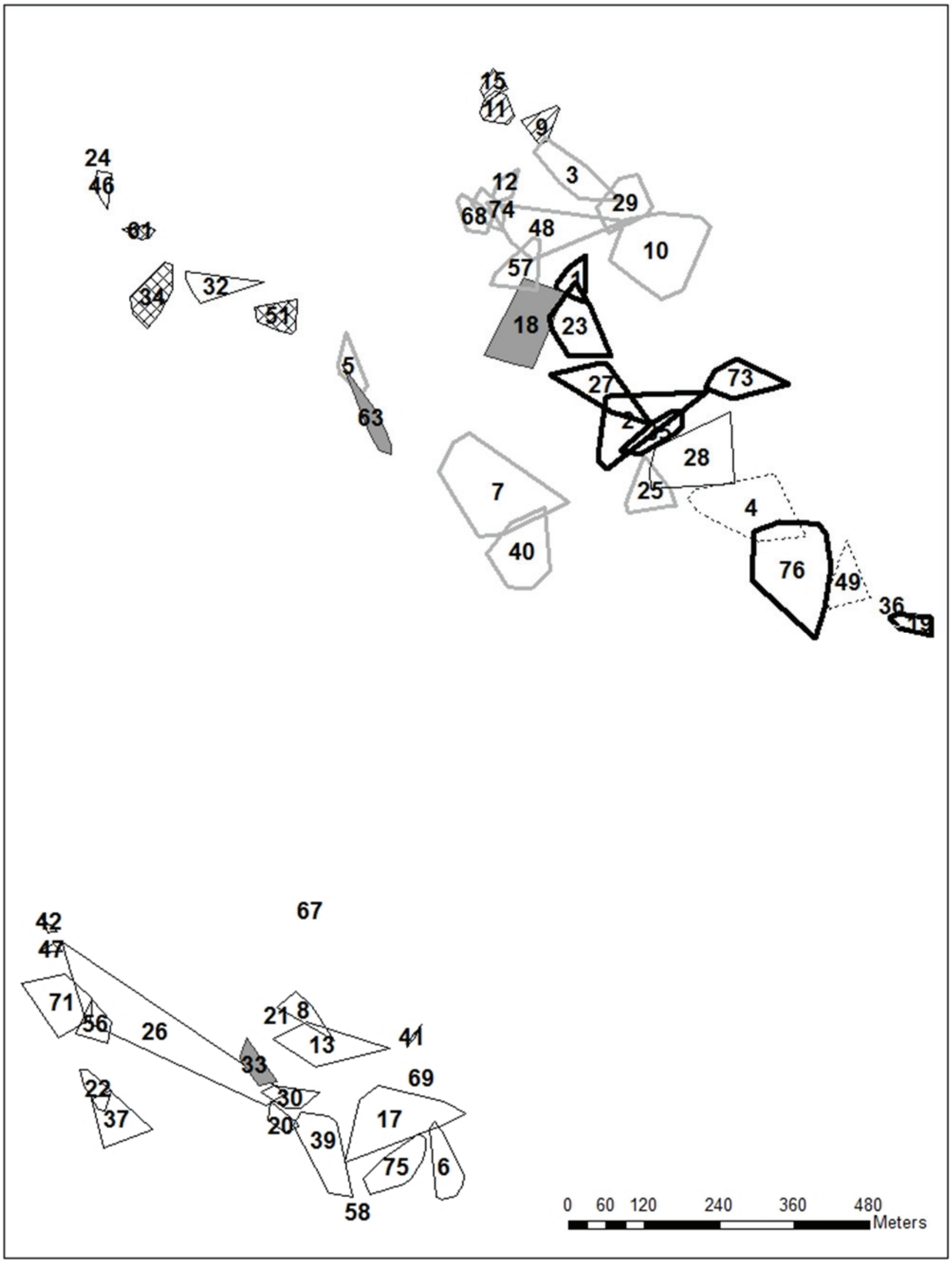

Figure 2.9 Canada Warbler territories in 2011 labelled by song neighbourhood. Upper plot territories are at top of figure; lower plot territories are at bottom. Territory numbers with no border indicate males with insufficient song data (<30 songs) to include in the analysis.

2.4 DISCUSSION

2.4.1 Repertoire Size

Male Canada Warblers had complex repertoires consisting of 7-16 phrases recombined to produce 11-134 song variants. Of 19 eastern North American parulid species reviewed by Lemon et al. (1983), the Canada Warbler is the only one without repeated sequences of individual elements, aside from rare exceptions such as multiple introductory notes. Canada Warbler song structure may approximate that of some eastern populations of Song Sparrows, where each male has a repertoire of syllables (analogous to phrases in Canada Warblers) used in multiple song types (Podos et al. 1992, Hughes et al. 1998).

The stability of repertoire size between years observed for individual male Canada Warblers, despite addition and deletion of phrases, has also been documented for other songbird species. In longitudinal studies of Great Tits (McGregor and Krebs 1989) and American Redstarts (Lemon et al. 1994), repertoire size did not change overall by male age, although males were most likely to increase or modify their repertoire between their first and second breeding seasons. Male sedge warblers (*Acrocephalus schoenobaenus*) showed larger repertoire sizes with age, yet within-season repertoire size did not change despite considerable song turnover (Nicholson et al. 2007). A longer-term study of Canada Warblers is needed to examine age effects on repertoire size and composition.

Discrete song types would be difficult to assign in Canada Warblers, as the number of new variants continually increased as more songs were produced. Quantitative methods such as cluster analysis (Podos et al. 1992) and transition matrices (Gil and Slater 2000) could potentially assign song types. However, analyzing sharing with all song variants appeared to adequately describe song neighbourhoods in this population while accounting for the maximum amount of within-individual variability. Since the majority of variants produced are rare, they have less weight than common variants in the Bray-Curtis index, and are thus unlikely to cause misleading results given the analysis methods used.

Canada Warbler phrases that were composed of elements of similar shape, but at a different frequency, in the same order, were not classified as being more similar to one another for song sharing analyses. Therefore, overall song sharing would be higher and individual repertoire sizes smaller, if these phrases were ‘lumped’. Playback experiments would be necessary to ascertain whether songs which appear more similar by human visual classification have behaviourally salient meaning to Canada Warblers. In Song Sparrows, males responded more strongly to between-song-type variation than within-song-type variation, although they did recognize the latter (Searcy et al. 1995). Song types with high syllable similarity were not perceived as more similar than song types with no syllables in common (Searcy et al. 1999).

No relationship was found in either year between fledging success and vocal characteristics. This suggests that factors other than repertoire size and song sharing, such as local breeding experience and territory quality, influence reproductive success in this population. Experienced males predominate at both Canada Warbler study plots, as evidenced by high site fidelity (Hallworth et al. 2008a, this study). Philopatric male great reed warblers (*Acrocephalus arundinaceus*) had higher lifetime reproductive success than immigrants, irrespective of age (Bensch et al. 1998). In collared flycatchers (*Ficedula albicollis*), philopatric males had higher mating success than immigrants, by using local familiarity to select and defend higher-quality nest boxes (Pärt 1994). Thus, females 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 within male territories in the study area (Goodnow and Reitsma 2011) likely contributes to high overall pairing and fledging success.

2.4.2 Song Sharing

Phrase sharing decreased linearly with distance, while variant sharing decreased exponentially. This meant that while many non-neighbours shared phrases, variants were typically shared only with immediate neighbours. A similar spatial pattern of whole-song sharing with neighbours has been described for other bird populations with low individual turnover between years, owing to year-round residency or high levels of breeding site fidelity (e.g., Hughes et al. 1998, Beecher et al. 2000a). Although migratory, Canada Warblers show high male return rates at the study site (Hallworth et al. 2008a, this study), which may promote continued use of specific songs in the population.

The increased mean and maximum variant sharing observed among males with more years at the site is consistent with other studies showing longer territory tenure for males with high sharing (e.g., Beecher et al. 2000a). Age is a related variable often used in song sharing studies (e.g., Cosens and Sealy 1986, Nicholson et al. 2007). Tenure was used here as a proxy, since exact age was not known 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 potentially allows increased aggression towards and dominance over territorial neighbours (Beecher et al. 2000b). Song data suggests that two males with phrases and variants different from those of local songs attempted to establish territories in mid-May 2010, but were displaced when the previous year's territory holder returned to the site 1-2 weeks later (A. Demko unpubl. data). In May 2011, unbanded males prospecting at the site with songs audibly distinct from the local songs were unable to establish territories (A. Demko pers. obs.).

Male Canada Warblers in their first breeding season appeared to alter their song repertoires to match their neighbours, as in other bird species who learn their songs (e.g., Payne 1982, Lemon et al. 1994, Nordby et al. 2007, Kiefer et al. 2010). For example, SY male Indigo Buntings typically copied a neighbouring ASY male to more closely match the local songs (Payne 1982). In ASY male Canada Warblers, repertoire modification was more subtle and infrequent. For example, the phrase added by ASY-35 between seasons differed only in frequency, not in element sequence or shape, from two other phrases in his repertoire. Still, Canada Warblers appear able to alter their repertoires after their first breeding season, perhaps in response to social influences from neighbours. 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).

Phrase turnover and element modification observed in this population suggests that phrases, elements, or both, may be the fundamental units of song learning in Canada

Warblers. An analysis of element and song type turnover in a population of Chestnut-sided Warblers over 19 years showed that cultural evolution of song involved rearrangement of elements to produce novel song types. Among the more variable 'unaccented' song types, 25% of elements present in year 1 were still present in year 19, yet over two-thirds (67.8%) of new songs that appeared contained both old and new elements (Byers et al. 2010). A long-term study of song in a population (e.g., 10 years: Lemon et al. 1994, 19 years: Byers et al. 2010) would be necessary to assess whether a similar pattern of song learning is present in Canada Warblers.

Song neighbourhoods among male Canada Warblers in this population appear to result primarily from longer territory tenure of males with shared song variant repertoires, and from song modification by newly-established SY males. The male return rate was higher at the upper study plot (88%) than the lower study plot in (58%) in 2011, which may have allowed more song neighbourhoods to develop and persist at the upper plot. First-year male Song Sparrows learned twice as many songs indirectly (i.e. from males they heard interacting vocally with other males) than through direct interactions with older males, highlighting the importance of social information in song learning from both neighbours and non-neighbours within a population (Beecher et al. 2007).

The results of the present study suggest that song sharing between neighbours may be selected for in Canada Warblers. Phrase repertoire size remained stable between years despite addition and loss of individual phrases, and neither phrase nor variant repertoire size was correlated with reproductive success, contrary to the repertoire hypothesis. High song sharing between neighbours, higher sharing with more years of territory tenure, and copying of shared songs by SY males, are more consistent with the song sharing hypothesis. Studies of female mate choice by song in Canada Warblers (e.g., whether females prefer local or shared songs versus large or complex repertoires) are needed to address both hypotheses directly.

CHAPTER 3: USE OF TWO SINGING MODES IN DIFFERENT SOCIAL CONTEXTS IN THE CANADA WARBLER

3.1 INTRODUCTION

Birds use their song repertoires to attract mates, defend territories, and communicate both species and individual identity. In species with a single song type, such as the White-crowned Sparrow (*Zonotrichia leucophrys*), one song conveys multiple messages (Nelson and Poesel 2007). In species with more than one song in their repertoires, all songs may convey the same message (e.g., Song Sparrows: Hughes et al. 1998), or particular songs may be used in different contexts (e.g., parulid warblers: Kroodsma 1981). Certain song types are preferentially used in specific social or behavioural circumstances in nightingales (Kunc et al. 2005), North American wood-warblers (Spector 1992), Old World warblers (Järvi et al. 1980), parids (Gaddis 1983, Wiebe and Lein 1999), vireos (Smith et al. 1978), and wrens (Trillo and Vehrencamp 2005).

Species with context-specific song use may divide their repertoires into distinct subsets (song categories), vary their patterns of song delivery (singing modes), or both (e.g., Nelson and Croner 1991, Spector 1992). Male Field Sparrows (*Spizella pusilla*) have two acoustically different song categories: one ‘simple’ song used for long-distance countersinging, and one ‘complex’ song for dawn singing or aggressive intrasexual interactions (Nelson and Croner 1991). Banded Wrens (*Thryothorus pleurostictus*) sing in high-switching serial mode (rapid switching between their repertoire of 15-24 song types) when undisturbed, but use low-switching serial mode (switching between 2-3 song types) or repeat mode (singing only one song) when countersinging (Molles and

Vehrencamp 1999). Hooded Warblers use their two song categories as separate modes: Repeat (one song type, sung at a low rate when unpaired) and Mixed (3-8 song types, sung at a high rate at dawn or near another male; Wiley et al. 1994).

Some genera of the Family Parulidae (North American wood-warblers) use one song type in both long-distance countersinging and short-range interactions with conspecifics. *Seiurus, Helmitheros, Parkesia, Protonotaria, Limnothlypis, Oreothlypis,* and *Geothlypis* species have one 'primary' or perch song; an extended or flight song is also reported for at least 11 species (Spector 1992). Males vary the rate of delivery (e.g., singing faster at dawn and during territorial encounters), or shorten, re-arrange, or mute songs (e.g., more short songs used near a female, or when feeding young) to convey different messages (e.g., Lein 1981). The extended song is more complex than primary song, but incorporates elements of it, and often includes chip notes and flight displays. Ovenbirds (Lein 1981) and Common Yellowthroats (Ritchison 1991) use extended song during aggressive or high intensity interactions.

Parulid species in the genera *Setophaga* (including all former *Dendroica* and *Parula*; Lovette et al. 2010)*, Mniotilta,* and *Vermivora* have two song categories, which they use in distinct behavioural contexts (Spector 1992). The first category, called Type A, Type I, Accented Ending, or Repeat, consists of simple, stereotyped, higher-frequency songs delivered at a slow rate with little immediate variety (Staicer 1989, 1996). It is most often sung by unpaired males, during the day at the territory centre or favourite song perches, after mate loss or nest failure, or when a female is present (Spector 1992). The second category, also known as Type B, Type II, Unaccented Ending, Mixed, or Serial, is comprised of complex, lower-frequency song types delivered intermittently at a rapid rate, with immediate variety and diversity (Staicer 1989, 1996). It increases in use after pairing and late in the season, and is sung either at dawn or during the day in territorial border disputes with conspecific males (Spector 1992). Some of these species, such as the Hooded Warbler (Wiley et al. 1994), American Redstart (Lemon et al. 1994, Staicer et al. 2006), and Yellow Warbler (*Setophaga petechia*; Spector 1991) also sing each category in a different mode.

The Canada Warbler is a member of the only North American parulid genus whose singing system has not yet been identified. The recent phylogenetic re-classification of the Parulidae placed the Canada Warbler in the genus *Cardellina* with the Wilson's, Red-faced (*C. rubrifrons*), Red (*C. rubra*), and Pink-headed Warblers (*C.versicolor*; Lovette et al. 2010, Chesser et al. 2011). According to their placement in this new phylogeny (Lovette et al. 2010), congeneric warbler species share a common singing system: either one- or two-category. Wilson's Warblers apparently have one song type per bird, and no flight song, although data on individual song variation and dawn song is lacking (Ammon and Gilbert 1999). No detailed analysis is available for the remaining three *Cardellina* species, inhabitants of Arizona, Mexico, and Central America (Curson et al. 1994, Martin and Barber 1995).

The limited information available on Canada Warbler song suggests that males have complex songs, with more individual notes per song and very little within-song note repetition in comparison to other warbler species (Lemon et al. 1983), and repertoires of more than one song type (Reitsma et al. 2010). There are anecdotal reports of a flight song (Ficken and Ficken 1962), and of variation in singing activity with breeding status (Reitsma et al. 2010). No quantitative data are available on song structure, repertoire size and use, or dawn song.

Knowledge of Canada Warbler singing behaviour has potential applications to conservation and monitoring of this species. The Canada Warbler has experienced a sharp population decline since the mid-1960s: 43% overall in Canada from 1997-2007, and 4.8% per year in the Atlantic Northern Forest region (Savignac 2008). It was listed as Threatened under Canada's Species at Risk Act (SARA) in 2010, prompting increased range-wide monitoring and recovery efforts. In American Redstarts, Repeat and Serial modes are distinguishable by ear, and paired males reliably used Serial mode more frequently than unpaired males (Staicer et al. 2006). If two singing modes are also audibly distinct in Canada Warblers, the singing mode used by a male could aid in estimation of population demographics (e.g., pairing success) and trends for this species of conservation concern.

In this study, I used two years of song data from male Canada Warblers at a study site in central New Hampshire to determine whether this species has song categories, singing modes, or both. Since Canada Warbler males have more than one song type each (Chapter 2), there are four potential scenarios of repertoire structure and use: (1) males use all songs interchangeably, as in Song Sparrows; (2) males have two or more song categories, but not distinct modes of delivery, as in Golden-winged Warblers *Vermivora chrysoptera*; (3) males use singing modes, but not categories, as in Banded Wrens; or (4) males have song categories and singing modes, as in Hooded Warblers.

3.2 METHODS

See Chapter 2.2 for details on the study site and general data collection methods.

3.2.1 Song Structure

I viewed spectrograms using Raven Pro 1.3 software (www.birds.cornell.edu/raven). I classified all vocalizations with a coding system described in Chapter 2.2.

3.2.2 Samples Used

I drew each sample from an uninterrupted sequence of continuous singing (‘song bout’). An inter-song pause of >30 seconds was considered to mark the end of a song bout (Wiley et al. 1994). Longer pauses often represent an interruption in singing activity based on a change in behaviour (e.g., interaction with another bird) which could produce a subsequent shift in vocal behaviour.

According to a cumulative plot of the number of new variants observed with total songs recorded from 36 males, the occurrence of new variants began to taper off after 20-30 recorded songs (Fig. 2.2). Thus, I randomly sampled segments of 20 consecutive songs from each recording, to standardize the number of variants in each sample.

I included a total of 231 recordings (60 dawn and 171 day) from 60 males in this analysis. I grouped dawn recordings separately, because dawn singing behaviour is distinct from daytime singing, even in species without song categories or singing modes (e.g., Lein 2007, Liu and Kroodsma 2007, Foote et al. 2008). ‘Dawn’ samples were recordings from the start of male vocal activity at approx. 0430-0445 EDT until the end of this continuous song bout. The end of the dawn bout varied among males, from approx. 5 min before sunrise until approx. 20 min after sunrise. Sunrise time ranged from 0506 EDT (11-20 June) to 0529 EDT (10 May). ‘Day’ samples were recordings made after the end of the dawn bout until approx. 1130 EDT (or 6 h after sunrise).

Through field observations and preliminary examination of recordings, song sequences appeared to be of two types, and thus potentially represented two singing modes (Fig. 3.2). Dawn samples included variants with low-frequency phrases, and frequent chipping between songs; some day samples shared this pattern. Most day singing did not include low-frequency phrases, or chips between songs. In other parulids with two singing modes, dawn and daytime singing of the same mode differ in acoustical features such as song rate (e.g., Bolsinger 2000, Staicer et al. 2006). Thus, I classified samples into one of three groups: (1) day I (no low-frequency phrases or chips between songs; Fig. 3.1a), (2) day II (low-frequency phrases and chips between songs; Fig. 3.1b), or (3) dawn (Fig. 3.1c). Each male had 1-3 low-frequency phrases in his total repertoire of 7-16 phrases.

I measured five structural and temporal song variables for each 20-song sample: song rate (songs/min), average song duration (s), number of different variants, average chip rate (chips/s), and cadence CV (%). These variables are known to differ between song categories and modes in other warbler species (Spector 1992). Song rate was the total number of songs (20) divided by the time from the beginning of the first song until the end of the 20th song. Song duration was the time from the beginning of its first element until the end of the final element. The number of different variants observed in each sample is an indicator of song variety and complexity, with a possible range from 1 (all songs the same) to 20 (all songs different). Chip rate was the number of chips between songs divided by the total time between them. Cadence, a measure of singing rhythm, was the time from the beginning of one song to the beginning of the next. Cadence CV (coefficient of variation) measures the degree of variation in this rhythm. Thus, singing at regular intervals would have a low cadence CV, and irregular singing would have a high cadence CV (Staicer et al. 2006).

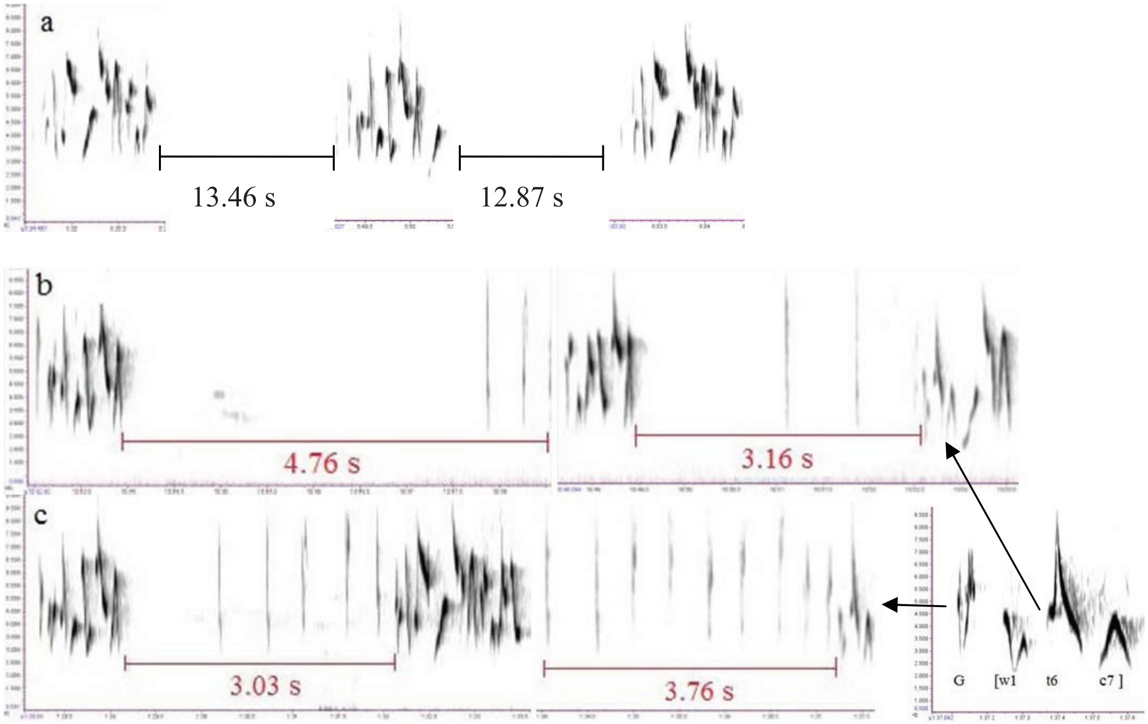

Figure 3.1 (a) Day I, (b) day II, and (c) dawn samples from male 14. This male used the low-frequency phrase [w1-t6-c7] in both day II and dawn singing.

Paired t-tests on a subsample of 10 birds with available dawn recordings from both years confirmed that none of the variables differed significantly between years for the same individual ($P > 0.05$). Thus, I pooled data from 2010 and 2011, and included recordings of individual males from both years if available, to maximize sample size. When more than one sample per bird was available in a given group, I averaged values to obtain a single data point per male. I used 38 dawn, 51 day I, and 32 day II samples in my analyses.

3.2.3 Principal Components Analysis

To assess whether Canada Warblers had distinct singing modes, I used principal components analysis (PCA) on the five variables described above. A correlation matrix was used for PCA, as it standardizes for different units and unequal variances among variables. Kruskal-Wallis and non-parametric Tukey's post-hoc tests were subsequently run by group on the most influential PC scores and the original variables.

Two influential principal components (PCs) were obtained using the correlation matrix. The first PC accounted for 61.9% of the total variance and had strong negative loadings for song rate, cadence CV, chip rate, and number of variants (Table 3.1). The second PC accounted for 21.2% of the variance, with strong negative loading for duration and weaker negative loading for number of variants (Table 3.1). All remaining principal components contributed less than 10% of the total variance.

PC 1 separated samples by group; the majority of dawn and day II samples had negative PC 1 scores, while day I samples had positive scores. PC 1 could be interpreted as the ‘singing mode’ component; positive scores correspond to slow, regular, less variable singing with few chips between songs, whereas negative scores represent fast, irregular, highly variable singing with rapid chipping between songs. PC 2 likely represents individual variation in song length and complexity. Samples with shorter songs and fewer variants have positive scores, while those with longer, more variable songs have negative scores. Because of apparent differences in song delivery described above, I hereafter refer to day I samples as “Mode I” and dawn and day II samples as “Mode II”.

Table 3.1 Loadings of variables for first two principal components.

Variable	PC 1	PC 2
Song rate	- 0.515	0.097
Cadence CV	- 0.485	0.053
Song duration	0.056	- 0.956
Chip rate	- 0.519	-0.002
No. of variants	- 0.476	- 0.270
Eigenvalue	1.76	1.03
% of total variance	61.9	21.2

3.2.4 Linear Discriminant Analysis

A key characteristic of two-singing-mode wood-warbler species is that both modes are used during daytime singing (e.g., Kroodsma et al. 1989; Staicer 1989, 1996; Wiley et al. 1994). Therefore, I used multivariate analysis of variance (MANOVA) and Discriminant

Function Analysis (DFA) with the leave-one-out cross-validation (LOOCV) procedure to determine whether a separate subset of paired 20-song day samples from 21 males (one Mode I and one Mode II from each) could be accurately grouped according to the variables, and which variable(s) were most diagnostic for differentiating the two groups.

3.2.5 Context of Use

Singing modes in other warbler species are typically used in distinct behavioural contexts (Spector 1992). I first used a Chi-squared test to assess whether the use of Mode I and Mode II singing varied according to time period. For daytime samples only, I used either Chi-squared or Fisher's exact tests (if $n \leq 5$ for any category) to examine whether singing behaviour differed with (1) presence of another male or female Canada Warbler nearby (i.e. male or female seen or heard within <10 m of the focal male either during or immediately after the recording), (2) pairing status (unpaired, paired, or post-fledging), or (3) breeding status: unpaired; early pairing, nest building, and egg laying; incubation; feeding young (nestlings or fledglings); after nest failure; or post-fledging (≥10 days after nest fledged, or ≥3 days after nest failure if the pair did not re-nest). A total of 339 recordings from 62 males, with sufficient songs and chips to classify the sample as Mode I or II, were available for these analyses. To ensure that each male was represented no more than once in a given category, I randomly sampled one recording per category per male for each analysis, if multiple recordings were available. I performed all statistical analyses using R 2.9.2 (www.R-project.org).

3.3 RESULTS

3.3.1 Principal Components Analysis

Dawn and day II samples had higher song and chip rates, more irregular delivery (larger cadence CV), and more variants than day I samples, and were thus more similar to one another than to day I samples (Table 3.2). The average PC 1 score differed significantly between groups (Kruskal-Wallis test: $\chi^2 = 88.65$, df =2, $P < 0.0001$; Fig. 3.2), and all three groups were significantly different from one another (Table 3.3). The average PC 2 score did not differ between any of the three groups ($\chi^2 = 0.98$, df =2, $P = 0.612$; Fig. 3.2). Four of the five explanatory variables (song rate, cadence CV, chip rate, and number of variants) were significantly different between groups. Two of these, cadence CV and number of variants, were similar between dawn and day II (Tables 3.2-3.3). Song duration did not differ significantly between groups ($\chi^2 = 1.24$, df =2, $P = 0.538$).

Table 3.2 Summary statistics of variables by group; all values are mean ± SD.

Sample group	Sample size	Song rate (songs/min)	Cadence CV (%)	Chip rate (chips/s)	No. of variants	Song duration (s)
Day I	51	5.7 ± 1.2	20.3 ± 8.8	0.2 ± 0.2	4.9 ± 2.1	1.2 ± 0.2
Day II	32	13.8 ± 4.1	46.6 ± 13.4	1.6 ± 0.7	10.3 ± 3.0	1.1 ± 0.2
Dawn	38	18.1 ± 5.0	48.8 ± 19.8	2.7 ± 1.0	10.6 ± 2.8	1.2 ± 0.2

3.3.2 Linear Discriminant Analysis

Linear discriminant analysis on 42 Mode I and II samples paired within males (n=21) effectively classified all Mode I and most Mode II samples. The two groups differed as a whole based on the five explanatory variables combined (Wilks MANOVA: W = 0.26, df =5 , p < 0.0001). The linear discriminant equation obtained was D = 0.226 (song rate) + 0.019 (cadence CV) + 0.993 (chip rate) + 0.009 (variants) - 1.441 (duration). Prediction analyses using all data correctly classified samples by group 95.2% of the time. All Mode I samples were classified correctly, while two Mode II samples were misclassified as Mode I. The jackknife method, where subsets of the original samples are used, had a lower accuracy (88.1%). Again, all Mode I samples were classified correctly, while 5 of 21 Mode II samples were classified as Mode I.

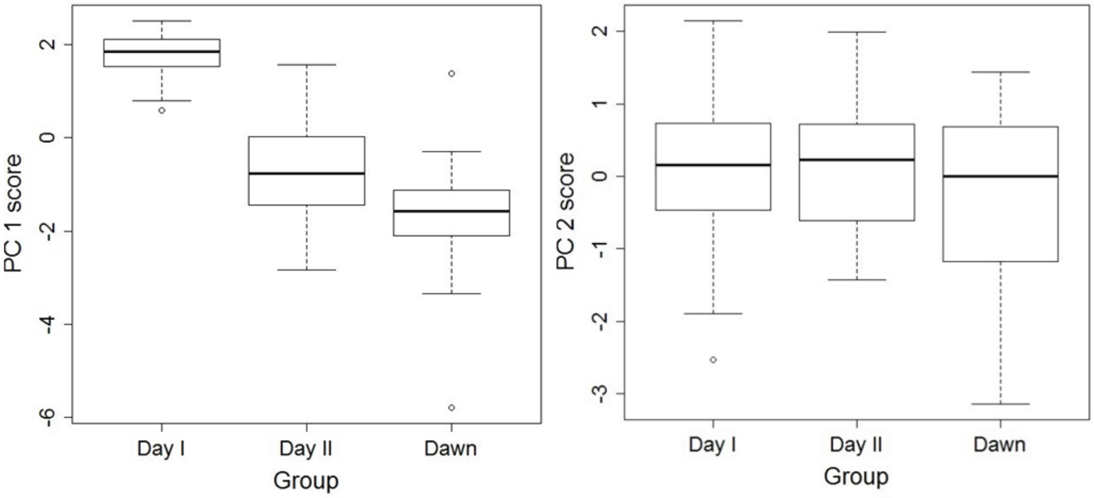

Figure 3.2 First PC scores showed considerable overlap between dawn and day II. Day I samples differed significantly from dawn and day II (left). Second PC scores did not differ between groups (right).

Table 3.3 Non-parametric Tukey's p-values for PC 1 and original variables.

Sample groups	PC 1	Song rate (songs/min)	Cadence CV (%)	Chip rate (chips/s)	No. of variants	Song duration (s)
Day I-Day II	0.000	0.000	0.000	0.000	0.000	0.902
Day I-Dawn	0.000	0.000	0.000	0.000	0.000	0.918
Day II-Dawn	0.005	0.002	0.950	0.000	0.917	0.576

Chip rate was the most important classifying variable, according to the stepwise LOOCV procedure. The linear discriminant equation was D = 2.112 (chip rate), and the prediction accuracy was 88.1%. All Group I samples were correctly grouped, while four Mode II samples were misclassified as Mode I.

3.3.3 Context of Use

Time of day- Males differed in their use of Mode I and Mode II at dawn and during the day ($\chi^2 = 49.65$, df = 1, $p < 0.0001$). Mode I was recorded in 75.4% of day samples, while Mode II predominated at dawn (Fig. 3.3). Only 1 of 41 dawn samples did not include Mode II: a sample from a male recorded in early July 2010, whose second nest attempt had recently failed, and whose female did not re-nest again. This male used Mode II in two other dawn recordings earlier in the 2010 breeding season, when his nests were still active.

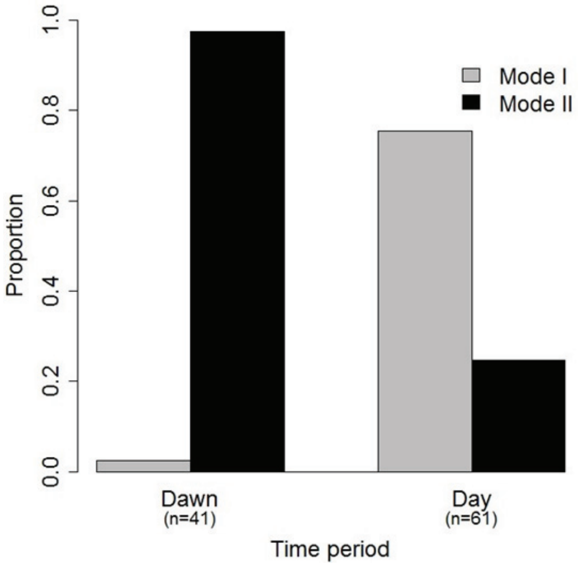

Figure 3.3 Proportion of Mode I and Mode II samples observed by time period.

Presence of female- Overall, males used Mode I more frequently regardless of whether or not a female was present (Fisher's test: $p = 0.565$). Mode I predominated when a female was nearby (81.8%), but also when the male was alone (72.9%; Fig. 3.4).

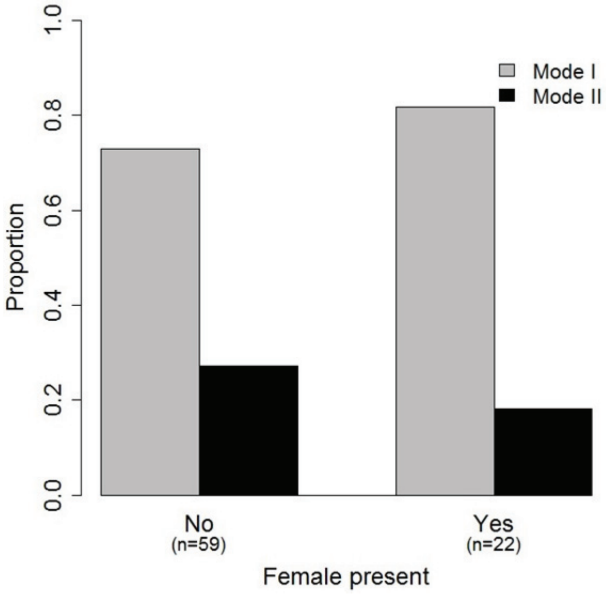

Figure 3.4 Proportion of daytime Mode I and Mode II samples based on presence of a female.

Presence of other males- During the day, males differed in their use of Mode I and II depending on whether or not another male was nearby ($\chi^2 = 13.48$, df = 1, $p = 0.0002$; Fig. 3.5). Mode II was observed in 66.7% of recordings where another male was present, yet in only 20.0% of cases without a second male.

Pairing status- Use of Mode I and II differed by pairing status (Fisher's test: $p < 0.0001$; Fig. 3.6). Mode II was rare in unpaired males (2.1%), increased in paired males during nesting (25.0%), and was most prevalent in the post-fledging period (59.5%).

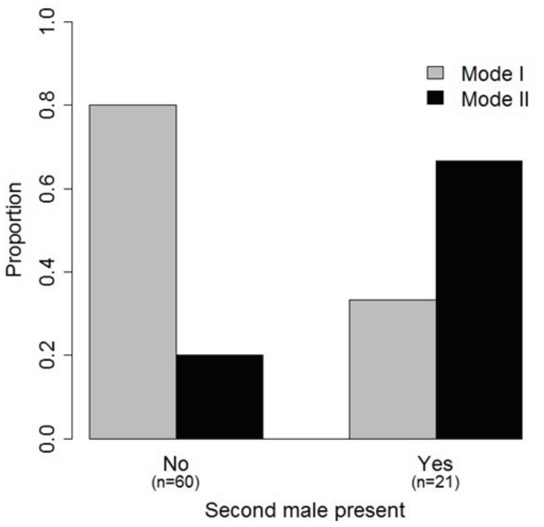

Figure 3.5 Proportion of daytime Mode I and Mode II samples based on presence of a second male.

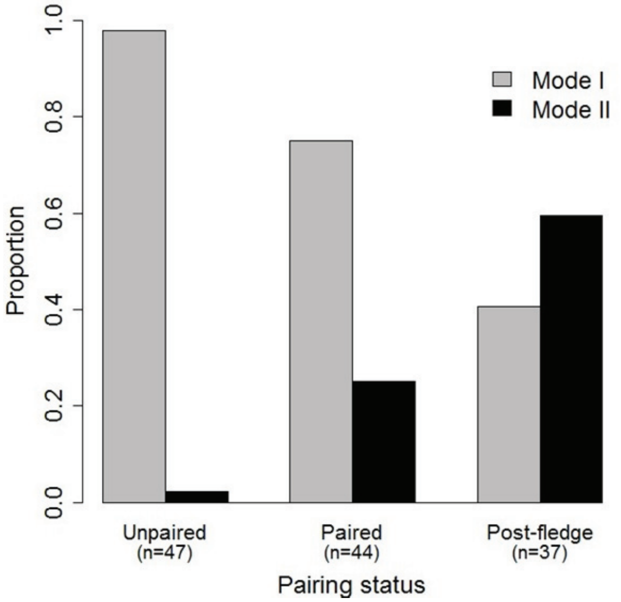

Figure 3.6 Proportion of daytime Mode I and Mode II samples based on male's pairing status.

Breeding status- Prevalence of Mode I and II differed with breeding status ($p < 0.0001$; Fig. 3.7). Males used Mode I more frequently when unpaired (95.7%), during nest-building and egg-laying (83.3%), and during incubation (85.7%). Mode I was less frequent while feeding nestlings and fledglings (56.5%) and post-breeding (42.9%). Sample size was small (n=3) for recordings after nest failure, although the majority (2/3) were Mode I.

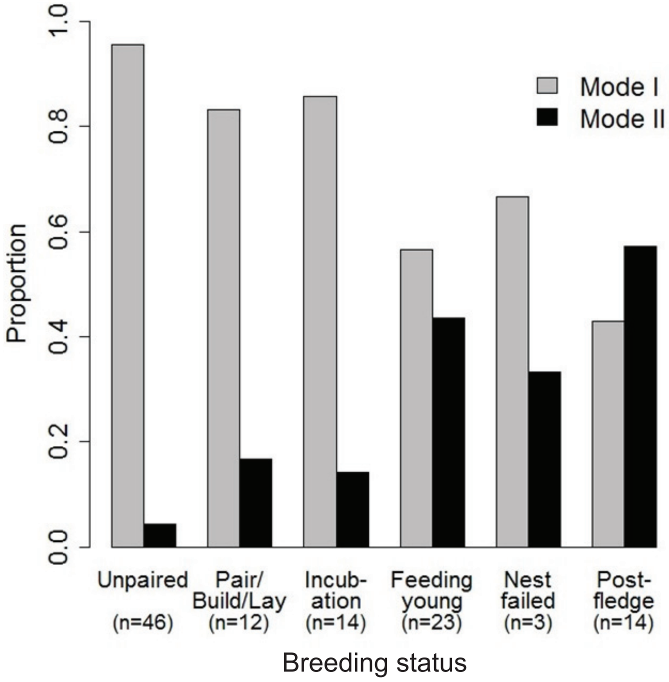

Figure 3.7 Proportion of daytime Mode I and Mode II samples based on males' breeding status.

3.4 DISCUSSION

3.4.1 Singing Modes: Song Structure and Delivery

Canada Warblers appear to have two singing modes, identifiable primarily by rhythm of song delivery, song complexity, and chipping between songs. Mode I, used almost exclusively during the day, had regular delivery (low cadence CV), few song variants per 20-song sample, and little chipping between songs. Mode II, used during dawn and day singing, had irregular delivery (high cadence CV), many variants per sample, and frequent chipping between songs. Variation in cadence (measured by its CV) between singing modes has been examined in few studies to date. Staicer et al. (2006) found that male American Redstarts sang Repeat mode with lower cadence CV when unpaired, early in the season, or after mate loss than when paired. Unlike other parulid species with more than one song type, Canada Warblers do not have two song categories. Only variants containing low-frequency phrases were unique to Mode II, while the remainder were used in both modes. Table 3.4 summarizes the terminology used for song categories and modes analogous to Canada Warbler Modes I and II, for other parulid species referenced in the text.

Canada Warbler singing behaviour shows the typical pattern of Mode II songs being more variable (i.e., a larger number of variants per song bout) than Mode I songs (Spector 1992). In most species with repertoires of more than one song in each category, such as Yellow Warblers (Spector 1991), American Redstarts (Lemon et al. 1994), and Hooded Warblers (Wiley et al. 1994), each male has more Mode II than Mode I songs in his repertoire. Song diversity, an index based on the number of variants observed per song sample, was greater for B song samples in Grace's Warblers (*S. graciae*; Staicer 1989). In Chestnut-sided Warblers, males produced many variants of UE song types (e.g., by adding or deleting introductory or terminal elements), while AE songs were more stereotyped. As well, individual elements were used in multiple UE song types, while AE elements were unique to one song type (Byers 1995).

Table 3.4 Terminology used in parulid song literature to describe song categories and singing modes analogous to Canada Warbler Mode I and Mode II.

Species	Mode I	Mode II
Singing mode		
American Redstart (*Setophaga ruticilla*)	Repeat mode	Serial mode
Hooded Warbler (*S. citrina*)	Repeat mode	Mixed mode
Song category		
Chestnut-sided Warbler (*S. pensylvanica*)	Accented Ending (AE)	Unaccented Ending (UE)
Yellow Warbler (*S. petechia*), Hermit Warbler (*S. occidentalis*), Golden-winged Warbler (*Vermivora chrysoptera*)	Type I	Type II
Grace's Warbler (*S. graciae*), Prairie Warbler (*S. discolor*), Golden-cheeked Warbler (*S. chrysoparia*)	Type A	Type B

Although song rates were significantly different between daytime Mode I, daytime Mode II, and dawn Mode II samples, Mode II samples were collectively more similar to one another than to Mode I samples, again consistent with other studies. Golden-cheeked Warblers (*Setophaga chrysoparia)* and American Redstarts sang B, or Serial songs, respectively, at significantly higher rates at dawn than during the day, and sang A, or Repeat songs, respectively, at a lower rate than either dawn or day B or Serial songs (Bolsinger 2000, Staicer et al. 2006).

A high chip rate is a distinctive feature of Canada Warbler Mode II singing, particularly at dawn. In Golden-cheeked Warblers, chips were also more frequent in B song bouts, since call notes usually preceded B songs, but not A songs (Bolsinger 2000). The dawn chorus of Golden-winged Warblers is characterized by continuous 30-40 min song bouts with frequent chipping between songs (Highsmith 1989).

Structural and temporal measures varied more among Mode II samples than among Mode I samples. This is evident in the LDA results; all Mode I samples were classified correctly, while some Mode II samples were classified as Mode I. Also, Canada Warblers do not have two separate song categories, as in all parulids with two modes studied to date (reviewed in Spector 1992). Canada Warblers use songs from Mode I singing in Mode II singing, although some songs are exclusive to Mode II. As in *Setophaga* species, one individual Canada Warbler may use a given song as Mode I, while another individual uses the same song, or individual phrases of the song, as Mode II (Staicer 1989, 1996; Lemon et al. 1994; Wiley et al. 1994).

Song sharing in the study population differs from sharing patterns observed for other warbler species with two singing modes. In Canada Warblers, both Mode I and II songs appear to exhibit high sharing among neighbours (Chapter 2). In Chestnut-sided Warblers (Byers 1996) and Yellow Warblers (Beebee 2002), AE/Type I songs showed no geospatial sharing pattern, while UE/Type II song sharing was highest amongst neighbours and decreased with distance between territories. Discrete Type I song dialects with geographical extents of 688-6300 km^2, and overlap zones of 6 km, were described for Hermit Warblers (*Setophaga occidentalis;* Janes and Ryker 2006). The

Canada Warbler study site in New Hampshire was < 2 km^2 in size, so information on large-scale geographic patterns of song sharing is currently unavailable.

3.4.2 Context of Use

Time of day- Despite differences in structural characteristics of singing modes between Canada Warblers and other species, temporal and behavioural contexts of use appear similar. Mode I singing was more common during the day, among unpaired males, during early nesting, and in the presence of a female, while Mode II predominated at dawn, late in the season, or when another male was nearby, as in other species (e.g., Highsmith 1989; Staicer 1989, 1996; Spector 1991; Bolsinger 2000). At dawn, the near-exclusive use of Mode II by paired males, and tendency towards Mode I singing early in the season by unpaired males, is prevalent in Canada Warblers and other parulid species (Highsmith 1989, Morse 1989, Bolsinger 2000). Three male Canada Warblers (two unpaired, and one after nest failure) did not use low-frequency phrases in their dawn chorus and sang at a lower rate with less song variation, suggesting that complete or partial use of Mode I singing may occur at dawn in some circumstances.

Presence of a female- Increased use of one singing mode in the presence of a female was not observed, although Canada Warbler males were typically either silent or used Mode I near females. Male Chestnut-sided (Kroodsma et al. 1989) and Yellow Warblers (Spector 1991) were usually silent near females, but AE/Type I songs predominated when males did sing. Canada Warbler males were often silent or just chipping when a pair was observed together, as has been noted in other wood-warbler studies (e.g., Lein

1978, Kroodsma et al. 1989, Staicer et al. 2006). My analysis included only samples where males sang at least 20 consecutive songs with <30 second inter-song pauses.

Presence of other males- Use of Mode II by male Canada Warblers in countersinging and territorial interactions is consistent with other parulid species (Nolan 1978, Staicer 1989, Spector 1991, Wiley et al. 1994). In Prairie Warblers (*Setophaga discolor*), 82% of observations where males sang during fights at boundaries included B songs (Nolan 1978). Yellow Warbler males sang Type II songs in intrasexual encounters, and switched to Type II from Type I when chasing another male, or approaching territory boundaries (Spector 1991). In early May, I observed neighbouring Canada Warblers singing Mode II during territory establishment. I had few high-quality recordings of this behaviour, however, because males often sang very softly, and perched < 1 m apart during these encounters. Other aggressive behaviours were observed on these occasions, including chases, physical contact, and wing-spreading while perched.

Breeding status- Canada Warblers varied use of singing modes according to breeding status in a similar fashion to other parulids (e.g., Spector 1992, Staicer et al. 2006). Unpaired males, and paired males early in the nesting cycle, use Type I singing most frequently (Kroodsma et al. 1989, Bolsinger 2000). However, a high proportion of Mode I singing was observed in all nesting stages for Canada Warblers. Nolan (1978) reported that the majority of singing by male Prairie Warblers during all stages of nesting was group A, although proportionally less than in unpaired males. The sampling strategy of my study (extensive recording throughout the population rather than intensive recording of a few individuals), the high rate of pairing in the population (> 90% in 2010 and

2011), and the lack of nesting data in 2011 precluded further analysis of singing behaviour according to breeding status.

During the post-fledging period, both failed and successful nesters sang a higher proportion of Mode II bouts. Kroodsma et al. (1989) found that Chestnut-sided Warbler males used some UE songs while feeding fledglings, but sang less overall. Nolan's (1978) study on Prairie Warblers documented male singing after young had fledged, and found that 81% of singing in the post-fledging period (August-September) was group B, even among molting males. Although singing behaviour of adult male warblers during the post-fledging and molting periods is little-studied, there are potential benefits of continued singing after the breeding season. Recently-fledged young males begin to learn and practice their songs during the post-fledging period (Marler and Peters 1982), so post-breeding song by adult males may facilitate song acquisition, particularly of local songs, in new recruits (e.g., Nordby et al. 2000). Recent evidence also suggests that post-fledging adult behaviour, particularly acoustic cues from singing, influences territory settlement of conspecifics in the following year, irrespective of actual territory quality (Betts et al. 2008).

3.4.3 Comparison with other *Cardellina*

Although Canada Warbler singing behaviour shares some common features with *Setophaga*, *Mniotilta*, and *Vermivora* species, vocalizations of other *Cardellina* species remain little studied. Wilson's Warblers apparently have a single song type composed of 4-15 individual notes in sets of repeated syllables (Ammon and Gilbert 1999). Males use partial, inverted, or soft versions of their song in different contexts, similar to other warbler species with one song type (e.g., Ovenbirds; Lein 1981). Minimal information is available on the Red Warbler of north and central Mexico and the Pink-headed Warbler of southern Mexico and Guatemala, although their songs are reported to be complex. The Red Warbler's song is described as a "series of warbling trills at different pitches, interspersed with rich warbling notes", while the Pink-headed Warbler's song is described as similar to that of the Yellow Warbler (Curson et al. 1994, p. 192).

The Red-faced Warbler, a high-elevation species of Arizona and Mexico, may have similar song structure, and potentially singing behaviour, to the Canada Warbler. Like Canada Warbler songs, Red-faced Warbler songs are said to be composed of 8-9 elements with little sequential repetition, and are within a frequency range of 3-7 kHz (Martin and Barber 1995). Sound files and spectrograms available on the Birds of North America account show that males can have more than one song type each, and considerable within-type variation (Martin and Barber 1995). Recordings of focal males during the dawn chorus and later in the morning would be necessary to check for the presence of singing modes, and to quantify Red-faced Warbler song complexity.

CHAPTER 4: BREEDING STATUS AND TEMPORAL EFFECTS ON DETECTABILITY OF TERRITORIAL MALE CANADA WARBLERS

4.1 INTRODUCTION

Point counts are a widely-used and cost-effective method for monitoring avian populations, yet many factors influence a bird's probability of detection (detectability) on a survey. Detection biases may be observer-related, such as species misidentification (Robbins and Stallcup 1981) and 'observer overload' resulting in count errors at high avian densities (Best and Schoultz 1984). Environmental and habitat variables impeding detection include dense vegetation (Schieck 1997, Pacifici et al. 2008), adverse weather conditions (Robbins 1981), and ambient noise (Simons et al. 2007). A suite of temporal and social factors such as time of day (Hayes et al. 1986), breeding status (Gibbs and Wenny 1993), and conspecific density (McShea and Rappole 1997) also affect detection by influencing avian vocal behaviour.

Over 90% of birds are identified and detected by ear during point counts, especially in dense forested habitats (Brewster and Simons 2009, Gale et al. 2009). A fundamental assumption in point count data analysis is that all males have an equal probability of detection (Thompson 2002). However, birds do not always vocalize when an observer is present at a site owing to temporal, socio-behavioural, and environmental factors, thus biasing population estimates and trends derived from point count data (Anderson 2001, Johnson 2008).

Breeding status and time of day are two factors known to influence detectability, often in an inter-related way. In species where mate attraction is a primary function of song, paired males sing less overall than unpaired males, and thus have a lower probability of detection on a point count (e.g., Best and Petersen 1982, Wilson and Bart 1985, Hayes et al. 1986, Gibbs and Wenny 1993, Staicer et al. 2006, Amrhein et al. 2007). Singing activity also differs with time of day between paired and unpaired males. For example, paired males often sing irregularly at low rates for the first two hours after sunrise, a time when unpaired birds are most vocal (Hayes et al. 1986, Bolsinger 2000). Thus, point counts may underestimate population density at sites with high pairing success, or overestimate density at lower-quality sites.

Conspecific density also influences singing behaviour and thus could affect probability of detection on a survey. Increased song output has been documented in areas of higher conspecific density (McShea and Rappole 1997, Penteriani et al. 2002). Yet, song output itself does not indicate a healthy population, since unpaired males are typically more vocal (e.g., Staicer et al. 2006). Density is positively correlated with reproductive success in some bird populations (e.g., Gibbs and Faaborg 1990), but not in others (Van Horne 1983, Vickery et al. 1992). Furthermore, observer errors in density estimates may increase at higher densities, resulting in underestimation of population declines (Bart and Schoultz 1984, Hayward et al. 1991, Howell et al. 2004).

Recent studies evaluating point count survey design and sources of variation in bird detectability have emphasized species-specific differences in singing behaviour (Diefenbach et al. 2007, Gonzalo-Turpin et al. 2008, Lee and Marsden 2008, Gale et al.

2009). For instance, forest songbird point count data consistently over- or under-estimated population density for particular species (Howell et al. 2004, Gonzalo-Turpin et al. 2008). To determine whether all males of a given species are equally detectable during point count surveys, identification of temporal and behavioural factors affecting that species' vocal behaviour is essential.

The Canada Warbler is a migratory songbird sustaining a long-term, range-wide population decline. This species' population has declined by 43% overall in Canada from 1997-2007, and by 4.8% per year in the Atlantic Northern Forest region (Savignac 2008). The Breeding Bird Survey (BBS) is a continent-wide avian monitoring program which currently provides the majority of data on Canada Warbler population trends. BBS observers conduct 3-min point counts of all birds seen and heard at 50 stops spaced 800 m apart along a prescribed route (Bystrak 1981). However, the BBS only covers 54% of the Canada Warbler's breeding range (Savignac 2008), and is conducted only once per year (Bystrak 1981). Little evidence is available to confirm that peak Canada Warbler vocal activity coincides with the BBS count period in its breeding range.

A shorter count interval (e.g., 3 min) allows observers to conduct more point counts within a given time period, but may also decrease the probability of detecting a territorial male who sings infrequently. Monitoring protocols should use a point count interval that is long enough to detect a singing male, yet short enough to both maximize the number of points surveyed daily and minimize bird movement out of the area during a count (Lee and Marsden 2008). Counts should also take place at the appropriate time of day and breeding season to increase the probability of detecting both paired and unpaired males.

The objective of this study was to determine if detectability of singing male Canada Warblers differed with breeding status, time of day, time of season (date), number of conspecific neighbours, and length of survey period. I used unsolicited recordings of males of known identity and breeding status from an area of high population density in central New Hampshire. I predicted that paired males would be less detectable than unpaired males, particularly during shorter count intervals, that detectability would decrease with time of day and season, and that males with more territorial neighbours would have higher detectability.

4.2 METHODS

See Chapter 2.2 for details on the study site and population.

4.2.1 Sampling Procedure

I recorded 35 territorial male Canada Warblers approximately once weekly from May-July 2010-2011, to document vocal behaviour at different stages of the breeding season. Weather permitting, I began recording at the start of the dawn chorus at 0.5 h before sunrise (0436-0508 EDT), and continued until approximately 5 h after sunrise (1006-1038 EDT). These times coincide with the period of peak morning vocal activity, and point count timing of regional BBS routes. In New Hampshire, BBS routes are run from 27 May-7 July, from one half-hour before local sunrise until 0930-1000 EDT (http://www.pwrc.usgs.gov/bbs/). Sunrise times ranged from 0506 EDT (11-20 June) to 0528 EDT (11 May). The duration of each sample was 10-65 consecutive minutes. I varied the order of subsequent visits to each male, unless his territory was far from trails, and therefore inaccessible before first light.

Sampling methodology aimed to minimize the effects of observer presence on male vocal behaviour. No song playbacks were used except for initial capture and banding of males, since playback use may result in increased dawn song output (e.g., Erne and Amrhein 2008) and earlier onset of dawn song (e.g., Foote et al. 2011). If the focal male was singing spontaneously upon arrival, I approached him and began recording for 20-30 min. If no male was heard, I quietly approached the territory and began recording in the area of known activity from previous observations. After recording, I confirmed each bird's identity by resighting colour bands, or actively searched the territory for 10-15 min to find the male if not already located.

4.2.2 General Analysis

I analyzed 97 recordings for which I could confirm the breeding status and identity of the territorial male. In 2011, when no active nest-searching efforts were underway, I only included recordings from visits where breeding status could be conclusively inferred from behaviour (e.g., feeding nestlings: adults delivering multiple food items to small localized area). Five of the 35 males were recorded in both years. I pooled data from both years for the analysis, because of comparable male arrival times (first arrival in both years: 10 May) and breeding chronology (first nest fledged: 13 June 2010, approx. 17 June 2011) across years.

4.2.3 Probability of Detection

To measure availability of territorial males for detection, I randomly selected one 1, 3, 5, and 10 min interval from each 10-65 min recording. Start times for each interval were selected with replacement, so the different intervals in recordings >10 min did not always overlap. I noted whether the territorial male sang at least once during each interval (i.e. he was detected). These time intervals correspond to standardized point count protocols: 3 min for the BBS (Bystrak 1981), 5 min for regional atlas programs (e.g., Maritimes Breeding Bird Atlas; http://www.mba-aom.ca/english/mbbaguide.pdf), and 10 min for other monitoring programs (e.g., BBIRD; Martin et al. 1997). I viewed spectrograms of recordings using Raven Pro 1.3 software (www.birds.cornell.edu/raven) in order to identify individuals based on their songs (see Chapter 2).

I categorized recordings by breeding status, time of day, time of season, and number of territorial neighbours. I grouped nesting stages into six categories: unpaired; early pairing, nest building, or egg laying; incubation; feeding young (nestlings or fledglings); after nest failure; and post-fledging (≥10 days after nest fledged, or ≥3 days after nest failure if the pair did not re-nest). Five time categories synchronous with BBS count times were used: dawn (30 min period before sunrise), and four 1.5 hour-long post-dawn categories: 0 to 1.5, 1.5 to 3, 3 to 4.5, and ≥4.5 hours after sunrise. I obtained sunrise times for Canaan, NH at the US Naval Observatory website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). If a recording overlapped two time categories, one category was randomly selected, and sub-samples were drawn from that category. Five time of season categories were each approximately two weeks long, and coincided with dates before, during, and after allowable NH BBS count dates: 11-26 May (before); 27 May-9 June, 10-23 June, and 24 June-7 July (during), and 8-19 July (after). I used three categories for number of neighbours: 1-2, 3-4, and 5-8 neighbours. To ensure independence of data points, I randomly selected one sample per category for each male in a given analysis, if more than one sample was available.

For each time interval, the probability of detection was calculated as the proportion of samples in a given category where the male sang at least once (Gibbs and Wenny 1993). I used generalized linear models (GLMs) with binomial distribution (0 = not detected, 1 = detected) to determine whether time of day, breeding status, and number of territorial neighbours influenced probability of detection at each time interval. I did not include time of season in the models because of uneven sample distribution across breeding status categories (e.g., 11-26 May samples were only from the unpaired and early pairing, nest building, and egg laying stages). I also excluded the after nest failure category owing to low sample size (n = 3). I selected the most parsimonious models according to Akaike's Information Criterion (AIC) value obtained from the 'step' model function in R. Models with lower AIC values have the best 'fit' to the data with the fewest number of parameters. Alternate models with a ΔAIC of ≤ 2 also have strong support (Burnham and Anderson 2002).

4.2.4 Song Rates

Probability of detection is potentially influenced not only by whether a bird sings within a time interval, but also by the rate and variability of song output (Wilson and Bart 1985).

I calculated song rates and variability of song output for all samples. First, I calculated the song rate (songs/min) for each minute of a given recording. I then calculated the mean song rate and the coefficient of variation (CV) of the song rate using all minutes of that recording. I determined whether mean song rate and CV differed with time of day, time of season, breeding status, and number of neighbours, using Kruskall-Wallis tests and non-parametric post-hoc tests to compare between levels of each factor (Gibbs and Wenny 1993). All values reported are mean ± SE. I performed statistical analyses using R 2.9.2 (www.R-project.org).

4.3 RESULTS

4.3.1 Probability of Detection

Overall detection probability of male Canada Warblers increased only slightly with longer duration of sampling time intervals: 0.61 at 1 min, 0.60 at 3 min, 0.66 at 5 min, and 0.70 at 10 min.

Time of day- Detectability decreased steadily with time of day relative to sunrise (Fig. 4.1). All males were detected at dawn (before sunrise) during the period of extensive dawn sampling (22 May-4 July). Detectability varied from 0.53-0.79 in early to mid-morning (sunrise to 4.5 h after), but only half of the territorial males were detectable by late morning (≥4.5 hours after sunrise, or 0936-0958 EDT).

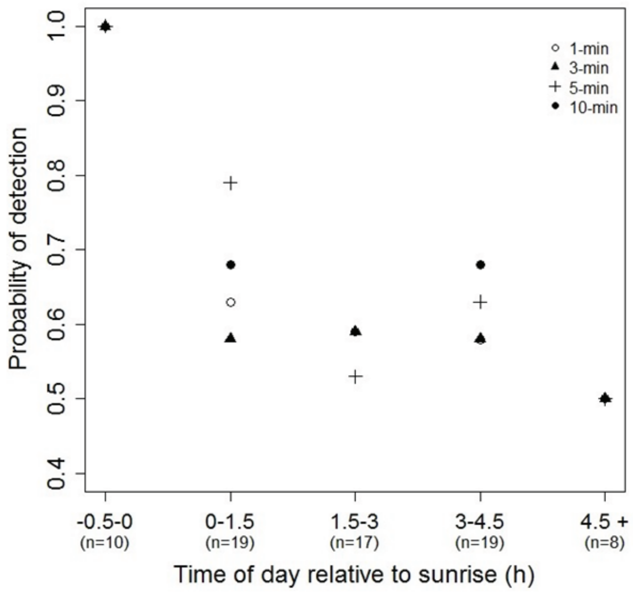

Figure 4.1 Probability of aural detection of territorial male Canada Warblers according to time of day relative to sunrise over four time intervals.

Breeding status- Considerable variation in detectability was observed with breeding status (Fig. 4.2). Detectability was high (≥0.89) for unpaired males and paired males whose nests had recently failed. Detectability was lower for paired males during nest-building and egg-laying (0.25-0.42), feeding young (0.22-0.56), and post-fledging stages (0.38-0.63), and was intermediate during incubation (0.60-0.73).

Time of season- Detectability varied less according to time of season (Fig. 4.3). Detectability was highest (0.74) from 11-26 May, ranged from 0.53-0.73 in late May to early July, and dropped to ≤ 0.5 by mid-July.

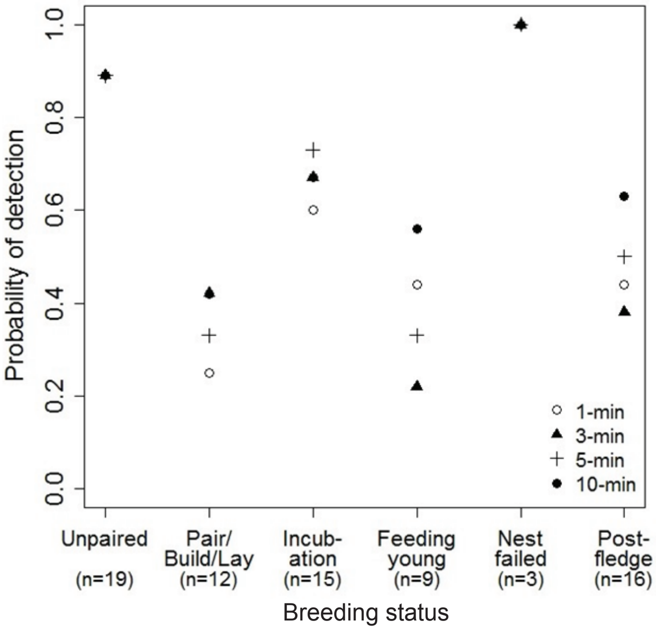

Figure 4.2 Probability of aural detection of territorial male Canada Warblers according to breeding status over four time intervals.

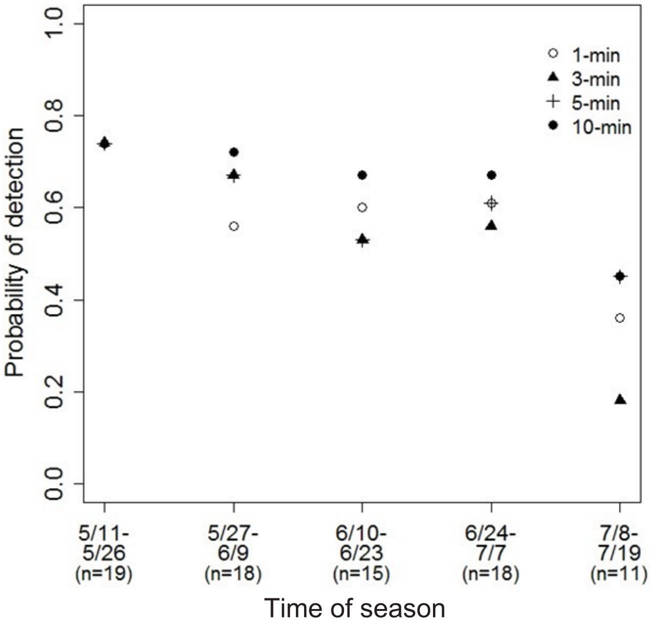

Figure 4.3 Probability of aural detection of territorial male Canada Warblers according to time of season over four time intervals. Time periods correspond to dates before (11-26 May), during (27 May-7 July), and after (8-19 July) allowable BBS survey dates in NH.

Number of neighbours- Detectability showed no consistent pattern with increased number of territorial neighbours, aside from higher detectability for all groups with the 10-min sampling interval (Fig. 4.4).

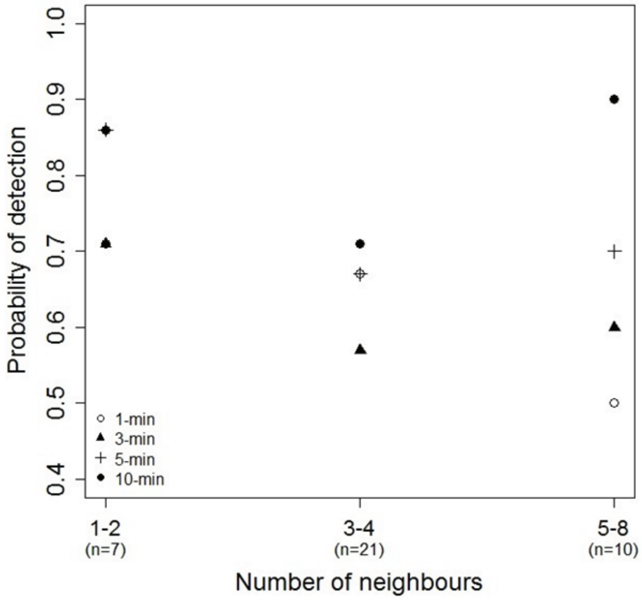

Figure 4.4 Probability of aural detection of territorial male Canada Warblers according to number of territorial neighbours over four time intervals.

Models- For all four time intervals, the most parsimonious model explaining probability of detection included breeding status and time of day (ΔAIC = 0.00; Table 4.1). The model including breeding status, time of day, and number of neighbours also had strong support at the 1-minute time interval (ΔAIC = 1.03; Table 4.1).

4.3.2. Song Rates

Time of day- Mean song rates differed significantly among the time of day categories (Kruskal Wallis test: $\chi^2 = 18.61$, df = 4, $P < 0.001$). Males sang faster at dawn than they did after sunrise: 0-1.5 h (non-parametric Tukey's: $P = 0.007$), 1.5-3 h ($P = 0.025$), and 3-4.5 h ($P = 0.005$). Song rate CV did not differ significantly by time of day ($\chi^2 = 2.48$, df = 4, $P = 0.648$; Fig. 4.5).

Table 4.1 Summary of best models explaining detectability of territorial male Canada Warblers.

Model[1]	AIC	ΔAIC
1-min interval		
status + time	104.79	0.00
status + neighb + time	105.82	1.03
status + neighb + time + neighb:time	115.10	9.28
3-min interval		
status + time	95.31	0.00
status + neighb + time	97.74	2.43
5-min interval		
status + time	102.35	0.00
status + neighb + time	105.08	2.73
10- min interval		
status + time	109.53	0.00
status + neighb + time	112.97	3.44

[1] status = breeding status; time = time of day; neighb = number of neighbours

Because of the much higher mean song rate at dawn compared to other time periods (Fig. 4.5), I ran all subsequent tests both with and without dawn samples. When effects were non-significant for both tests, I report results only for tests using all samples.

Breeding status- Mean song rates differed significantly among breeding status categories both including ($\chi^2 = 14.89$, df = 4, $P = 0.005$) and excluding ($\chi^2 = 16.59$, df = 4, $P = 0.002$) dawn samples. In both analyses, males feeding young sang at a lower rate than did unpaired males ($P = 0.017$; Fig. 4.6). Song rate CV also differed significantly according to breeding status both including ($\chi^2 = 20.34$, df = 4, $P < 0.001$) and excluding ($\chi^2 =$

22.54, df = 4, P < 0.001) dawn samples. Unpaired males sang at a less variable rate than did males feeding young (with dawn: P = 0.023, without dawn: P = 0.021), and post-fledging males when dawn samples were excluded (P = 0.016). Song rate CV did not differ significantly between unpaired males and males during incubation (with: P = 0.060; without: P = 0.080; Fig. 4.6).

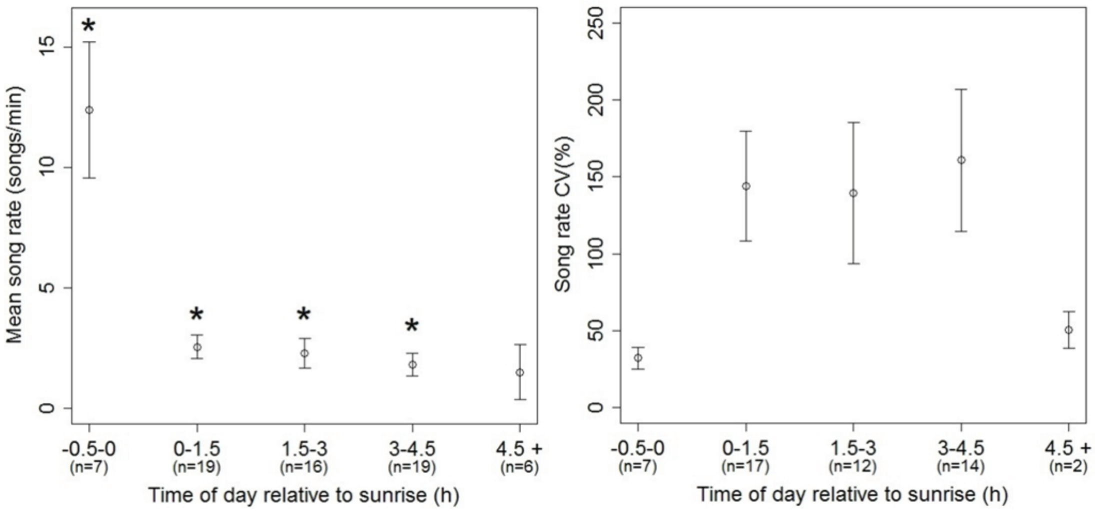

Figure 4.5 Mean song rate (left) and song rate CV (right) of male Canada Warblers according to time of day relative to sunrise. All values are mean ± SE. Asterisks represent significant effects ($\alpha = 0.05$).

Time of season- Although mean song rate did not differ among the time of season categories ($\chi^2 = 4.72$, df = 4, P = 0.318), song rate CV did differ, both with ($\chi^2 = 17.46$, df = 4, P = 0.002) and without ($\chi^2 = 17.68$, df = 4, P = 0.001) dawn samples (Fig. 4.7). With dawn recordings included, song rate CV was higher for the 8-19 July category than for 24 June-7 July (P = 0.072). With dawn recordings excluded, song rate CV was higher for the 24 June-7 July category than for 11-26 May (P = 0.081).

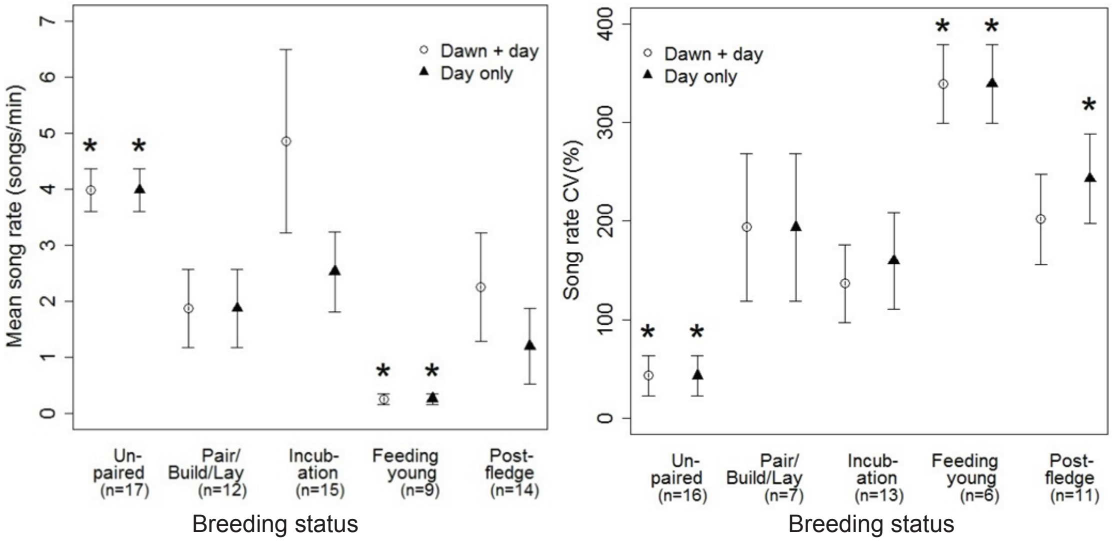

Figure 4.6 Mean song rate (left) and song rate CV (right) of male Canada Warblers according to breeding status. All values are mean ± SE. Asterisks represent significant effects ($\alpha = 0.05$).

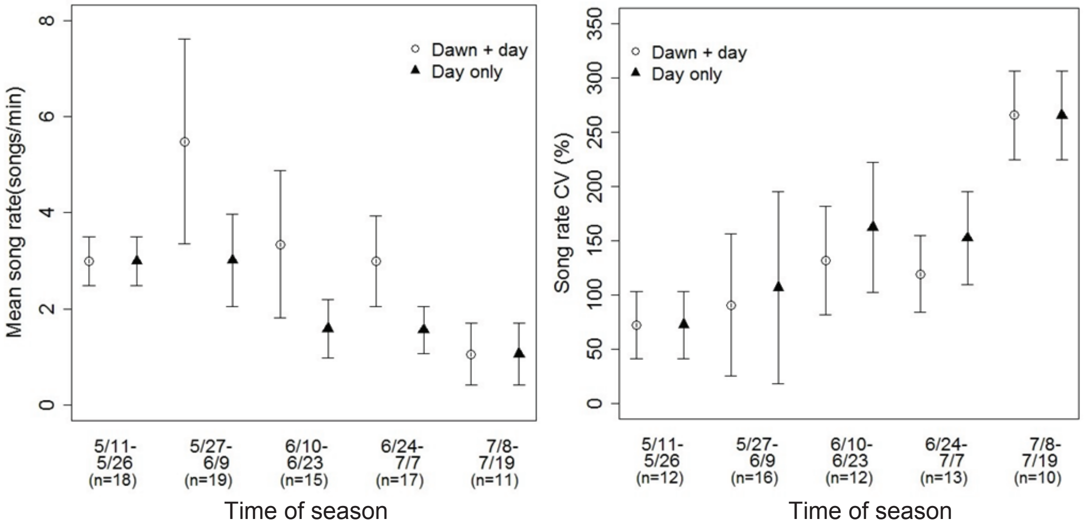

Figure 4.7 Mean song rate (left) and song rate CV (right) of male Canada Warblers according to time of season. All values are mean ± SE.

Number of neighbours- There was no significant difference in either mean song rate ($\chi^2 = 1.48$, df = 2, P = 0.477) or song rate CV ($\chi^2 = 0.89$, df = 2, P = 0.642; Fig. 4.8) according to number of territorial neighbours.

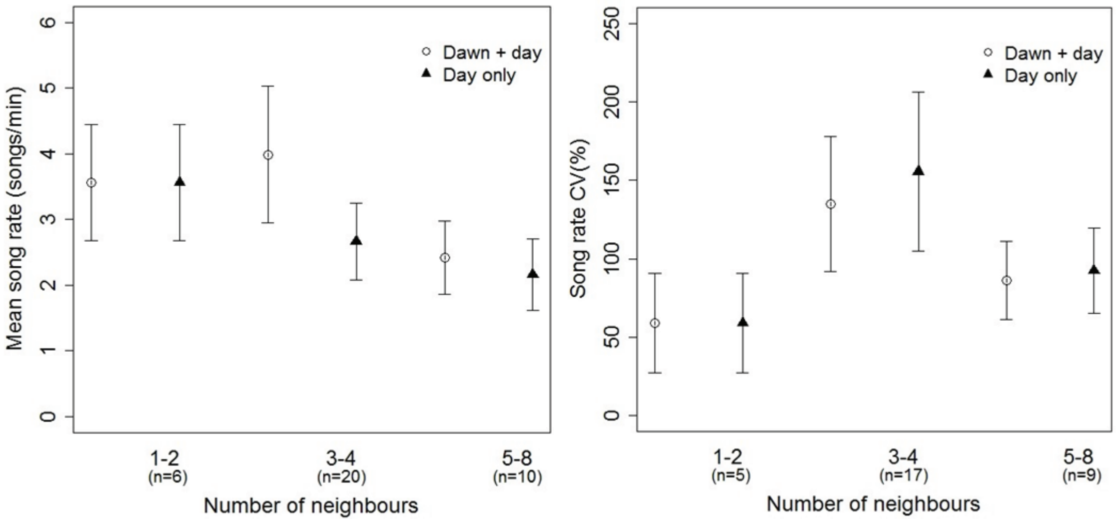

Figure 4.8 Mean song rate (left) and song rate CV (right) of male Canada Warblers according to number of territorial neighbours. All values are mean ± SE.

4.4 DISCUSSION

The present study demonstrated that male Canada Warblers at a high-density site are easily detectable at dawn, when they sing continuously at high rates. Dawn singing behaviour is known to vary according to conspecific male density, thus affecting detectability. Other studies indicate that a primary context of dawn song is intrasexual interaction (Staicer et al. 1996, Liu 2004, Sexton et al. 2007, Foote et al. 2008). Removal experiments on Chipping Sparrows (*Spizella passerina*) found that males either did not sing at dawn or reduced dawn chorus length and song rate after neighbour removal, and resumed usual dawn singing behaviour following neighbour return (Liu 2004). Male Eastern Kingbirds (*Tyrannus tyrannus*) with few neighbours were more often silent at dawn, while those with more neighbours sang faster and longer dawn bouts (Sexton et al. 2007). If male Canada Warblers also reduce or cease dawn singing at low-density sites, their probability of detection at dawn would be lower than found here. A detailed comparison of dawn singing from Canada Warblers in both high- and low-density populations throughout the breeding season is needed to quantify these effects.

Unpaired male Canada Warblers were 90% detectable overall, and sang regularly (low CV) at a high mean rate (4.0 songs/min). Males were only 22-63% detectable during early pairing, nest building, egg laying, when feeding young, and post-fledging, when they sang intermittently (high CV) at a low rate (range: 0.3-2.3 songs/min). Detectability was intermediate during incubation, when males sang at a higher rate (range: 2.5-5.0 songs/min), but infrequently (high CV). Thus, the probability of detection varied according to differences in song rate variability associated with breeding status. This pattern is consistent with studies where detectability of paired birds was examined by nest stage. Detectability of male House Wrens (*Troglodytes aedon*) during 3-min count periods was approximately 0.7 during pre-pairing and incubation, but dropped to 0.5-0.6 during early nesting, and <0.5 when feeding young (Wilson and Bart 1985). Paired male Sage Sparrows (*Amphispiza belli*) and American Redstarts were only half as detectable (0.45-0.5) as unpaired males (>0.85; Best and Petersen 1982, Staicer et al. 2006).

The breeding status of male Canada Warblers did not appear to influence diel patterns of vocal activity. This is in contrast to the considerable diel variation in song output by pairing status reported for other warbler species. In Golden-cheeked Warblers, paired males were detected on 89% of 20-min counts at dawn or during mid-morning (2+ hours after sunrise), but on only 64% of counts in the first two hours after sunrise (Bolsinger 2000). Paired male Kirtland's Warblers (*S. kirtlandii*) also sang little post-sunrise (0630-

0800), when unpaired males were most vocal (Hayes et al. 1986). For Canada Warblers in this study population, detectability was slightly lower overall in mid-morning (1.5-3 hours) than post-sunrise (0-1.5 h). However, detectability did not drop below 50% until 4.5 hours after sunrise (approximately 0935-1000 EDT), which coincides with the official end time of regional BBS counts.

The number of conspecific neighbours did not explain differences in detectability in this population of Canada Warblers. However, conspecific density was high, and all males had at least one territorial neighbour (mean ± SD: 3.4 ± 1.5 in 2010; 3.1 ± 1.5 in 2011). In Ovenbirds, Northern Cardinals (*Cardinalis cardinalis*), and Wood Thrush (*Hylocichla mustelina*), males had higher song rates in areas of high conspecific density (McShea and Rappole 1997). During nocturnal Eagle Owl (*Bubo bubo*) surveys, detectability averaged 95.7% for males at a high-density site, but only 47.8% at a low-density site (Penteriani et al. 2002). Data on Canada Warbler song output in low-density areas is needed, since the species is scarce or declining in most of its breeding range (Savignac 2008).

Observer errors during point counts (e.g., recording fewer individuals than are detectable) may also increase at higher densities. In 3-min aural point counts conducted in the lab and in the field, experienced observers declined by 32-49% in efficiency (proportion of individuals detected) when species density at the survey point increased from 1 to 4 individuals (Bart and Schoultz 1984). Direction and extent of survey errors may also be species-specific, as point count data over-estimated density for Acadian Flycatchers (*Empidonax virescens*) and Worm-eating Warblers (*Helmitheros vermivorum)*, but under-estimated it for Wood Thrush (Howell et al. 2004). Comparison of point count surveys at areas of known high and low Canada Warbler density would be useful to measure the effect of observer errors on population estimates and trends in this species.

Obtaining clear recordings for this study necessitated being within approx. 10-20 m of the focal male for ≥10 consecutive minutes. Observer presence can influence male singing behaviour and detectability, especially for longer count periods. Song rates were 1.3-4.0 times higher for all three focal species in the McShea and Rappole study (1997) when observers were >50 m away from the bird, suggesting that observer proximity reduced song output. During Eagle Owl surveys, five males stopped calling when they noticed a nearby observer (Penteriani et al. 2002). Lee and Marsden (2008) found that overall density estimates were >50% lower for 5 of 6 forest bird guilds, including insectivores, when a 10-min pre-count ‘settling-down period’ was used, primarily from bird movement away from the observer. Canada Warbler habitat is dominated by dense vegetation which can impede visual detection, so males may make evasive movements or reduce vocal activity without the observer’s knowledge.

Breeding status is closely tied to time of season for migratory songbirds, so selection of Canada Warbler survey dates should be appropriately timed to the species’ breeding cycle. In New Hampshire, male Canada Warblers arrive on territory from mid-late May, with eggs laid on average by 1 June, and nests fledging around 23 June. However, nest-building and egg-laying can occur in mid-June for re-nests, which fledge in mid-July (Reitsma et al. 2010); this produces asynchrony between breeding status and calendar date. Furthermore, Canada Warblers are single-brooded throughout their range (Reitsma et al. 2010), so males with early successful nests may become less territorial and thus not available for detection past mid-June. In 2010, 31% (17/54) of territorial males at the study site had fledged young by 24 June, meaning they were no longer territorial. Overall detectability dropped after 7 July, when most males were either feeding young or had completed breeding, and sang infrequently. Although detectability of males who were present was high in early-mid May, many males did not arrive until late May. To maximize availability for detection, preferred survey times for Canada Warblers near the study area are approximately 27 May (majority of males have established territories) to 24 June (majority of nests active and males still territorial). However, owing to temporal variation in breeding status of males in the population, and annual variation in breeding phenology, it is challenging to choose an optimal survey date maximizing detectability.

Since Canada Warbler detectability increased by only 10% overall as the count time interval increased from 1 to 10 min, the 3 min counts currently used by the BBS appear to effectively maximize the number of counts per day. Variation in detectability by count length was >20% during the feeding young, post-fledging, and late-season periods, when song rate CV was high. This result indicates that results from point counts are more likely to be inaccurate when males sing intermittently. Other studies suggest that detectability of males who sing intermittently can be maximized by increasing the number of surveys conducted per season at a site rather than the point count duration (Gibbs and Wenny 1993, Penteriani et al. 2002). Assuming similar length of nesting stages range-wide, Canada Warbler surveys should ideally include more than one count over a four-week period, beginning approximately two weeks after territory settlement by the earliest-arriving males.

This study's small sample size and limited geographic range mean that results should be interpreted cautiously in regards to range-wide monitoring of Canada Warblers. Since I was not able to sample focal males at least once during each nesting stage, individual variation in vocal output (Mayfield 1981, Biro and Dingemanse 2009) warrants further investigation. For example, Mayfield (1981) noted that some individual male Kirtland's Warblers were more 'elusive' than others regardless of breeding status. During the late season (after 24 June), approximately 1/3 of male Canada Warblers had completed breeding, and were thus not reliably available for detection on territory. The study site was small (< 2 km^2), with high conspecific density and pairing success of ≥90% in both years. Applicability of results to areas with low density and pairing status is limited, owing to social influences on Canada Warbler vocal behaviour (Chapters 2 and 3). Nevertheless, results suggest that breeding status of male Canada Warblers does influence vocal activity, and thus detectability, on standardized point counts. Further studies are recommended to compare detectability of males at the high-density study site to those at low-density sites.

CHAPTER 5: CONCLUSION

This study revealed that Canada Warblers have a complex vocal communication system, including repertoires of multiple songs shared with neighbours (Chapter 2). Males delivered their songs in distinct singing modes used in different social contexts (Chapter 3). Male song output, and thus probability of aural detection by an observer, varied with breeding status and time of day (Chapter 4). In this chapter, I summarize the main implications of these results, and suggest avenues for future research on Canada Warblers and related species.

Male Canada Warblers showed spatial clustering of territories into song neighbourhoods and higher overall song sharing with longer territory tenure. First-year breeders (SYs) also modified songs to more closely match their older neighbours. Therefore, young Canada Warbler male likely learn or modify songs from neighbouring males during establishment of their first breeding territories. The song neighbourhoods observed in this study are potentially products of high site fidelity and conspecific density in the New Hampshire study population. Additional studies would help to quantify song sharing at sites with lower density, site fidelity, and average male age.

The presence of two singing modes in the Canada Warbler, but not two discrete song categories, appears to be a unique system of repertoire organization among the Parulidae. All other species studied to date have either one primary multi-purpose song, or two song categories (Spector 1992). In the updated phylogeny of the Parulidae (Lovette et al. 2010), species within a genus share either the one- or two-category singing system.

Cardellina may be an exception, since Canada Warblers have complex songs and singing behaviour, while Wilson's Warblers apparently have only one song type per male (Ammon and Gilbert 1999). Further studies on the remaining three congeners, which reportedly have variable songs (Curson et al. 1994, Martin and Barber 1995), are necessary to determine whether Canada Warbler repertoire structure and vocal behaviour are typical of, or unique within, the genus *Cardellina.*

Classification of singing modes in Canada Warblers by presence or absence of low-frequency phrases and chips between songs was effective in most cases. This method required sufficient recordings of a given male, typically from a dawn recording, to identify low-frequency phrases and chipping pattern. In some ambiguous cases, males used low-frequency phrases as part of Mode I songs, or used specific 'regular' phrases only in Mode II. The presence of chipping between songs was then used to classify samples, instead of both criteria. Daytime recordings from two Canada Warbler males in Nova Scotia confirmed that singing modes could be differentiated in 2-11 min continuous song samples. Mode II song bouts were identifiable by both chipping between songs and use of low-frequency phrases, and switches between Mode I and II were observed within the same recording. This suggests that singing modes could be distinguished by ear in male Canada Warblers in other populations, particularly on the basis of conspicuous chipping between songs.

My results suggest that male Canada Warblers have high song output at dawn, and that detectability of paired males does not decrease sharply until early July. However, males sang Mode II, which is faster and more conspicuous, more often in the presence of other males during dawn and daytime song bouts. High conspecific density at the study site likely resulted in increased Mode II use, and potentially higher detectability, although I did not test this hypothesis explicitly. The high population density at the New Hampshire site is atypical for Canada Warblers range-wide (Savignac 2008). Canada Warbler detectability studies which also measure singing mode use at low-density sites would be useful to quantify density effects on vocal behaviour.

Acoustical monitoring techniques such as automated recording units and microphone arrays would be valuable tools for future vocal behaviour research on this species. In 2011, I used a SongMeter SM2 automated recorder (Wildlife Acoustics, Inc.) to record male vocal activity throughout the day at 10 locations within known Canada Warbler territories. The recordings were of sufficiently high quality to confirm identity of one or more individuals based on song, and to classify song bouts by mode. I did not include these recordings in my analyses, because supplementary data such as breeding status and presence of conspecifics (males, females, or fledglings) were not available. An array of SongMeters or similar devices could be used to record use at dawn of shared songs by individual males within a neighbourhood (e.g., Lapierre et al. 2011). As well, remote microphones could objectively measure singing mode use and detectability based on temporal, behavioural, and environmental factors, without possible effects of observer presence on vocal activity.

In male songbirds, vocal traits such as repertoire size, dawn song complexity, singing consistency, and song rate have been correlated with success at fathering extra-pair young (e.g., Hasselquist et al. 1996, Kempenaers et al. 1997, Byers 2007, Chiver et al.

2008). Analysis of extra-pair paternity (EPP) data from the study site is currently underway (L. Reitsma pers. comm.). The prevalence of song ‘clusters’ (high sharing with some, but not all, neighbours) suggests that new males preferentially incorporated songs of specific neighbours into their repertoire. Thus, it would be interesting to examine whether young males settling in a neighbourhood copy the shared songs of nearby males with high reproductive success. Many banded females at the study site were site-faithful, and even showed mate fidelity between breeding seasons. EPP data could address whether female Canada Warblers prefer males with larger, more complex, and more shared repertoires as social and extra-pair mates.

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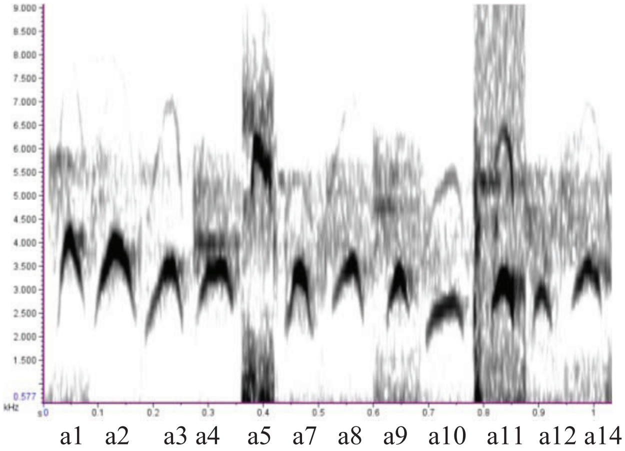
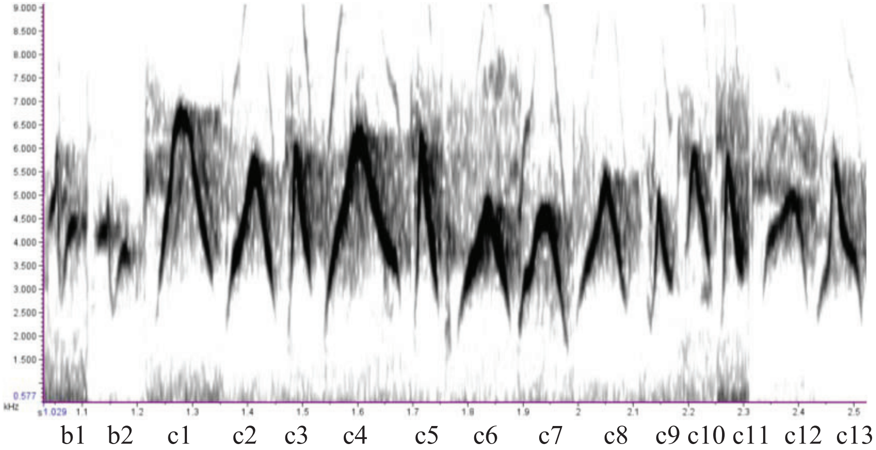
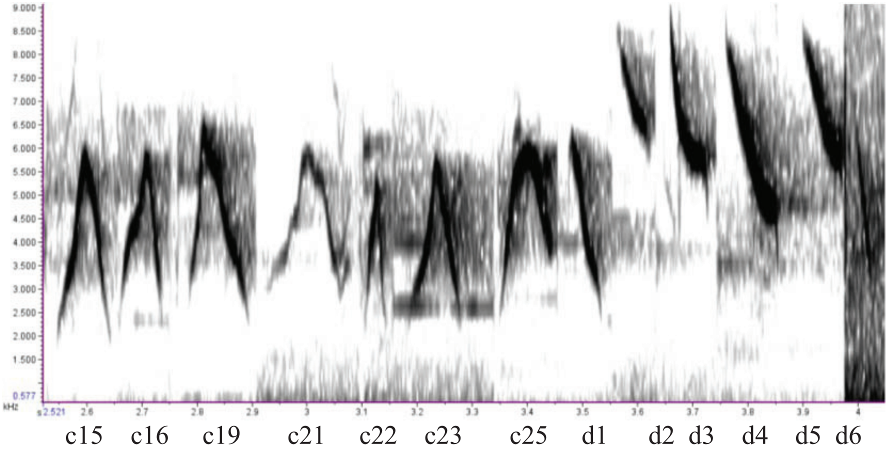
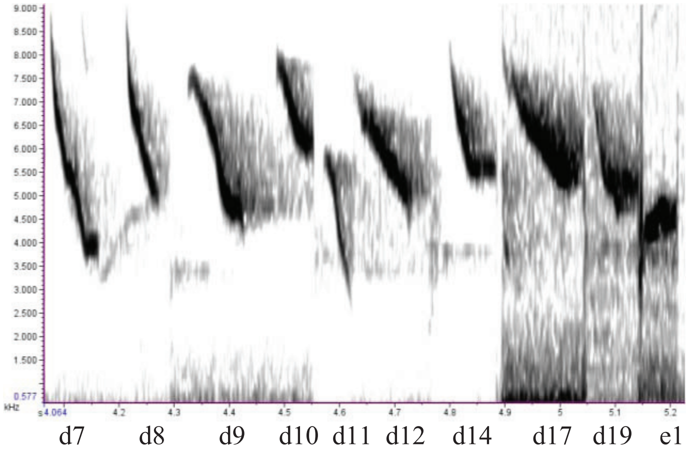
APPENDIX A: Catalogue of Elements Used.

Song elements





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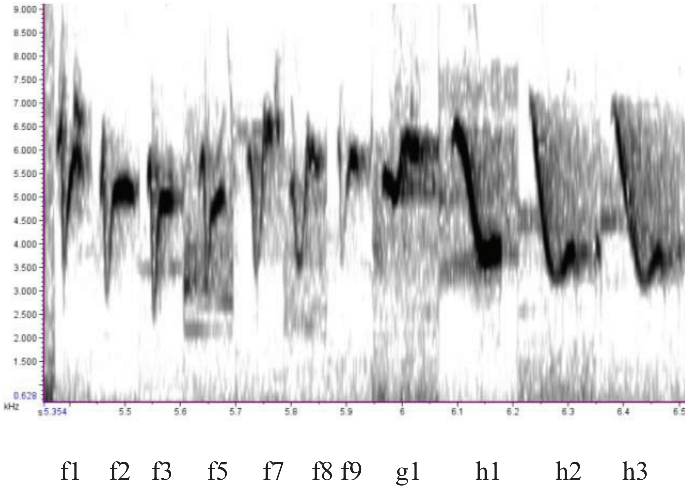
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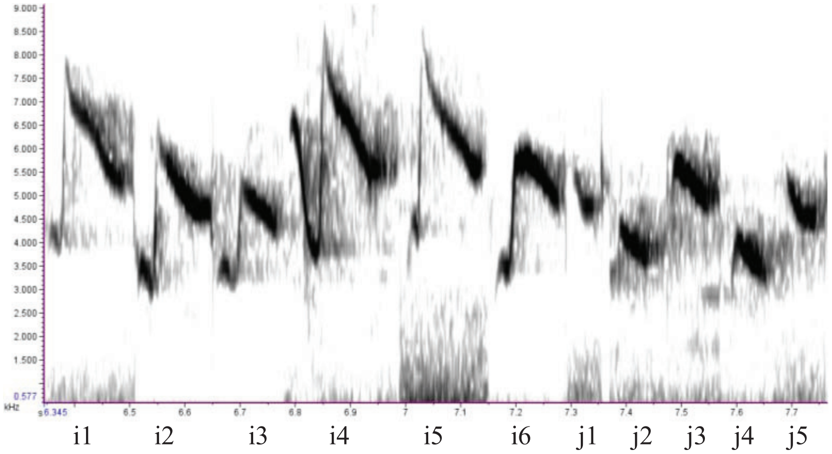
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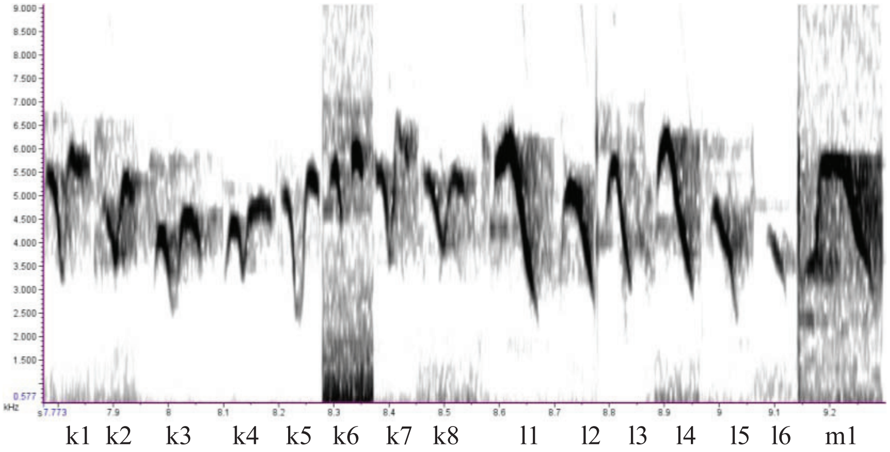
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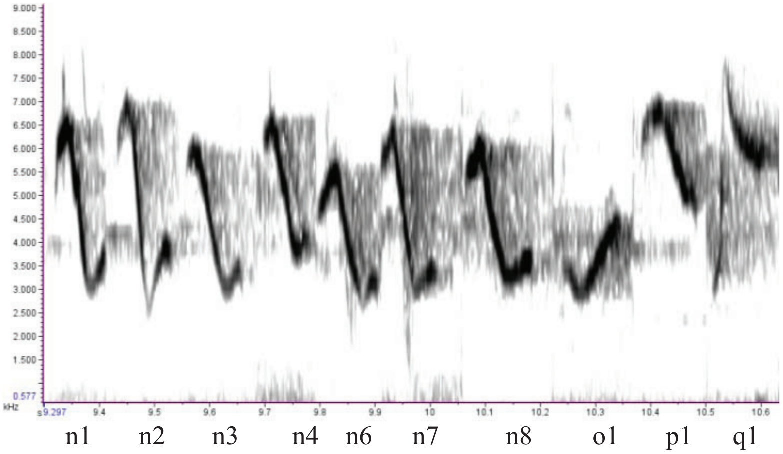
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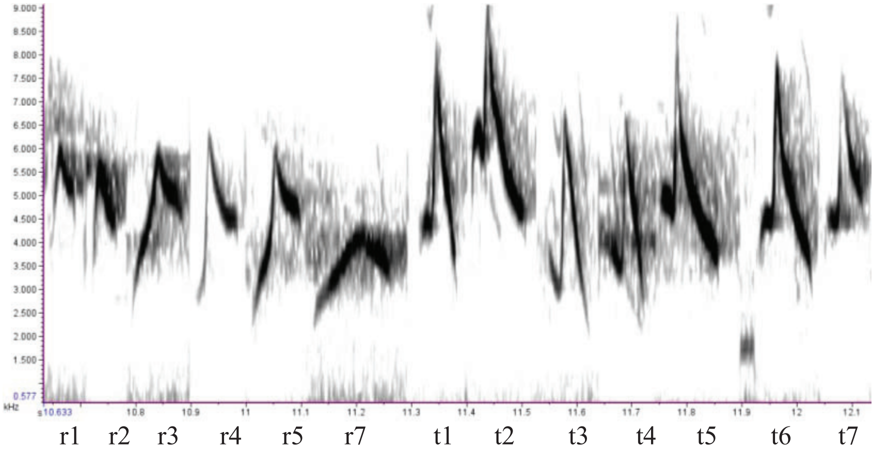
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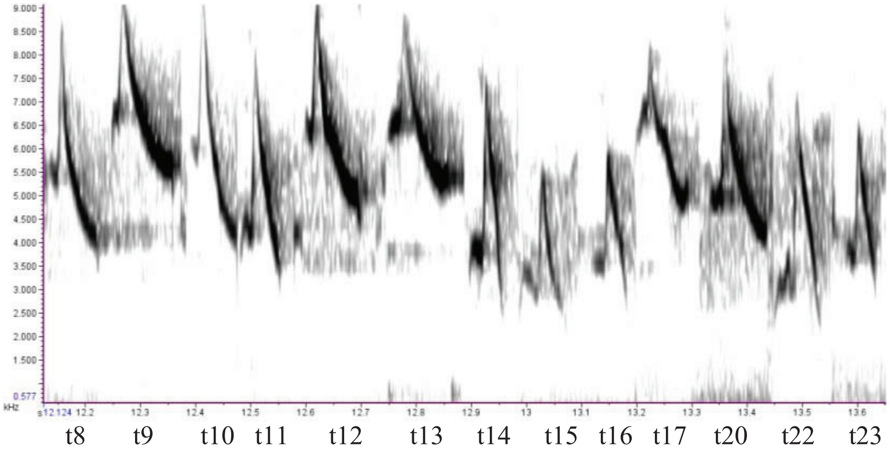
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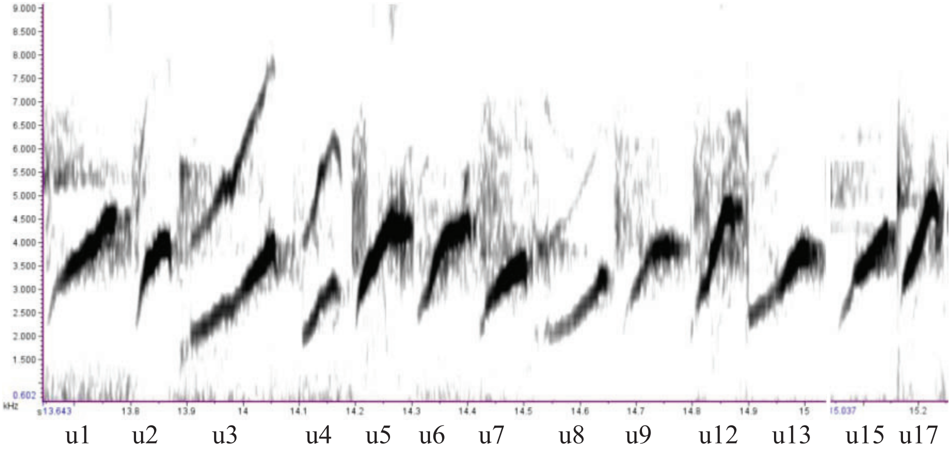
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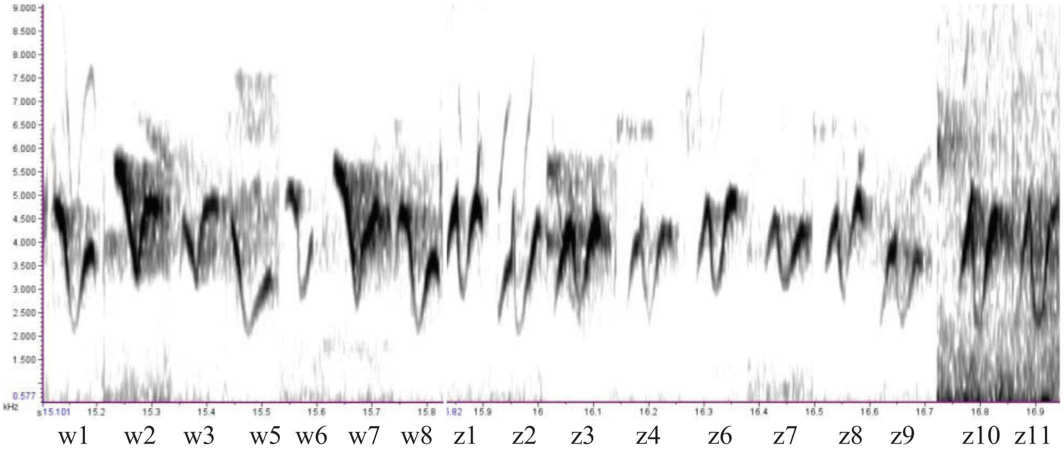
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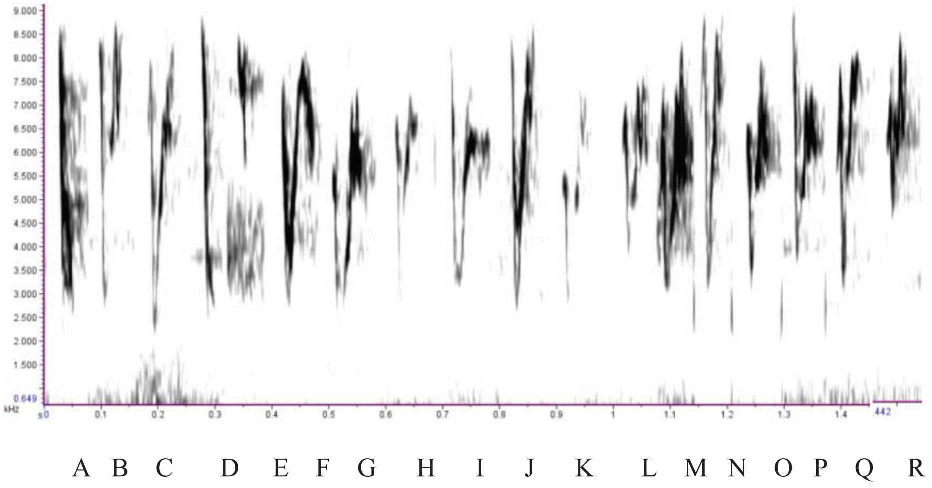
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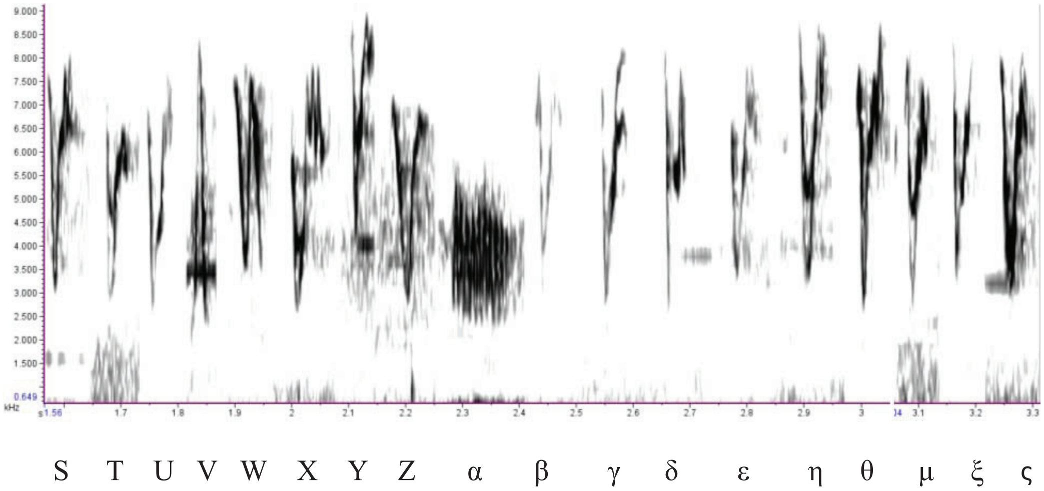
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APPENDIX B: List of Phrases Used.

Phrase	Number of notes	Note code[1]
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b1-d1-d17-u1	4	i-iv
b1-d1-i1-u1	4	i-iv
b1-i1-u1	3	i-iii
b1-i4	2	i-ii
b2-d11	2	i-ii
b2-d1-i3	3	i-iii
b2-i2-u1	3	i-iii
b2-i3	2	i-ii
d11-i6-u15-d3-c19	5	i-v
d19-m1	2	i-ii
d2-(r1/a5/c10/l3)-c1	3	i-iii
d4-d5-c5-u5	4	i-iv
d7-d8-c9-u7	4	i-iv
d8-c9-r7	3	i-iii
f1-z1-t1-u2	4	i-iv
f2-k4-t7-u2	4	i-iv
f3-z8-t14-a3	3	i-iii
f5-w1-t11-a2	4	i-iv
f7-f8-z4-t16-a8	5	i-v
f7-z8-t1-u2	4	i-iv
f9-j1-l6-e1-h2	5	i-v
g1-c22-j3	3	i-iii
h1-t12-c15	3	i-iii
h1-t2-c2	3	i-iii
h3-t10-c13	3	i-iii
k1-a1-r3	3	i-iii
k1-a1-u6	3	i-iii
k1-a1-u6-d1	4	i-iv
k1-z2-t3-u4	4	i-iv
k1-z3-t4-a4	4	i-iv
k2-a7-r5	3	i-iii
k2-a7-t3-u4	4	i-iv
k5-a11-r4	3	i-iii
k6-i5-c21	3	i-iii
k7-l5-o1	3	i-iii
k8-a1-u6	3	i-iii

Phrase	Number of notes	Note code[1]
l1-t5-c6	3	i-iii
l2-t5-c6	3	i-iii
n1-t12-c2	3	i-iii
n1-t2-c2	3	i-iii
n2-p1-c16	3	i-iii
n2-t13-c16	3	i-iii
n2-t17-u17	3	i-iii
n3-t20-c8	3	i-iii
n3-t8-c8	3	i-iii
n4-t13-c8	3	i-iii
n4-t2-c2	3	i-iii
n4-t9-c12	3	i-iii
n4-t9-c15	3	i-iii
n6-t5-c6	3	i-iii
n7	1	i
n8	1	i
u13-d14-r2-c25-k3	5	i-v
u3-d3-c3-c4	4	i-iv
u8-d9-d10-c11-u9-l4-i3	7	i-vii
w1-t6-c7	3	i-iii
w2-a9-j2	3	i-iii
w3-a12-j4	3	i-iii
w5-t22-a10	3	i-iii
w7-a14-j5	3	i-iii
w7-z3-t3	3	i-iii
w8-t6-c7	3	i-iii
z10-t6-c7	3	i-iii
z11-d6-d6	3	i-iii
z2-t3-d12-u1	4	i-iv
z2-t3-u4	3	i-iii
z6-t11-a2	3	i-iii
z7-t23-a14	3	i-iii
z9-t15-a10	3	i-iii
z9-t6-c7	3	i-iii

[1] Uniquely identifies each note when labelling partial phrases in a variant.

APPENDIX C: Summary Statistics for Repertoire Size and Song Sharing of Male Canada Warblers According to Pairing and Fledging Success in 2010 and 2011.

		Repertoire size		Song sharing			
	n	Phrases	Variants	Mean phrase	Maximum phrase	Mean variant	Maximum variant
2010							
Fledged	8	11.1 ± 2.7	47.5 ± 20.3	0.44 ± 0.05	0.90 ± 0.12	0.10 ± 0.03	0.52 ± 0.17
Failed	10	12.6 ± 1.8	56.9 ± 19.5	0.41 ± 0.09	0.81 ± 0.20	0.08 ± 0.04	0.33 ± 0.19
2011							
Fledged	24	12.3 ± 1.5	52.5 ± 23.5	0.42 ± 0.07	0.90 ± 0.13	0.05 ± 0.03	0.37 ± 0.17
Failed	6	12.2 ± 2.3	54.8 ± 23.9	0.38 ± 0.05	0.80 ± 0.06	0.04 ± 0.04	0.29 ± 0.20
2010							
Paired	20	12.1 ± 2.3	55.9 ± 22.2	0.42 ± 0.08	0.84 ± 0.17	0.08 ± 0.04	0.37 ± 0.21
Unpaired	1	14	97	0.44	0.87	0.09	0.53
2011							
Paired	30	12.3 ± 2.3	56.1 ± 26.8	0.40 ± 0.07	0.87 ± 0.16	0.05 ± 0.03	0.35 ± 0.18
Unpaired	2	11.0 ± 0.0	33.0 ± 31.1	0.36 ± 0.08	0.83 ± 0.00	0.02 ± 0.00	0.25 ± 0.30

APPENDIX D: Song Neighbourhood Assignment and Eigenvalues.

	2010			2011	
Bird	Eigenvalue	Cluster	Bird	Eigenvalue	Cluster
3	-0.3376	grey border	3	-0.2515	grey border
29	-0.3127	grey border	5	-0.1949	grey border[1]
38	-0.3221	grey border	7	-0.2249	grey border
40	-0.3408	grey border	10	-0.1961	grey border
53	-0.3815	grey border	12	-0.0821	grey border[1]
9	-0.3672	striped	25	-0.0004	grey border
11	-0.3653	striped	29	-0.3412	grey border
15	-0.3629	striped	40	-0.2364	grey border
1	0.0580	wide black border	48	-0.0502	grey border[1]
2	0.1657	wide black border	57	-0.0557	grey border
23	0.2029	wide black border	68	-0.1005	grey border[1]
27	0.2735	wide black border	74	-0.0965	grey border[1]
35	0.1110	wide black border	6	0.0191	thin black border
50	0.2830	wide black border	8	-0.0893	thin black border
59	0.3441	wide black border	13	-0.0823	thin black border
72	0.2888	wide black border	17	-0.0112	thin black border
76	0.3536	wide black border	20	-0.0969	thin black border
5	0.2497	dotted[1]	22	-0.1861	thin black border
12	0.2958	dotted[1]	26	-0.1651	thin black border
18	0.2931	dotted[1]	28	-0.0065	thin black border
48	0.1651	dotted[1]	30	-0.0797	thin black border
60	0.2498	dotted	32	0.1329	thin black border
68	0.2148	dotted[1]	37	-0.1493	thin black border
74	0.2264	dotted[1]	39	-0.0815	thin black border
6	0.1928	thin black border	41	-0.0737	thin black border
8	0.0447	thin black border	42	-0.1345	thin black border
13	0.0304	thin black border	46	-0.0437	thin black border
14	0.1943	thin black border	47	-0.2170	thin black border
16	0.1635	thin black border	56	-0.0856	thin black border
17	0.2012	thin black border	71	-0.1347	thin black border
26	0.0152	thin black border	75	0.0085	thin black border
31	0.1874	thin black border	1	0.0746	wide black border
37	-0.0178	thin black border	2	0.4833	wide black border
52	0.1772	thin black border	19	0.0216	wide black border
55	0.1268	thin black border	23	0.2494	wide black border
56	0.1277	thin black border	27	0.3606	wide black border
62	0.0410	thin black border	35	0.1830	wide black border
69	0.1598	thin black border	73	0.3620	wide black border
75	0.1958	thin black border	76	0.0959	wide black border
4	0.5451	dotted border	9	-0.3700	striped
49	0.5503	dotted border	11	-0.3590	striped
			15	-0.3664	striped
			34	0.3591	checked
			51	0.4912	checked
			61	0.6262	checked
			18	0.4384	grey shaded[1]
			33	0.4167	grey shaded
			63	0.4060	grey shaded
			4	0.5474	dotted border
			49	0.5480	dotted border

[1] Assigned to different clusters in 2010 and 2011.

APPENDIX E: Identity and Age of Territorial Male Canada Warblers Recorded in 2010 and 2011.

Bird ID	Band Combination	Study Plot	New/ Return 2010[1]	Age in 2010	New/ Return 2011[1]	Age in 2011
1	ABi-B	upper	R	ASY	R	ASY
2	A-BkP	upper	R	ASY	R	ASY
3	AG-W	upper	R	ASY	R	ASY
4	AGy-B	upper	N	ASY	R	ASY
5	A-GyGy	upper	N	ASY	R	ASY
6	AGy-PY	lower	N	SY	R	ASY
7	ALb-Bk	upper	N	SY	R	ASY
8	AP-WW	lower	R	ASY	R	ASY
9	A-PY	upper	N	SY	R	ASY
10	AR-B	upper	N	SY	R	ASY
11	AR-BkBk	upper	R	ASY	R	ASY
12	AR-RG	upper	R	ASY	R	ASY
13	AV-PP	lower	R	ASY	R	ASY
14	AW-RY	lower	N	SY	-	-
15	AW-VY	upper	R	ASY	R	ASY
16	AY-GP	lower	N	SY	-	-
17	BA-G	lower	R	ASY	R	ASY
18	BB-BA	upper	R	ASY	R	ASY
19	BGy-A	upper	-	-	N	ASY
20	BkA-WBk	lower	-	-	N	SY
22	BkB-VA	lower	N	SY	R	ASY
23	BkGy-A	upper	R	ASY	R	ASY
25	BkY-AW	upper	N	SY	R	ASY
26	BkY-OA	lower	N	SY	R	ASY
27	B-OA	upper	R	ASY	R	ASY
28	BR-WA	upper	-	-	N	ASY
29	BY-AG	upper	N	SY	R	ASY
30	G-ALb	lower	-	-	N	ASY
31	GA-OGy	lower	R	ASY	-	-
32	GA-Y	upper	N	SY	R	ASY
33	GBk-ABk	lower	-	-	N	SY
34	GO-WA	upper	N	SY	R	ASY
35	G-PA	upper	N	ASY	R	ASY
36	GW-AR	upper	R	ASY	R	ASY
37	GW-RA	lower	N	SY	R	ASY
38	Gy-ALb	upper	R	ASY	-	-

Bird ID	Band Combination	Study Plot	New/ Return 2010[1]	Age in 2010	New/ Return 2011[1]	Age in 2011
39	GyA-P	lower	-	-	N	ASY
40	GY-GA	upper	N	ASY	R	ASY
41	GyV-GyA	lower	-	-	N	SY
42	GyY-A	lower	-	-	N	ASY
45	Unbanded	upper	N	Unknown	-	-
46	LgA-Lb	upper	-	-	N	SY
47	OA-G	lower	-	-	N	ASY
48	OA-GP	upper	R	ASY	R	ASY
49	O-AGy	upper	R	ASY	R	ASY
50	O-AY	upper	R	ASY	-	-
51	OB-A	upper	-	-	N	SY
52	OGy-GA	lower	R	ASY	-	-
53	OW-BkA	upper	R	ASY	-	-
55	PBk-AW	lower	R	ASY	-	-
56	PO-A	lower	N	SY	R	ASY
57	PP-PA	upper	N	SY	R	ASY
59	PV-AP	upper	R	ASY	-	-
60	RA-GY	upper	N	ASY	-	-
61	RA-OY	upper	-	-	N	ASY
62	RBk-AR	lower	N	SY	-	-
63	RV-ABk	upper	N	SY	R	ASY
65	RY-VA	upper	N	ASY	-	-
68	VA-R	upper	R	ASY	R	ASY
69	VA-RGy	lower	N	SY	R	ASY
71	WA-WR	lower	N	SY	R	ASY
72	W-GyA	upper	R	ASY	-	-
73	WR-A	upper	-	-	N	SY
74	Y-AY	upper	R	ASY	R	ASY
75	YO-BkA	lower	R	ASY	R	ASY
76	YO-LgA	upper	R	ASY	R	ASY

[1] N (new): first year at site; R (return): at site in previous year; dash: male not present at site during that breeding season.