

THE BREEDING ECOLOGY OF THE CANADA WARBLER
IN CENTRAL NEW HAMPSHIRE

BY

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B.S. Biology, Plymouth State University, 2004

THESIS

Submitted to Plymouth State University

in Partial Fulfillment of

Master of Science

in

Biology

June, 2007

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ACKNOWLEDGEMENTS

I would like to thank Jim Chace for providing the methodology to map male territories. I would like to thank Erik Anderson, Phred Benham, Chris Bordonaro, Scott Betorney, Nic Dalzell, Keith Doran, Mo Goodnow, Kyle Parent, Clint Parish, and Amy Ueland for helping get 30's and collect vegetation data. I would also like to thank Kerry Yurewicz and Dan Lambert for serving on my thesis committee and providing helpful insights and comments on previous drafts. I would like to thank New England Institute for Landscape Ecology for funding over the length of the project. I would also like to thank Len Reitsma for everything he helped me with from countless hours in the field over the last four years, to dedicating many hours to read and comment on previous drafts, to allowing field crews to stay in the Gnome home during the field season, without Len this project would not have been possible.

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ABSTRACT

THE BREEDING ECOLOGY OF THE CANADA WARBLER IN CENTRAL NEW HAMPSHIRE

by

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The breeding bird communities associated with the southern regions of the North American boreal forest are among the richest and most diverse in North America (Hobson and Bayne 2000). Migratory species in the Northeastern United States comprise between 80% and 90% of the breeding birds, many of which are Neotropical or long distance migrants (Peters et al. 2005).

Birds are commonly the focus of population level studies. Many of these population studies focus upon habitat selection (Block et al. 1987) as it is one of the determining factors of avian distribution and abundance. However, geographic variations in habitat use within a single species may differ from region to region (Graves 2002). To date there is no published research that solely focuses on the habitat selection of the Canada warbler (*Wilsonia Canadensis* Lambert and Faccio 2005), despite the Northeastern

U.S. regional decline in the breeding population. The focus of this thesis is on habitat selection, reproductive success, return rates, and site fidelity of Canada warblers. This study also focuses on the differences of male Canada warbler territories, success rates, return rates, and site fidelity between a relatively mature red maple (*Acer rubrum*) swamp, and early successional forest directly north of the swamp.

This study was conducted on Canaan Town Forest and Bear Pond Natural Area in central New Hampshire (43.690, -72.0371). From 2003-2006, male territories were delineated using handheld Global Positioning Systems (GPS) between May 27 and July 10. Over 94% of territorial males were banded throughout the study (87 of 92). Pairing and fledging success was documented for each male. Vegetation characteristics were sampled both within male territories and non-territories. These vegetation characteristics were used to determine which habitat features best predict the presence of Canada warblers. Kullback-Leibler information and the Akaike information criterion (AIC) were used to evaluate the vegetation characteristics models, and AICc was used to correct for small sample sizes (Burnham and Anderson 2001).

Shrub density was the best predictor for the presence of Canada warblers. The total number of shrubs, the number of perch sites, canopy height, and the shrub density from 2-2.5m in height

was also a strong predictor of Canada warbler presence. The total number of shrubs did not differ between the red maple swamp and the early successional forest. The average territory size was smaller in the red maple swamp and larger in the early successional forest. The reproductive rates on the study plots were high in comparison to other Neotropical migratory warblers that breed throughout the eastern United States. After second year (ASY) males paired at higher rates than second year (SY) birds but there was no difference in the fledging rates. The return rates (50% - 49 of 98) were higher than both the American redstart (*Setophaga ruticilla*) and the black-throated blue warbler (*Dendroica caerulescens*) breeding in Hubbard Brook Experimental Forest, but similar to the hooded warbler (*Wilsonia citrina*) breeding in northwestern Pennsylvania.

The most important vegetative habitat characteristic for Canada warblers is the density of shrubs. The shrub density did not differ between a red maple swamp and an early successional forest created by forest management. Forest management practices create habitat that is ephemeral and may not sustain the high shrub stem densities Canada warblers prefer. The reproductive success also did not differ between the two habitat types. These results suggest that early successional stands create an understory that enables Canada warblers to breed successfully.

CHAPTER 1

INTRODUCTION

Determining the factors that are necessary for any animal population to persist and the factors that limit or regulate populations is difficult to quantify without having an in-depth knowledge of the organism of interest. Birds have long been the focus of population level research, not only because they occur throughout most habitats, but also because most are easy to detect. There are two main categories of birds throughout North America, resident and migratory. Migratory species in the Northeastern United States comprise between 80% and 90% of the breeding birds, many of which are Neotropical or long distance migrants (Peters et al. 2005).

An in-depth population study of marked individuals is arguably the best way to quantify changes in the population numbers and to assess demographic parameters, site fidelity, habitat requirements and the reproductive success of individuals. Population dynamics and the factors that regulate populations of long distance Neotropical migrants are not well known, despite their dominance during the breeding season in the Northeastern United States (Sherry and Holmes 1989). There are many factors that determine the number of individuals in any given population,

including both interspecific and intraspecific competition, climate, food availability (Sherry and Holmes 1995) and the amount of suitable habitat (Rotenberry et al. 1995). Habitat use, or the way a species uses habitats to meet its life history needs (Jones 2001), is one of the major focuses in bird ecology (Block et al. 1987). Habitat selection is a hierarchical process that results in a disproportionate use of habitats that increases survival and fitness of individuals (Jones 2001).

Habitat selection is one of the determining factors of avian distribution and abundance; however, geographic variations of habitat selection within a single species may differ from region to region (Graves 2002). For example, Collins (1983) found that forest dwelling birds in Maine were occupying habitats that were different from the same species in Minnesota. During the breeding season individual birds will occupy a particular territory within a broad zone of a particular habitat type (Wilson et al. 1998). Selection of territories may occur at different scales within the same habitat type, and this selection process likely includes such features as song perches, adequate substrate for foraging, and suitable nest sites. Jones and Robertson (2001) demonstrated that male cerulean warblers (*Dendroica cerulea*) try to defend multiple nest patches or nest sites within their territory to increase the likelihood of a female settling with them. Loegering and Anthony (2006)

indicated that both large (distances to human activity) and small (distance between ledge and rock overhang where the nest was located) spatial scales disproportionately influenced American dipper (*Cinclus mexicanus*) nest site selection. Territories serve multiple needs throughout the breeding season and thus the habitat selection decisions at different scales are important in the selection of a territory (Barg et al. 2006).

Habitat selection based upon suitable habitat is only one variable contributing to the presence or absence of individuals. Social cues such as conspecific attraction, settling in close proximity to other conspecifics, and assessing conspecific reproductive success (Doligez et al. 2002) may also influence the selection of a territory. For example, Ward and Schlossberg (2004) attracted an endangered Neotropical migrant, the black-capped vireo (*Vireo atricapilla*), into areas of suitable habitat using conspecific cues. Males that responded to the playback returned the following year despite the absence of the playback. Hahn and Silverman (2006) found using conspecific playbacks during arrival to the breeding grounds resulted in higher densities of American redstarts (*Setophaga ruticilla*) in those sites compared to control sites, although return rates were lower than expected the subsequent year.

Age of individuals also influences the suitability of the habitat within which an individual establishes a territory. Hunt (1996) indicated that older males predominated in habitats with high redstart densities, and because after-second-year (ASY) males are dominant over second-year (SY) males, older males dominated the better habitat. Age of an individual is also related to pairing and fledging success, because the SY birds are typically forced to settle in sub-optimal habitat. Zanette (2001) showed that younger more inexperienced eastern yellow robin (*Eopsaltria australis*) males were eight times more likely to occur in small fragmented forests than older more experienced males, in Australia. Bayne and Hobson (2001) found that young male ovenbirds (*Seiurus aurocapillus*) had a lower probability of attracting a mate than older males. There are also age effects in relation to reproductive success. Green (2001) found that reproductive performance increased with age for both male and female brown thornbills (*Acanthiza pusillia*) in Australia. Zanette (2001) found that older experienced male eastern yellow robins produced as much as seven and a half more fledglings on average than younger inexperienced males. Holmes et al. (1996) also found that older, more experienced black-throated blue warbler (*Dendroica caerulescens*) males produce more fledglings than young, inexperienced males. Sherry and Holmes (1995) suggest that the

higher habitat quality on older males' territories strongly affects the reproductive success of individual black-throated blue warblers, and that adequate food supply, sufficient cover and nest sites are the most important factors influencing habitat quality.

Turnover rates are yet another way to measure the quality of habitats. Many migratory passerines exhibit a high degree of breeding-site fidelity (Howlett and Stutchbury 2003, Holmes and Sherry 1989). Many factors influence site fidelity including surviving migration and the overwinter period, sex, age and the previous years breeding performance. For example, Howlett and Stutchbury (2003) documented that male hooded warblers (*Wilsonia citrina*) exhibit greater site fidelity than females, although females that returned to the breeding site tended to have higher nesting success the previous year than females that did not return. Holmes and Sherry (1989) showed that ASY American redstarts returned to breeding sites significantly more than SYs. In northern hardwood forests of New Hampshire, some species, for example, the black-throated blue warbler, there is no difference between ASY and SY return rates (Holmes and Sherry 1989).

The Canada warbler (*Wilsonia canadensis*) is a small (10-12g) sexually dimorphic warbler. Rappole (1983), using both museum and live specimens, found that the Canada warbler has five different plumages, including adult male basic (winter), adult

male alternate (breeding), adult female basic and alternate, male basic, and female basic. The Canada warbler (CAWA) is a Neotropical-Nearctic migrant that breeds from northern Georgia, along the Appalachian Mountain range into Northeastern, United States and throughout the majority of Canada. The CAWA overwinters throughout Northern South America as far South as Peru (see figure 1.1). The CAWA population has been declining at 2.7% year⁻¹ throughout its breeding range (Sauer 2004). They belong to the ground-nesting (Norton and Hannon 1997) and low shrub/ground foraging guild. It is also considered an early successional species in Maine (Hagan and Meehan 2002). In Michigan, CAWAs use relatively young, disturbed forests (Sodhi and Paszkowski 1995). Robbins et al. (1989) suggests that the minimum habitat area requirement for 50% occurrence probability for the CAWA is forests that are 400 ha. In Rhode Island, CAWAs were one of the most abundant species breeding in red maple (*Acer rubrum*) swamps, and the amount of upland forest within 1 km of red maple swamps was positively correlated with the abundance of CAWAs (Golet et al. 2001). Hagan and Meehan (2002) found that the amount of late-successional forest in a landscape was negatively correlated with the presence of CAWAs. In New Hampshire and Maine the CAWA occurs in early-successional

forest stands but they also occur within the deciduous under-story of mature forests during the breeding season (DeGraaf et al. 1998).

Few studies have been conducted on the CAWA at the population level. Working on the same population in central New Hampshire as this study, Ueland (2004) found that CAWA territories had significantly more shrubs (< 2.5 and > 2.5 cm diameter at breast height - dbh) than non-territory areas. A study on the same population indicated that paired CAWA males had significantly more shrubs (< 2.5 cm dbh), and snags (8-22.9 cm dbh) within their territory than unpaired males (Anderson 2005). In Vermont, Chace et al. (in manuscript) found that a lower average canopy height was also associated with CAWA as well a higher percent of ground cover which included shrubs. Other than the studies indicated above, no other population level studies have been published on the CAWA. There are many habitat variables that contribute to the selection of a territory, and for the CAWA the two above vegetation structure components to date have been found to be important, shrub density and canopy height (Anderson 2005, Ueland 2004). The focus of this thesis is to quantify other habitat variables that contribute to habitat selection. This thesis also assesses reproductive success, measures site fidelity and return rates of CAWAs utilizing two adjacent but distinct habitat types,

early successional upland forest selectively harvested in 1985 and a mature red maple swamp interspersed with mixed mature forest.

I hypothesized that habitat features, in addition to shrub density, such as the number of perch sites, and the density of the shrub stratum from 0-2.5m will affect territory selection. After second-year, more experienced males will have a higher shrub density and more perch sites within their territories than SY males. There would be a higher shrub density in the red maple swamp and older males will select the red maple swamp over the early successional forest. The pairing and fledging success would be higher within the red maple swamp compared to the early successional forest because of the predicted higher shrub densities and older more experienced males within the red maple swamp.

METHODS

Study Site

This study was conducted in central New Hampshire (43.690, -72.0371). In the Canaan Town Forest (81 ha, hereafter referred to as the lower plot) and the adjacent Bear Pond Natural Area (BPNA 416 ha, hereafter referred to as the upper plot) in Canaan (see figure 1.2). The lower plot (Canaan Town Forest and southern BPNA) is a red maple (*Acer rubrum*) swamp dominated by red maple, balsam fir (*Adies balsamea*), red spruce (*Picea rubens*) with interspersed mixed upland forest. The understory (2.5-7.99 cm dbh) is dominated by winterberry (*Ilex verticillata*), mountain holly (*Nemppanthos mucronatus*) and balsam fir (Ueland 2004), and the ground cover is comprised of mosses, ferns, grasses, and forbs (see Van de Poll 2006 for species list). The upper plot (all within BPNA) is a mixed deciduous upland forest, which was heavily harvested in 1985. The trees (>8.0 cm dbh) of the upper plot are now dominated by red maple, balsam fir, eastern hemlock (*Tsuga canadensis*), red spruce, and big-toothed aspen (*Populus grandidentata*). Balsam fir dominates the smallest size class of shrubs and saplings (<2.5cm dbh) on the upper plot followed by a cohort of *Ilex* and *Viburnum* spp., white birch (*Betulla papyrifera*), and red maple. The larger size class of shrubs and saplings (2.5 –

7.99 cm dbh) is mainly comprised of balsam fir, white birch, red maple and quaking aspen (*Populus tremuloides*). *Ilex* and *Viburnum* species were combined into one category for analyses because the species of the substrate seems to be less important to CAWAs than the overall stem density (Ueland 2004, and personal observation). The average ground cover for ferns, moss and grass are 20%, 14%, and 6% respectively (see Van de Poll 2006, for species list).

Field Methods

Male Territories

From 2003-2006, territorial males were captured using an audio playback, which was recorded on the study site with a tape player and a microphone. If a bird did not respond to another CAWA song, that individual was recorded and his song was used as a playback. A carved decoy was used in capture attempts in 2005 and 2006. All birds received a US Fish and Wildlife Service aluminum band and a unique color-band combination, which allowed for subsequent field identification of individuals. Over 94% of territorial males were banded throughout the study (66 of 71). Standard morphometric measurements were taken, including unflattened wing cord (mm), length of tarsus (mm), amount of subcutaneous fat (0-4 scale) and weight (g). The birds were aged

according to their plumage characteristics (Pyle et al. 1987, Rappole 1983). Male territories were mapped from May 27-July 10 each year. Every territorial male was observed for two 30-minute periods in each of three consecutive 15-day observation periods. Birds were not followed in consecutive days. During each observation period, the bird's location was recorded with a Garmin 72 or a Garmin 76 Global Positioning System (GPS) at five-minute intervals. This resulted in a total of six 30-minute observation bouts and 42 data points for each territorial male. If a bird was in the same location for longer than ten minutes, that location was entered twice. Precautions were taken not to alter birds' movements while observing. All observations were in the morning after sunrise, and the last 30-min observation sequences started no later than 0930. Males without a complete set of six 30-min observation bouts were not used in analyses. Pairing and fledging success was documented for each male within these observation bouts. A male was considered paired if one of the following was observed: a female was seen within the territory, a non-vocal female was seen within 10m of the male, a female chip note was heard in the presence of a singing male (Lambert and Hannon 2000), or an active nest was found within a territory (Bayne and Hobson 2001). Males singing from high perches throughout the breeding season and with no female seen or heard within the

territory were considered unpaired. A nest was considered fledged if at least one fledgling was seen (Howlett and Stutchbury 2003), or if males and females delivered food to multiple areas within the territory. Adaptive Kernel (ADK) was used to calculate the territory boundaries (95% ADK) and the “core” territory areas (50% ADK) of each individual (Barg et al. 2005). Territory boundaries and sizes were calculated using CALHOME home range analysis program (Kie et al. 1994). Territories were overlaid onto a digital aerial photograph using ESRI ArcMap 9.1 (www.esri.com) to plot territories.

Vegetation Sampling

Male territories were constructed using minimum convex polygons calculated by CALHOME (Kie et al. 1994), for compatibility with Ueland’s (2004) and Anderson’s (2005) data for future publication. Only males with the full set of six complete observation bouts were used in vegetation analyses. All vegetation characteristics were quantified using a modification of the Breeding-Bird [BBIRD] protocol (Martin and Conway 1994). Thirty-nine sets of vegetation plots, each set consisting of 4 subplots, were located within territories and are considered territory plots. Each subplot has an 11.3m radius and an area of 0.04 ha. The first circular vegetation plot within a territory was located in the center of the minimum convex polygon. The centers of the other three subplots

were placed in the direction of 0, 120, and 240 degrees from the original plot (see figure 1.3). The subplots were at least 30 m from the center of the first subplot. At least half of the subplot needed to fall within the territory boundary to be considered a territory plot. If a subplot fell outside of the territory it was shifted accordingly, with a minimum distance of 30m from the original subplot and with the additional criterion of containing at least two location data points from that territorial male from that breeding season. If a territory was too small to fit all four subplots, the maximum number of subplots was created given the size of the territory. Thirty-two sets of plots each containing four subplots, were located randomly and are considered non-territory vegetation plots. Non territory plots were generated using a random number generator to create coordinates. Those coordinates were then overlaid onto a map of the study site. Every 20th coordinate was placed on this map. If the selected coordinate fell outside of an existing territory it was considered the center of a non-territory vegetation plot and the three subplots were constructed as described above (see figure 1.4). Within each subplot the number of trees, identified to species, and snags (standing dead wood) in three different size classes were tallied (8-22.9, 23-37.9, >38cm dbh).

Average canopy height and the number of song perches were also quantified. A song perch tree was any tree that emerged

at least 3 m above the surrounding canopy, with a crown radius that was not overlapping (>5m radius) with the surrounding canopy .

These perch sites are presumed to provide high visibility and during singing maximize the distance at which a song may be heard by conspecifics. Within a five meter radius the number of small (<2.49 cm dbh and >1m in height) and large (>2.50 and <7.99cm dbh and >1m in height) size class shrubs and saplings were counted. The percent of moss, grass, and fern cover was estimated within a five-meter radius. Other ground cover characteristics were not quantified because they were not a significant variable predicting CAWA presences in two previous analyses performed with data from this site (Anderson 2005, Ueland 2004). The density of the shrub strata was quantified using a pole (2.5m long and 2.5cm diameter) marked at half meter intervals. Within each half-meter interval, the plant species and number of times its branch or leaf touched the pole was recorded. The pole was placed one meter from the center of the plot in each of the four cardinal directions. See Appendix 1 for a summary of the vegetation variables characterized. For analysis, all four subplots, for each territory or non-territory analog were averaged to best approximate the habitat in the area sampled.

Prey Abundance

An index of prey abundance was collected during two sample periods throughout the 2006 breeding season (5/31 – 6/18 and 6/27 – 7/10). Samples were collected using malaise traps, an index of the prey base for CAWAs because 70% of foraging maneuvers involve capturing arthropod prey while in flight (Sodhi and Pazkowski 1995, personal observation). A total of sixteen locations were sampled, eight territory (4 lower, 4 upper) and eight non-territory (4 lower, 4 upper). Each location was sampled once per sample period. Non-territory locations were created again using a random number generator. As with vegetation sampling plots, prey sample points were considered non-territory if the location did not fall within an existing territory. Malaise traps were set up in the morning after dawn between 0500-0700, and disassembled in the evening between 1800-2000, in order to avoid capturing nocturnal species because CAWAs do not forage at night. Samples were not collected on rainy days. Pest Stop® was used as the killing agent. After the sample was collected, the contents were preserved in 70% ethanol. The contents were emptied over a metal screen (2 x 2mm) to separate insects that were smaller than the mesh of the metal screen. Insects smaller than the mesh size are assumed not to be part of the CAWA diet.

All samples were identified using a dissecting scope. Individuals were identified to family.

The following three chapters describe different aspects of the breeding ecology of CAWAs reporting the results from the methods described above. The chapters address habitat selection and site fidelity, differences in habitat and reproductive success according to the age of individual males, and the differences in the breeding ecology between red maple swamps and early successional forest stands.

CHAPTER 2

HABITAT SELECTION AND SITE FIDELITY OF THE CANADA WARBLER IN CENTRAL NEW HAMPSHIRE

Introduction

In recent years, a major focus of bird ecology has been the analysis of habitat use. Within a species population individuals select parts of the environment that provide for certain life requirements during the breeding season and these selected habitats share some common characteristics (Block et al. 1987). Habitat selection is an important determinant of avian distribution and abundance. Within different habitat types, individual birds during the breeding season will select particular areas within a vegetative community type to establish their territories (Wilson et al. 1998). The selection of a territory occurs at different scales and combines the individual importance of site-specific factors including woodland or forest area and isolation, edge effects, social and demographic features of conspecifics, and stand structure and floristic composition (McCollin 1998). For example, Hunt (1996) found that American redstart (*Setophaga ruticilla*) densities were highest in early successional habitats and lowest in mature coniferous forests, indicating that early successional habitats are

more suitable for the American redstart based upon the assumption that higher quality habitats are occupied first. Jones and Robertson (2001) focused on structural differences between territory and non-territory habitat features of the cerulean warbler (*Dendroica cerulea*) and found that territories had higher mean basal areas, basal-area to stem ratios, foliage cover between 12-18 m, and maximum tree height. Peters et al. (2005) found that the number of vines and the presence of cane (*Arundinaria gigantea*) were the best predictors of presence or absence of the Swainson's warbler (*Limnothlypis swainsonii*) in South Carolina. These examples illustrate how birds use specific habitat features in selecting territory locations.

Many migratory passerines exhibit high breeding site fidelity, presumably for as long as they survive (Howlett and Stutchbury 2003). Returning to the same location to breed may decrease the need to seek out necessary habitat requirements such as nest sites. Holmes and Sherry (1989) found that 39% of black-throated blue warblers (*Dendroica caerulescens*) returned to the breeding site after the year of banding. They also found that 27% of American redstarts returned the breeding season following banding. Howlett and Stutchbury (2003) showed that 48% of hooded warblers (*Wilsonia citrina*) breeding in Pennsylvania returned the following year.

The Canada warbler (*Wilsonia canadensis*) is a small (10-12g) Neotropical-Nearctic migrant. In New Hampshire the Canada warbler (CAWA) occurs in early-successional forest stands but they also occur within the deciduous under-story of mature forests during the breeding season (DeGraaf et al. 1998). In the forests of the mid-Atlantic States, CAWAs occur in moist areas such as swamps and flood plains (Robbins et al. 1989). In Massachusetts, the CAWA is among the most abundant breeders in red maple swamps (Swift et al. 1984). In Maine, Hagan et al. (1997) found that the CAWA utilizes areas that have been clear-cut or partially harvested 6-20 years post harvest. Hagan and Meeghan (2002) found that CAWA presence was positively correlated with understory stem density.

The Breeding Bird Survey (BBS) indicates that the CAWA has been declining at 2.7% year⁻¹ throughout its breeding range; however, in New Hampshire the CAWA has been declining at 4.7% year⁻¹ since 1966 (Sauer et al. 2004). Despite the declines, little research has been conducted at the population level to determine habitat requirements for CAWAs. Ueland (2004) found that shrub stem densities in two size classes (<2.5 and >2.5 cm dbh) are higher within territories than non-territories. Chace et al. (in manuscript) found that a high percent of ground cover (which included shrubs) and a low canopy height was associated with

CAWA presence. Anderson (2005) found that successful males had higher small shrub stem (<2.5 cm dbh) densities than non-successful males. The purpose of this study is to determine the habitat requirements of the CAWA in New Hampshire and to determine the amount of site fidelity exhibited by the CAWA. The hypothesis is that CAWAs will select territories in areas with high shrub stem densities. Other factors such as lower canopy height, which may increase the visibility when an individual is singing, and higher shrub foliar density, to provide increased foraging substrate, will also affect the selection of territories.

Methods

Territories

Male territories were characterized and measured using the methods described in chapter 1. The same vegetation sampling technique was employed as described in chapter 1.

Site Fidelity

The average territory movements for individuals between years were calculated using ESRI ArcMap 9.1. For each returning male, the distance from the furthest point of the territory in each cardinal direction was measured to the corresponding point of the previous year's territory (see figure 2.1). This method was employed for both the territory (95% ADK) and the core area (50% ADK). All measurements were averaged to get the territory

movement from the previous year. If an individual had more than one core area, all possible combinations were measured and then averaged. There were no individuals that had multiple core areas in one year and only a single core area the next. If an individual had one core area one year and two core areas the next, the distance from the single core area to the two core areas was measured and then averaged.

Statistical Analyses

Male territories with a complete set of six, 30 min. observation bouts were used during analysis ($n = 92$). Mann Whitney U was used to analyze territory and core area sizes between the two age classes (ASY and SY). Territory size (Kolmogorov-Smirnov stat = 0.149 df = 90 $p = < 0.001$) and core area (Kolmogorov-Smirnov stat = 0.171 df = 90 $p < 0.001$) were not normally distributed. Mann Whitney U was used to analyze territory movements between years. All statistical analyses were conducted using SPSS 14.0.

An information-theoretic approach was used to construct models for the habitat selection analysis. The information-theoretic approach is based on the principle of parsimony, which suggests that the model variables, the structure and the number of variables should be as simple as possible (Burnham and Anderson 2001). Twelve variables that seem to be biologically relevant (personal

observations) for CAWAs were selected *a priori* for the analysis. Four variables were also selected based on the results of previous studies (Anderson 2005, Ueland 2004). The variables included the sum of all shrubs (sumshrub, >1m <7.99 cm dbh,), small size class shrubs (<2.5, >1m , < 2.5cm dbh), large size class shrubs (>2.5, >1m, 2.5-7.99cm dbh Anderson 2005, Ueland 2004), average canopy height (canhgt), sum of coniferous (conif) and deciduous (decid) trees, the small size class snags (smsnag, 8-23cm dbh, Anderson 2005, Chace et al. in manuscript), the sum of all snags (sumsnag), number of perch trees (perch), three ground cover types (fern, grass, moss Ueland 2004) and three shrub strata density measurements (shrubstrat 3, 1-1.5m, shrubstrat4, 1.5-2m, shrubstrat5, 2-2.5m). Binary logistic regressions were calculated with SPSS 14.0. Kullback-Leibler information and the Akaike information criterion (AIC) was used to evaluate the models, AICc was used to correct for small sample sizes (Burnham and Anderson 2001). The lowest AIC value indicates the model that best fits the empirical data; therefore the combination of variables included in the model with the lowest AIC value best predicts the presence or absence of CAWAs.

A two-way analysis of variance (ANOVA) was used to compare the prey abundance between territory and non-territory locations. ANOVA was also used to compare prey abundance

samples that were collected between 5/27-6/18 and 6/27-7/10 (early v late).

For all statistical tests $\alpha \leq 0.05$ was considered significant. The mean value is reported with the standard error, unless stated otherwise.

Results

Ninety-two male territories had a complete set of six, 30-min. observation bouts, 78 ASYs and 14 SYs over the 4 years (see figure 2.2). Over 94% (66 of 71) of the males were uniquely color banded to identify individuals in the field. The five unbanded individuals were surrounded by marked males making it possible to map their territories.

The average territory size (95% ADK) was 1.12, 0.70, 1.17, and 1.24 ha for 2003, 2004, 2005 and 2006, respectively (see table 2.1). There was no significant difference in territory size between years ($f = 1.71$ $df = 3$ $P = 0.17$). The average core area (50% ADK) was 0.25, 0.11, 0.19, and 0.24 ha for 2003, 2004, 2005, and 2006, respectively. In 2004 the core area was significantly smaller than 2003, 2005 and 2006 ($f = 2.82$ $df = 3$ $P = 0.044$).

Site Fidelity

The return rates for territorial males from 2003-2004, 2004-2005, 2005-2006, were 57.1%, 50.0% and 47.4%, respectively (see table 2.2). Birds continued to return to the same area to breed year

after year. The return rate for birds from 2003 to 2005 was 25% and 10% of birds banded in 2003 returned all three years.

The mean territory shifts for all males (2003-2004, 2004-2005, 2005-2006) were $27.55(\pm 5.43)$, $36.89 (\pm 11.15)$ and $31.14 (\pm 6.48)$ m, respectively (see table 2.3). There was no significant difference between years ($f = 0.29$ $df = 2$ $P = 0.75$).

Habitat selection

The high density of shrubs (>1m in height and <8.0cm dbh) was a strong predictor of CAWA presence ($\Delta AICc = 0.00$ see table 2.4). The model including high density of shrubs, low canopy height, a high shrub density in the vertical layer 2-2.5m, and number of perch trees within a territory was also a strong predictor of presence of CAWAs ($\Delta AICc = 0.04$). Together these models explain 75.4% of the variation. Models that were moderate predictors of CAWA presence were sum of shrubs, canopy height, number of perch sites ($\Delta AICc = 2.04$), shrubs greater and less than 2.5 cm dbh ($\Delta AICc=3.73$), shrubs greater and less than 2.5 cm dbh, number of perch sites, and canopy height ($\Delta AICc = 5.80$).

Prey Abundance

A total of 4799 individuals from 54 families were captured (see table 2.5). There was no significant difference in the amount of available prey between territories and randomly assigned non-territory locations ($F = 0.341$, $df = 1$ $P = 0.561$). There was also no

significant difference between the prey abundance early (5/31-6/18) and late (6/27-7/10) in the breeding season ($F = 0.361$, $df = 1$ $P = 0.549$).

Discussion

This study focused on the different habitat characteristics within territories and randomly assigned non-territory vegetation plots, as well as calculating the degree of site fidelity exhibited by CAWAs. The hypothesis was that CAWAs select territories with high shrub stem (>1m in height and <8.0cm dbh) densities based on the results of Ueland (2004) and Anderson (2005), and based upon birds of North America description of preferred habitat (Conway 1999). However, other factors including canopy height and vertical shrub density also influence the presence or absence of CAWAs. The degree of site fidelity (51.5%) is higher than other Neotropical-Nearctic migrants (hooded warbler: 48% Howlett and Stutchbury 2003, black-throated blue warbler: 39% Holmes and Sherry 1989, American redstart: 27% Holmes and Sherry 1989). The Canada warbler arrives later than most species to the breeding ground, and establishing territories must occur fast. Thus, returning to the same territory may decrease the amount of time searching for a new territory.

The results of the analyses of vegetation characteristics indicate that CAWAs are found in areas with high shrub densities,

which is consistent with Ueland (2004) and Anderson (2005), with a lower canopy (Chace et al. in manuscript) and higher numbers of perch sites than non-territory locations, and a denser shrub stratum between 2-2.5m above the ground. Perch sites were used by the CAWA as song perches when attempting to attract females and to establish territory boundaries. Perch sites were also an important habitat characteristic in the core area of the cerulean warbler in Ontario, Canada (Barg et al. 2006). A low canopy was also associated with the presence of the CAWA. This low canopy, which may be a result of the hydric soils (lower and upper plot) or successional age (upper plot), may facilitate high shrub densities due to higher sunlight exposure to the understory, as well as provide more emergent trees used as perch sites and display locations. Sodhi and Paszkowski (1995) found that male CAWA mean foraging height in early successional forests was 4.06 (\pm 0.25) m. Female mean foraging height was 3.07 (\pm 0.27) m. The high density of the shrub layer from 2-2.5m within territories provides ample substrate for foraging and cover (personal observation). Anderson (2005) found that successful males had more small snags (8-22.9 cm dbh) on territories than unsuccessful males; however the results of this study, with higher sample sizes indicate that small snags are not strongly associated with presence or absence of CAWAs.

Prey Abundance

This study indicates that the food availability was not different between territories and non-territories. The food availability characterized in this study accurately depicts the prey that CAWAs are utilizing because male CAWAs hawk or capture prey on the wing 70% of the time (Sodhi and Paszkowski 1995). Rodenhouse and Holmes (1992) indicated that food availability influences habitat quality and reproductive success in the black-throated blue warbler (*Dendroica caerulescans*). However, the food availability was not significantly different between territories and non-territories suggesting that the food availability is sufficient for fledging young but does not vary significantly between areas that are used by CAWAs and areas that are not.

Site Fidelity

Site fidelity of the CAWA has not previously been quantified. The results of this study indicate that male CAWAs (50% 49 of 98) exhibit strong site fidelity, higher than the American redstart, black-throated blue warbler, and similar to its congener the hooded warbler. If a CAWA does survive the non-breeding season it returns to within an average of 32 meters of its previous year's territory. This may significantly reduce the time spent looking for suitable

habitats and other characteristics within areas that are defended because the territories are so similar to previous years.

Future research should focus on the return rates, and site fidelity of females and how these influence reproductive success for both sexes. This work focused only on male CAWAs. Focused research on females will allow for a better understanding of the species as a whole.

CHAPTER 3

DOES AGE INFLUENCE TERRITORY SIZE, HABITAT SELECTED AND REPRODUCTIVE SUCCESS OF MALE CANADA WARBLERS IN CENTRAL NEW HAMPSHIRE

Introduction

Habitat features and/or food availability affect the quality of a territory, which in turn influences territory size, return rates, and reproductive success (Rodenhouse and Holmes 1992). The age of male great tits (*Parus major*) has been shown to affect laying date, the number of young fledged, and the number of fledglings that survived, although the age of the male did not affect clutch size (Perrins and McCleery 1985). For the pied flycatcher (*Ficedula hypoleuca*) a migratory passerine that breeds in northern Europe and northern Africa, age is correlated with laying date, clutch size and fledging success (Harvey et al. 1985). Nol and Smith (1987) found that older song sparrows (*Melospiza melodia*) began breeding earlier, and raised more young to independence than younger song sparrows. There is also an age effect on reproductive success in warblers. The age of ovenbirds (*Seriurus aurocapillus*) has been shown to correlate with habitat quality and positively affect pairing success of individuals. Older males acquire higher quality habitats and pair at higher rates than younger males (Bayne and Hobson 2001). Holmes et al. (1996) found that the black-

throated blue warbler (*Dendroica caerulescens*) in areas of high shrub density contained proportionally more older males which fledged significantly more young, and returned at higher rates than yearlings occupying areas with a more open shrub layer. These findings indicate that habitat variables and age may influence the breeding success and return rates of warblers. This study focuses on the Canada warbler (*Wilsonia canadensis*) a small (10-12g) Neotropical-Nearctic migrant. The Canada warbler breeds in areas with high shrub density like that typical of forested red maple (*Acer rubrum*) swamps (see results from chapter 2). In New Hampshire the Canada warbler occurs in early-successional forest stands, but they also occur within the deciduous under-story of mature forests during the breeding season (DeGraaf et al. 1998). The purpose of this study is to determine if differences exist in the habitat characteristics, breeding success, and territory sizes between after-second-year (ASY) and second-year (SY) males within the same breeding population.

Methods

The male territories were characterized and measured using the methods described in chapter 1. The same vegetative characteristics were measured using the method described in chapter 1. Chi-square analysis was used to compare pairing and fledging rates between ASY males and SY males.

Results

Over four years, (2003-2006) a total of 92 territories of 71 males were mapped with a complete set of six 30-min observation bouts (minimum of 42 location points per individual, see Methods) including 17 males mapped in two consecutive years and four males mapped in three consecutive years. Of the 92 male territories mapped over four years, 76 were held by ASYs (83%), 14 by SYs (15%), and 2 were held by individuals of unknown age (2%). These two were excluded from all analyses (see figure 3.1). Over 94% (66 of 71) of the males were uniquely color banded to identify individuals in the field.

The average territory size (95% ADK) of ASYs was 1.12, 0.67, 1.11, and 1.18 ha for 2003, 2004, 2005 and 2006, respectively. The average territory size of SYs was 1.16, 1.36, and 1.27 ha for 2004, 2005 and 2006, respectively (see table 3.1). There were no SYs that had a complete set of six, 30min. observation bouts in 2003. There was no significant difference in territory size between the two age classes, although the mean SY territory was larger in each year (Wilcoxon $W = 3351$ $Z = -1.191$ $P = 0.23$). The average core areas (50% ADK) for ASYs were 0.249, 0.107, 0.152, and 0.232 ha for 2003, 2004, 2005, and 2006, respectively. The average core areas for SYs were 0.150, 0.286, and 0.203 ha for 2004, 2005, and 2006, respectively. There was

no significant difference in the core area size between the two age classes (Wilcoxon $W = 3378$ $Z = -0.891$ $P = 0.373$).

Reproductive Success

There was a significant difference between the pairing success of ASYs and SYs. ASYs (97% 61 of 63) paired at significantly higher rates than SYs (63% 10 of 16; $\chi^2 = 16.52$ $df = 2$ $P < 0.001$, Table 3.2). However the proportion of individuals fledging at least one young did not significantly differ between the two age classes ($\chi^2 = 0.07$ $df = 2$ $P > 0.05$).

Habitat Characteristics

A total of 21 habitat characteristics were measured. Of the 21 characteristics, three variables were significantly different between the two age classes. ASYs had a significantly lower canopy height than SYs (Wilcoxon $W = 1491$, $Z = -2.13$, $P = 0.03$, see table 3.3). The density of the shrub layer from 0-0.5m and 0.5-1.0m was significantly lower on ASY territories than SY territories. (0-0.5m, Wilcoxon $W = 1452$, $Z = -2.27$, $P = 0.023$, 0.5-1.0m, Wilcoxon $W = 1464$, $Z = -2.06$, $P = 0.04$). ASYs had fewer deciduous trees of the small size class (8-22.9cm dbh) located within their territories than SYs but the difference was not significant (Wilcoxon $W = 1467.5$, $Z = -1.92$, $P = 0.055$).

Discussion

Many studies have shown that age correlates with fitness and that older birds occupy better habitat. ASY Canada warblers (CAWA) paired at significantly higher rates than SYs. This is consistent with other warbler species such as the black-throated blue warbler (Holmes et al. 1996), and ovenbird (Hobson and Bayne 2001). Although ASYs paired at higher rates than SYs there was no significant difference in the fledging rate, as measured by fledging one or more nestlings, suggesting that the limiting factor for SYs is females in the Canaan Town Forest and BPNA. ASY males may secure territories in habitats that females find more attractive, possibly, because ASY territories contain a higher number of nest sites. However, female selection of partners may also be influenced by phenotypic traits such as plumage or song repertoire.

The habitat characteristics differ between ASY and SY territories in some interesting ways. The shrub densities from 0-0.5m and 0.5-1m on SY territories were higher than on ASY territories. Holmes et al. (1996) found that higher shrub density was found on black-throated blue warbler ASY territories when compared to SY territories. The lower shrub density from 0-0.5m, and 0.5-1m on ASY territories may influence nest site selection; however, it likely does not add substrate for foraging. Sodhi and Paszowski (1995) found that the average foraging height of male

CAWAs was 4.06 (\pm 0.25) m and for females was 3.18 (\pm 0.27) m. Many of the nest sites were found in sphagnum moss hummocks, which seems to be a preferred nesting substrate (personal observation). The high shrub stratum densities between 0-0.5m and 0.5-1m within SY territories may prevent the formation of sphagnum hummocks, potentially decreasing the preferred substrate for CAWA nests within SY territories.

The average canopy height was significantly lower within ASY compared to SY territories, consistent with Chace et al. (In manuscript). The lower canopy height may increase the substrate for foraging. There was no significant difference in the number of perch sites between ASY and SY territories. The number of perch sites within the territories of the two age classes suggests that females may assess more than just a male's song, and that other plumage characteristics, such as length and fullness of a male's necklace, may be important when choosing a mate. Females may assess habitat quality located within an individual male's territory. Among the variables that were measured, only three were significantly different: canopy height, and shrub foliage densities between 0-0.5 and 0.5-1m; however, ASY males paired at significantly higher rates than SYs. Females may assess other habitat characteristics such as the number of suitable nest sites as well when determining the quality of the territory.

There was no significant difference in size of territories (95% ADK) or core areas (50% ADK) between ASYs and SYs. After-second-year males paired at significantly higher rates than SY males, however, no significant difference existed between ASYs and SYs in the rate of fledging at least one young which may indicate similar food resources in the territories of both age classes. Rodenhouse and Holmes (1992) found that habitat quality is reflected in greater food availability, which in turn positively influences reproductive success for black-throated blue warblers. But those SY CAWAs that did pair had similar success to ASYs post-pairing in this study, at least as measured by observing males with at least one fledgling.

Future studies should focus on the food availability between ASY and SY territories to quantify the food resource for both size classes, and characterize the return rates and site fidelity of SYs returning to breed in subsequent years. CAWA nests are difficult to find and this limited the measure of reproductive success. These analyses compared males who fledged at least one young to those who did not. With an average clutch size of greater than four, CAWA males are likely to have differences in clutch sizes, nestling growth rates, and the number of nestlings fledged. Of 18 nests found in 2005 (n=5) and 2006 (n=13) combined, 13 successfully fledged young and 5 failed. Nest predation was the cause of the

failures. Future studies should quantify the number of young per nest fledged by both age classes as best as possible to determine whether ASY males fledge more young per nest than SY males, as shown by many other studies (Perrins and McCleery 1985, Harvery et al. 1985, Nol and Smith 1987). On the other hand, if the food availability is similar throughout the study area, and if nesting substrate is not limiting, then females may be the single most limiting factor to a male's reproductive success. The study area appears to be of relatively high quality to CAWAs in that 80% of the males are ASYs, and the return rates, pairing (ASY: 97%, SY: 63%) and fledging (ASY: 70%, SY: 75%) rates are higher than in other Neotropical-Nearctic migratory warblers. Holmes et al. (1992) found that nest success for black-throated blue warblers was 63.3%. Future studies should compare ASY and SY reproductive performance in areas with different demographic ratios assuming that within population differences are likely to be more pronounced in more marginal habitat.

CHAPTER 4

DIFFERENCES IN THE BREEDING ECOLOGY OF CANADA WARBLERS IN EARLY SUCCESSIONAL FOREST STANDS COMPARED TO RED MAPLE SWAMPS

Introduction

The gradient of habitat quality among suitable habitats for species, especially avifauna in the Northeastern United States, has been the focus of many studies (Holmes et al. 1996, Rodenhouse and Holmes 1992). Various types of forest management are common throughout the Northeastern United States, including clear cuts, selective harvesting and strip cutting. These forest management strategies influence the bird community differently (Norton and Hannon 1997). Clear-cut harvesting is the most common practice of forest management in the White Mountain National Forest in New Hampshire (Costello et al. 2000). Forest management practices affect the habitat structure of the areas harvested and in turn this affects the species composition from pre- to post-harvest. Costello et al. (2000) found that clear-cutting provides habitat for a more diverse group of early successional species than group selection. Many early successional species in the Northeast are Neotropical migrant birds (NTMB). Migratory species in the Northeastern United States comprise

between 80% and 90% of the breeding birds, many of which are NTMBs or long distance migrants (Peters et al. 2005).

Habitat selection during the breeding season has been shown to affect the reproductive output of NTMBs such as the black-throated blue warbler (*Dendroica caerulescans* Holmes et al. 1996). The creation of areas suitable for early successional species, many of which are NTMBs, raises the question: How does early successional forest resulting from group selection or clear-cutting compare to areas of thick forest with high stem densities that occur naturally? In other words, can harvest regimes create potentially high quality breeding sites for NTMBs?

Reproductive success has been shown to affect the return rates of hooded warblers (*Wilsonia citrina*). Successful males returned at higher rates than unsuccessful males. Female hooded warblers had a tendency to return to the same breeding site after they were successful the previous year (Howlett and Stutchbury 2003). If forest management practices create suitable habitat for NTMBs, and if they are successful during the breeding season in these new habitats a new breeding population that returns to that site year after year may be established. If forest management establishes a new breeding population, then group selection and clearcut harvesting may be a suitable forestry practice that increases breeding habitats for many NTMBs and sustains breeding populations.

The Canada warbler (*Wilsonia canadensis*) is a small (10-12g) NTMB. The Canada warbler (CAWA) breeds throughout the Northeastern

United States and prefers areas with high shrub densities during the breeding season (see chapter 2). CAWAs arrive in New Hampshire prior to complete leaf out (personal observation) so species composition of the shrub layer may not play a role in where they establish territories; however, the density of shrub stems (<8.0 cm dbh) does. Current harvesting strategies such as group selection, harvesting a group of trees resulting in a gap of < 2 ha (Kilgo et al. 1999), and clear cutting create areas of high stem densities.

The purpose of the current study is to determine whether areas that are created by forest management are suitable areas for breeding CAWAs. This study focuses on age ratios, territory sizes, reproductive success, and return rates between an area that was selectively harvested in 1985 and a red maple swamp with a naturally dense understory. The objective is to determine whether the quality of habitat created by forest management can act as a surrogate for declining forested swamp habitat. This is especially important for this species given it is in a 4.7% annual decline in the Northeastern United States region (Sauer et al. 2004).

Methods

Male territories were characterized and measured using the methods described in chapter 1. The same vegetative characteristics were sampled using the methods described in chapter 1.

Return rates for 2004 (birds from 2003 returning in 2004), and 2005 (birds from 2004 returning in 2005) were not relevant on the upper plot

because the study was not expanded to the upper plot until 2005, and only 4 birds were banded on the upper plot prior to 2005. Only birds banded in 2005 on the upper plot were used during return rate analysis.

Results

Ninety-two male territories had a complete set of six, 30-min. observation bouts, 76 territories were held by ASYs (83%) and 14 held by SYs (15%) and 2 of unknown age (2%, not used in analyses) over the four years (see figure 4.1). Over 94% (66 of 71) of the males were uniquely color banded to identify individuals in the field. Fifty-seven percent of ASY males established territories on the lower plot, while 63% of SY males established territories on the upper plot but the difference was not statistically significant ($\chi^2=3.02$ df = 1 P > 0.05 see table 4.1).

A total of 14 habitat variables within established territories were measured to compare the two study plots. There were a total of seven habitat characteristics that were significantly different between the two plots (see table 4.2). The total number of shrubs within territories was not significantly different between the two study areas (Wilcoxon W = 1121, Z = -1.10, P = 0.27). However there were significantly more small size class (<2.5 cm dbh) deciduous shrubs on the lower plot (Wilcoxon W = 885.5, Z = -4.52, P < 0.001). There were significantly more deciduous (Wilcoxon W = 523, Z = -3.37, P = 0.001) and coniferous (Wilcoxon W = 534.5, Z = -3.20, P = 0.001) shrubs of the larger size class (>2.5>8.0cm dbh) on the upper plot. The density of the shrub layer between 1.5-2m (Wilcoxon W =

988.5, $Z = -2.84$, $P = 0.005$) and 2-2.5m (Wilcoxon $W = 992$, $Z = -2.80$, $P = 0.005$) was significantly greater on the lower plot compared to the upper plot. There were also significantly more coniferous trees in all size classes on the upper plot than on the lower plot (Wilcoxon $W = 959$, $Z = -3.44$, $P = 0.001$).

There were a total of 4799 individual insects collected from 54 families. The prey abundance was not significantly different between the two plots ($F = 0.773$, $df = 1$, $P = 0.381$, Lower: 23.97 ± 5.82 , Upper: 22.45 ± 6.39).

The territory (Kolmogorov-Smirnov stat = .156 $df = 92$ $p < 0.001$) and core area (Kolmogorov-Smirnov stat = 0.180 $df = 92$ $p < 0.001$) sizes were not normally distributed. Non-parametric Mann Whitney U tests were used to compare the territory and core area sizes between the two plots. The average territory (95%) size was significantly smaller on the lower plot compared to the upper plot (Wilcoxon $W = 1936$, $Z = -4.95$, $P < 0.001$). The average core area (50% ADK) was also significantly smaller on the lower plot than it was on the upper plot (Wilcoxon $W = 1943$, $Z = -4.89$, $P < 0.001$). ASY male territories (Wilcoxon $W = 1472$, $Z = -4.50$, $P < 0.001$) and core areas (Wilcoxon $W = 1503$, $Z = -4.16$, $P < 0.001$) were significantly smaller on the lower plot compared to the upper plot. The territory (Wilcoxon $W = 32$, $Z = -1.68$, $P = 0.093$) size of SYs did not differ between the two plots but the core area (Wilcoxon $W = 29$, $Z = -2.07$, $P =$

0.039) was significantly smaller on the lower plot compared to the upper plot.

There was no significant difference between the reproductive success (fledging at least one young) on the lower plot and the reproductive success on the upper plot (see table 4.3). There were higher rates of pairing on the upper plot but the difference was not significant ($\chi^2 = 3.52$, $df = 1$, $P > 0.05$). There was also no significant difference in fledging at least one young between the upper and the lower plot ($\chi^2 = 0.133$, $df = 1$, $P > 0.05$).

In 2006, return rates on the lower plot were not significantly different from the return rates on the upper plot ($\chi^2 = 0.38$ $df = 1$ $P > 0.05$ see table 4.4).

Discussion

The total number of shrubs was not significantly different between the two plots; however, the number of coniferous and deciduous stems was. This indicates that the species composition of the shrub layer plays a negligible role in CAWA habitat selection, and that harvesting can increase shrub stem densities in ways that attract CAWAs.

Ficken and Ficken (1966) suggest that older, more experienced males inhabit better areas and often force younger inexperienced males into suboptimal habitats where the probability of attracting a mate is reduced. The lower plot had a greater proportion of the total ASY males in the entire study (36 of 63), and the upper plot had a greater proportion of

SY males (10 of 16). However, male CAWAs on the upper plot (36 of 37) tended to pair at higher rates than males on the lower plot (47 of 55), indicating that creation of early successional stands establishes habitat features that are suitable for breeding CAWAs. The fledging rate on the two plots was not significantly different suggesting that the two plots provide ample resources for fledging young successfully. The average territory (95% ADK) and core area (50% ADK) size was smaller on the lower plot. Males on the lower plot may defend smaller territories because the shrub layer and sphagnum hummocks may increase the number of suitable nest site locations. There was no significant difference between ASY and SY territory or core area sizes (see chapter 3), indicating that the difference in the size of the territories between the two plots is due to the resource base. Kilgo (2005) found that arthropod abundance decreased in forest gaps created by group selection harvests and arthropod abundance increased within mature bottomland hardwood forest. However, there was no significant difference in the prey base between the upper and lower plot. This finding suggests that the smaller territories on the lower plot are because of other factors such as more available nest sites or social characteristics that influence conspecific interactions.

Holmes and Sherry (1989) suggest that site fidelity reflects habitat suitability, habitat variability and, competition. When competition becomes too great for better habitat, return rates and site fidelity may decrease because of dispersion. Males that are forced out of high quality habitats

may leave the study site to find areas where the intraspecific competition is less. The return rates are similar for both study plots suggesting that the successional stage of the upper plot contains suitable habitat for the CAWA. The return rates and site fidelity in the future may decrease as the forest matures and the shrub layer decreases. Hagan et al. (1997) found that CAWA abundance was highest from 6-20 years post harvest. DeGraaf (1985) found that abundance of CAWAs increases as the post harvest stand ages from 5-15 years.

Although early successional stands may not support suitable habitat for CAWA reproduction in perpetuity, forest management practices that create early successional stands increase the areas in which CAWAs can breed successfully for a number of years. Creation of areas with high shrub densities, ample song perches (see chapter 2), shorter canopies and thick shrub layers may increase the number of forest stands in which CAWAs are able to successfully breed. It is conceivable that this could be accomplished on an economically viable silvicultural rotation. The CAWA population has been declining at 2.7% per year and in New Hampshire at 4.7% annually since 1966 (Sauer et al. 2004). There are many silvicultural practices that are used in New Hampshire; however clear-cutting is most often used throughout the White Mountain National Forest (DeGraaf et al. 1998). To help promote areas that are conducive for CAWAs, silvicultural practices creating a dense understory and leaving residual trees for perch sites may enhance CAWA breeding within areas currently being clear-cut

and slow the decline in New Hampshire. If such practices can be implemented at the landscape scale so as to maintain early successional stands, then CAWA recruitment may increase within this Northeast region where the population is currently in notable decline.

CHAPTER 5

CONCLUSIONS

Selecting habitat for breeding territories involves many variables from the landscape level (Hagan and Meehan 2002) down to the number of nest sites (Jones and Robertson 2001) that are contained within the territory boundaries. There have been no studies to date that focus solely on the habitat selection of the Canada warbler, however there are a few habitat selection studies that include the Canada warbler (Hagan et al. 1997, Hagan and Meehan 2002, Robbins et al. 1989). There are no published population level studies on the Canada warbler (CAWA) that elucidate finer habitat selection characteristics to date. Ueland (2004) found that there were significantly more shrubs in the territories of male Canada warblers compared with non-territories. Anderson (2005), also working on the same breeding population found that paired males had significantly more small (<2.5 cm dbh) shrubs contained within their territories than males that did not pair. These studies elucidated an important habitat characteristic of the CAWA, but there are many habitat variables that contribute to habitat selection, as evidenced by the work of this thesis. The total number of shrubs (>1m and <8.0 cm dbh) was the best model predicting the presence of CAWAs. The total number of shrubs may increase the amount of cover for nest sites, enhance evasion of

predators and increase foraging substrate. Another model, which also predicted the presence of CAWAs, was the total number of shrubs, number of perch sites, lower canopy height, and a high shrub layer density at 2-2.5m. Barg et al. (2006) also found that the number of perch sites were ten times higher within the core area than non core areas in the territories of cerulean warblers (*Dendroica cerulea*). These perch sites are presumed to provide adequate visibility and maximize the distance at which a song may be heard by conspecifics. The lower canopy height may be a function of the hydric soils, which are widespread throughout the lower study plot. A lower canopy height may increase foraging substrate and may lead to or be correlated with the creation of perch sites. To date this is the most comprehensive study on the habitat selection of the CAWA. Further research is still needed to determine the habitat characteristics that influence nest site selection.

The age of individuals influences many factors during the breeding season, from territory selection (Holmes et al. 1996, Hunt 1996) to the number of young produced (De Forest and Gaston 1996, Perrins and McCleery 1985). Habitat characteristics and the rate of pairing differed between the two age classes of CAWAs. The average canopy height was significantly lower within ASY male territories compared with SY territories. Having a lower canopy height may increase the distance that an individual song may be heard from a perch site, because higher canopy density at the height of singing males may decrease the distance that a song may be

heard. The density of the shrub layer from 0-0.5m and 0.5-1.0m was significantly more dense within SY territories than ASY territories. The density of shrubs from 0-0.5m and 0.5-1m is not likely to affect the foraging substrate of male CAWAs. Sodhi and Paszowski (1995) found that male CAWAs forage at an average of 4.06 (\pm 0.25)m above the ground.

ASY males paired at significantly higher rates than SYs. This result is consistent with Green (2001, brown thornbill, *Acanthiza pusillia*), Holmes et al. (1996, black-throated blue warbler *Dendroica caerulescans*), and Bayne and Hobson (2001 ovenbirds *Seiurus aurocapillus*). A potential reason for the difference in pairing between the age classes could relate to habitat quality. Sherry and Holmes (1995) suggest that habitat quality strongly affects the reproductive success of individuals, and that adequate food supply, sufficient cover and nest sites are the most important factors influencing habitat quality. Zanette (2001) showed that younger more inexperienced males were eight times more likely to occur in small fragmented forests than older more experienced males. ASYs may force SYs into suboptimal habitats where the chances of finding a mate are reduced. Holmes and Sherry (1995) suggest that food availability influences habitat quality. The food availability on the territories of the two age classes was not a part of the scope of this thesis. The proportion of males fledging at least one young did not differ between the age classes and this suggests there are ample food resources within both ASY and SY

territories (but see Discussion Chapter 3). However, the number of young fledged per nest by each age class is not known, and ASY males may fledge more young per brood and have larger average clutch sizes than SYs.

There have been many studies that focus on the bird communities that are affected by forest management practices (Costello et al. 2000, Degraaf et al. 1998, Flaspohler et al. 2002, LaRue et al. 1995, Norton and Hannon 1997). There are far fewer studies that focus on one focal species and the effects of forest management practices (Lambert and Hannon 2000, Warkentin et al. 2003, Bayne and Hobson 2001). Timber harvesting in the Northeastern United States is an integral part of the regional economy, especially in the Northern New England states. In the White Mountain National Forest, clear-cutting is the most prevalent type of timber harvest, and so this industry has significant influence on landscape scale changes in habitat structure.

There were seven within-territory vegetation variables that differed between the harvested study site and the relatively mature red maple (*Acer rubrum*) swamp. The two study plots had a similar number of total shrubs, which was the strongest single habitat feature attracting CAWAs. This finding indicates that early successional stands create a shrub layer that supports suitable habitat for CAWAs. The vegetative characteristics that differed between the two plots indicate that the structure of the understory and shrub layer is what influences habitat selection of CAWAs

and not the species composition of the shrub layer or the trees. There was no difference in the pairing or fledging rates between the two study plots indicating that creation of early successional stands may benefit CAWAs. However, the average territory and core area size was smaller on the lower plot than the upper plot, suggesting that resources are more abundant on the lower plot and CAWAs need to defend smaller territories to meet their resource needs. Holmes and Sherry (1996) argue that age ratio and return rates may reflect habitat quality, and that birds return to areas of high habitat quality more often than areas of poor habitat quality. There were proportionally more ASYs on the lower plot and proportionally more SYs on the upper plot but the results were not significantly different. This may reflect the overall high quality of the habitat for CAWAs throughout the entire study area. A study involving the American redstart (*Setophaga ruticilla*) found that ASY densities were higher in areas of high habitat quality and SYs were forced into suboptimal habitats such as mature forest stands (Hunt 1996). The return rates between the upper and lower plot were not significantly different, suggesting that the habitat quality on the upper plot is similar to the habitat quality on the lower plot, despite territories being smaller on the lower plot. These findings suggest that creating early successional stands that have residual trees that can be used as perch sites may benefit the CAWA. Red maple swamps are the most common inland wetland type throughout the glaciated Northeastern United States and are an example of where the habitat

characteristics that CAWAs utilize occur in their natural state (Golet et al. 2001). However, red maple swamps have been heavily impacted by human activities including residential development, highway construction and other human land use practices, despite legal protection at the state and federal level (Golet et al. 2001). Increasing the protection of red maple swamps and creating areas of early successional forests with thick understories, especially if in close proximity to red maple swamps, may help reduce the rate of decline that the Canada warbler has been facing over the last forty years in New Hampshire.

LITERATURE CITED

- Anderson, Erik 2004., M.Ed. thesis, Plymouth State University, Plymouth NH 03264.
- Barg, J. J., D. M. Aiama, J. Jones, R. J. Robertson. 2006. Within-territory habitat use and microhabitat selection by male cerulean warblers (*Dendroica cerulea*). *Auk* 123(3):795-806.
- Barg, J. J., J. Jones, R. J., Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology* 74: 139-149.
- Bayne, E. M., and K. A. Hobson. 2001. Effects of habitat fragmentation on pairing success of ovenbirds: Importance of male age and floater behavior. *Auk* 118(2): 380-388.
- Block, W. M., K. A. With, M. L. Morrison. 1987. On measuring bird habitat: influence of observer variability and sample size. *Condor* 89(2): 241-251.
- Borror, D. J., R. E. White. 1970. A field guide to Insects America North of Mexico. Peterson Field Guide. Houghton Mifflin Company, Boston. New York.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28: 111-119.
- Chace, J. F., S. D. Faccio, A. Chacko, (In manuscript). Canada warbler habitat use in Vermont: Influence of forest community type, Canopy structure and understory density.
- Collins, S. L. 1983. Geographic variation in habitat structure for the wood warblers in Maine and Minnesota. *Oecologia* (Berlin) 59: 246-252.
- Conway, C. J. 1999. Canada Warbler (*Wilsonia canadensis*). In *The birds of North America*. No. 421. (A. Poole and F. Gill, eds.) The Birds of North America, Inc., Philadelphia, PA.
- Costello, C. A., M. Yamasaki, P. J. Perkins, W. B. Leak, C. D. Neefus. 2000. Songbird response to group selection harvest and clearcuts in a New Hampshire northern hardwood forest. *Forest Ecology and Management*. 127: 41-54.
- De Forest, L. N, and A. J. Gaston 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* 77(5): 1501-1511.

DeGraaf, Richard M. 1985. Breeding bird assemblages in New England northern hardwoods. Pp. 5-22 *in* The Impact of Timber Management Practices on Nongame Birds in Vermont, Conference Proceedings (R. J. Regan and D. E. Capen, eds.). Johnson State College, Johnson, VT.

DeGraaf, R. M., J. B. Hestbeck, M. Yamasaki. 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine. *Forest ecology and management* 103: 217-233.

Doligez, B., E. Danchin, J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. *Science* vol. 297 p. 1168-1170.

eNature Canada warbler (*Wilsonia canadensis*) www.enature.com

ESRI ArcMap 9.1 © 1995-2005 ESRI Inc. www.esri.com

Ficken, M., and R. W. Ficken. 1966. Notes on mate and habitat selection in the Yellow warbler. *Wilson Bulletin* 78: 232-233.

Flaspohler, D. J., C. J. Fisher Huckins, B. R. Bub, and P.J. Van Dusen. 2002. Temporal patterns in aquatic and avian communities following selective logging in the upper great lakes region. *Forest Science* 48(2): 339-349.

Graves, G. R, 2002 Habitat characteristics in the core breeding range of the swainson's warbler. *Wilson Bulletin* 114(2): 210-220.

Green, D. J. 2001. The influence of age on reproductive performance in the Brown Thornbill. *J. Avian Biol.* 32: 6-14.

Golet, F. C., Y. Wang, J. S. Merrow, and W. R. DeRagon. 2001 Relationship between habitat and landscape features and the avian community of red maple swamps in southern Rhode Island. *Wilson Bulletin* 113(2): 217-227.

Hagan, J. M., P. S. McKinley, A. L. Meehan, and S. L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* 61: 718-735.

Hagan, J. M., A. L. Meehan. 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. *Forest science* 48(2): 231-242.

Hahn, B. A., E. D. Silverman. 2006. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biol. Lett.* 2: 337-340.

Harvey, P. H., M. J. Stenning, B. Campbell. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (*Ficedula hypoleuca*). *Journal of Animal Ecology* 54(2): 391-398.

Hobson, K. A. and E. Bayne. 2000. Effects of forest fragmentation by agriculture on avian communities in the southern boreal mixedwoods of western Canada *The Wilson Bulletin* 112(3): 373-387.

Holmes R. T., P.P. Marra, and T. W. Sherry. 1996. Habitat specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): Implications for population dynamics. *Journal of Animal Ecology*. 65(2): 183-195.

Holmes, R. T. and T. W. Sherry. 1989. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation Manomet symposium 1989 Published in Ecology and conservation of neotropical migrant landbirds. Ed. Hagan III, J.M., D. W. Johnston, Smithsonian Institution Press.

Holmes, R. T., T.W. Sherry, P.P. Marra, K.E. Petit 1992. Multiple brooding and productivity of a neotropical migrant (*Dendroica caerulescens*) In an unfragmented temperate forest. *Auk*, 109(2): 321-333.

Howlett, J. S. and B. J. M. Stutchbury. 2003 Determinants of between-season site, territory, and mate fidelity in Hooded warblers (*Wilsonia citrina*). *Auk* 120(2): 457-465.

Hunt, P. 1996. Habitat selection by American redstarts along a successional gradient in Northern hardwoods forest: evaluation of habitat quality *Auk* 113(4): 875-888.

Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* 118(2): 557-562.

Jones, J., Robertson R. J. 2001. Territory and nest site selection of Cerulean warblers in Eastern Ontario. *Auk* 118(3): 727-735.

Kie, J. G., J. A. Baldwin, C. J. Evans. 1994. CALHOME Home range analysis program. United States Forest Service, Pacific Southwest Research Station. California Department of Fish and Game.

Kilgo, J. C. 2005. Harvest-related edge effects on prey availability and foraging of hooded warblers in a bottomland hardwood forest. *Condor* 107: 627-636.

Kilgo, J. C., Miller K. V, and Smith W. P., 1999. Effects of group selection timber harvest in bottomland hardwoods on fall migrant birds. *Journal of Field Ornithology* 70(3): 404-413.

Lambert, J. D. and S. Faccio. 2005. Canada warbler, population status, habitat use, and stewardship guidelines for northeastern forests. VINS technical report 05-4.

Lambert, J. D. and S. J. Hannon. 2000. Short term effects of timber harvest on abundance, territory characteristics, and pairing success of ovenbirds in riparian buffer strips. *Auk* 117(3): 687-689.

LaRue, P., L. Bélanger, and J. Huot. 1995. Riparian edge effects on boreal balsam fir bird communities. *Canadian Journal of Forest Research* 25: 555-566.

Loefering, J. P., and R. G. Anthony. 2006. Nest-site selection and productivity of american dippers in the Oregon coast range. *Wilson Journal of Ornithology* 118(3): 281-294.

Martin, T. E., and C. J. Conway. 1994. Breeding Bird (BBIRD) field protocol. Montana Cooperative Wildlife Research Unit. University of Montana, Missoula MT.

McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* 21: 247-260.

Nol, E. and J.N.M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology*. 56: 301-313.

Norton, M. R., and S. J. Hannon 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Can. J. For. Res.* 27: 44-53.

Perrins, C.M. and R. H. McCleery. 1985 The effect of age and pair bond on the breeding success of great tits *Parus major* *Ibis* 127(3): 306-315.

Peters, K. A., R. A. Lanica, J. A. Gerwin. 2005. Swainson's Warbler habitat selection in a managed bottomland hardwood forest. *Journal of Wildlife Management* 69(1): 409-417.

Pyle, P. 1997. Identification guide to North American birds, part I Columbidae to Ploceidae. Slate Creek Press. Bolinas California.

Rappole, J. H., 1983. Analysis of plumage variation in the Canada warbler. *Journal of Field Ornithology* 54(2): 152-159.

Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of Middle Atlantic States. *Wildl. Monogr.* 103: 1-34.

Rodenhouse, N. L., R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. *Ecology* 73(1): 357-372.

Rotenberry, J. T., R. J. Cooper, J. M. Wunderle, K.G. Smith. 1995. When and how are populations limited? The Roles of insect outbreaks, fire, and other natural perturbations. *Ecology and Management of Neotropical Migratory Birds, A synthesis and review of critical issues*. Ed. Martin T. E., D. M. Finch New York, Oxford University Press

Sauer, J. R., J. E. Hines, and J. Fallon. 2004. The North American Breeding Bird Survey, Results and Analysis 1966-2003. Version 2004.1. USGS Patuxent Wildlife Research Center, Laurel, MD.

Sherry, T. W., R. T. Holmes. 1989. Population fluctuations in a long-distance neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. *Manomet Symposium 1989*. Published in *Ecology and conservation of neotropical migrant landbirds*. Ed. Hagan III, J.M., D. W. Johnston, Smithsonian Institution Press.

Sherry, T. W. and R. T., Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? *Ecology and Management of Neotropical Migratory Birds, A synthesis and review of critical issues*. Ed. Martin T. E., D. M. Finch New York, Oxford University Press.

Sodhi, N. S., and C. A. Paszkowski. 1995. Habitat use and foraging behavior of four parulid warblers in a second growth forest. *Journal of Field Ornithology* 66(2): 227-288.

Swift, B. L., J. S. Larson, and R. M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. *Wilson Bulletin* 96:48-59.

Ueland, Amy. 2005. Habitat selection of Canada Warblers in a forested wetland in Canaan NH. M.Ed. thesis, Plymouth State University. Plymouth NH 03264.

Van de Poll, R. 2006. 2005 Final report on a partial natural resources inventory of the bear pond natural area. In *Natural Resource Inventory of the Bear Pond Natural Area 2003-2005*. Pg 8-38.

Ward, M. P. and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds *Conservation Biology* 18(2): 519-525.

Warkentin, I. G., A. L. Fisher, S. P. Flemming, and S. E. Roberts. 2003. Response to clear-cut logging by northern waterthrush. *Can. J. For. Res.* 33: 755-762.

Wilson, Jr. H. W., R. E. Zierzow, A. R. Savage. 1998. Habitat selection by peatland birds in central Maine bog: The effects of scale and year. *Journal of Field Ornithology* 69(4): 540-548.

Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *J. Avian Biol.* 32: 38-46.

APPENDIX

Appendix 1. List of vegetative habitat characteristics sampled within both territories and non-territory subplots.

Habitat Characteristics

11.3m Radius

Canopy Height (m)

Song Posts (0.04 ha)

Trees

Small (8-22.9cm dbh)

Medium (23-37.9 cm dbh)

Large (>38 cm dbh)

Snags

Small (8-22.9cm dbh)

Medium (23-37.9 cm dbh)

Large (>38 cm dbh)

5m Radius

Shrubs and Saplings (>1m <7.9m)

<2.5

>2.5

Ground Cover (%)

Moss

Fern

Grass

1 m Radius

Shrub Vertical Density

0-0.5m

0.5-1m

1-1.5m

1.5-2m

2-2.5m

FIGURES

Figure 1.1 The range map of the Canada warbler (*Wilsonia canadensis*), with breeding range indicated in red and overwintering in yellow (www.enature.com).



Figure 1.2. Aerial photograph, with topographic map overlaid, showing the study site. The Bear Pond Natural Area is 415 ha (Northwest section not shown) and the adjacent Canaan Town Forest is 36.5 ha. The privately owned property is currently under conservation easement. Bear Pond is in the middle of the study plot separating the upper and the lower plots. The area that appears gray is a quaking bog and serves as a habitat barrier between the populations on the upper and lower plots.



Figure 1.3. A male's territory created by a minimum convex polygon, with the territory vegetation subplots enclosed. The first subplot is located at the center of the male's territory, the subsequent subplots are constructed at 0, 120, and 240 degrees, and at least 30m away from the center of the first subplot. The red circles indicate the 11.3m radius in which the vegetation was sampled.

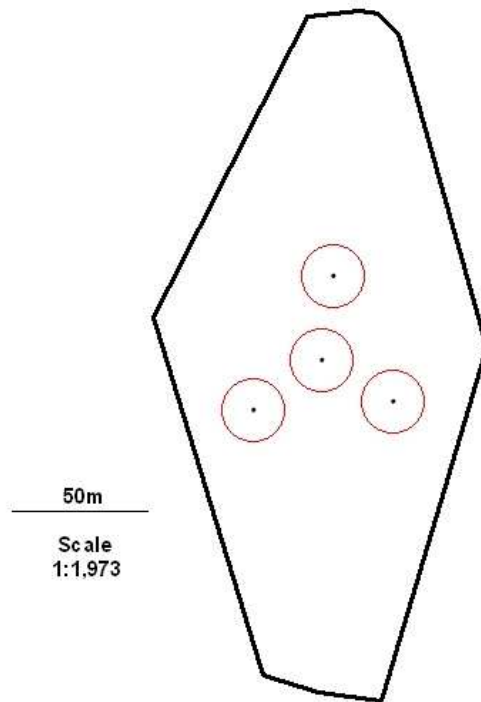


Figure 1.4. Aerial photograph of the study plot, overlaid by a topographic map showing territory (white dots n= 39) and non-territory (yellow triangles n = 37) vegetation plots.



Figure 2.1. Measuring the territory shift of a male's territory in 2005 (Red circles) to the same male's territory in 2006 (Blue triangles). The arrows represent where the measurement was taken and the value in meters. This method was also used to calculate the core area (indicated by smaller areas within the territory boundaries).

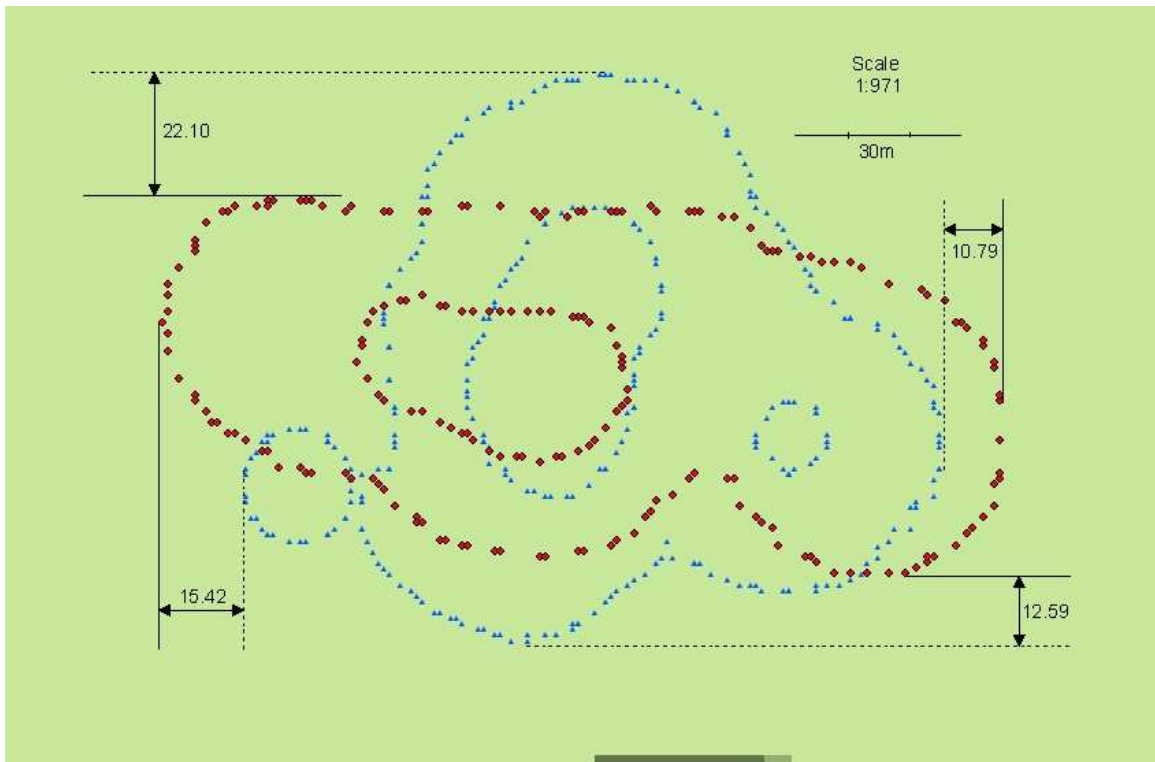


Figure 2.2. Map of the study plot in Canaan NH with male territories overlaid. Male territories in 2003 are indicated in red, 2004 in yellow, 2005 in blue and 2006 in white. Both territory (95% ADK) and core area (50% ADK) are shown for all individuals with a complete set of six, 30-min observation bouts (see Methods for details).

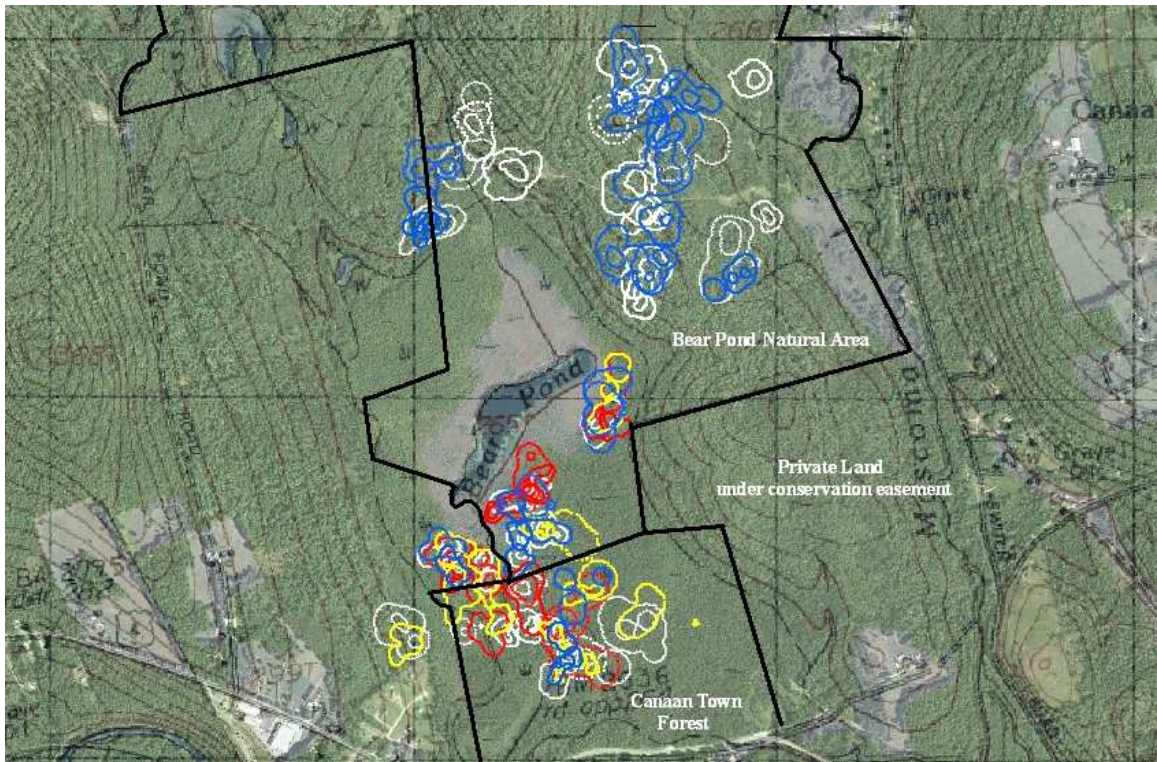


Figure 3.1. Canada warbler territories from 2003-2006, only males with a complete set of six, 30-min. observation bouts. After-second-year (ASY) males are shown in red, second-year (SY) male territories are shown in white.

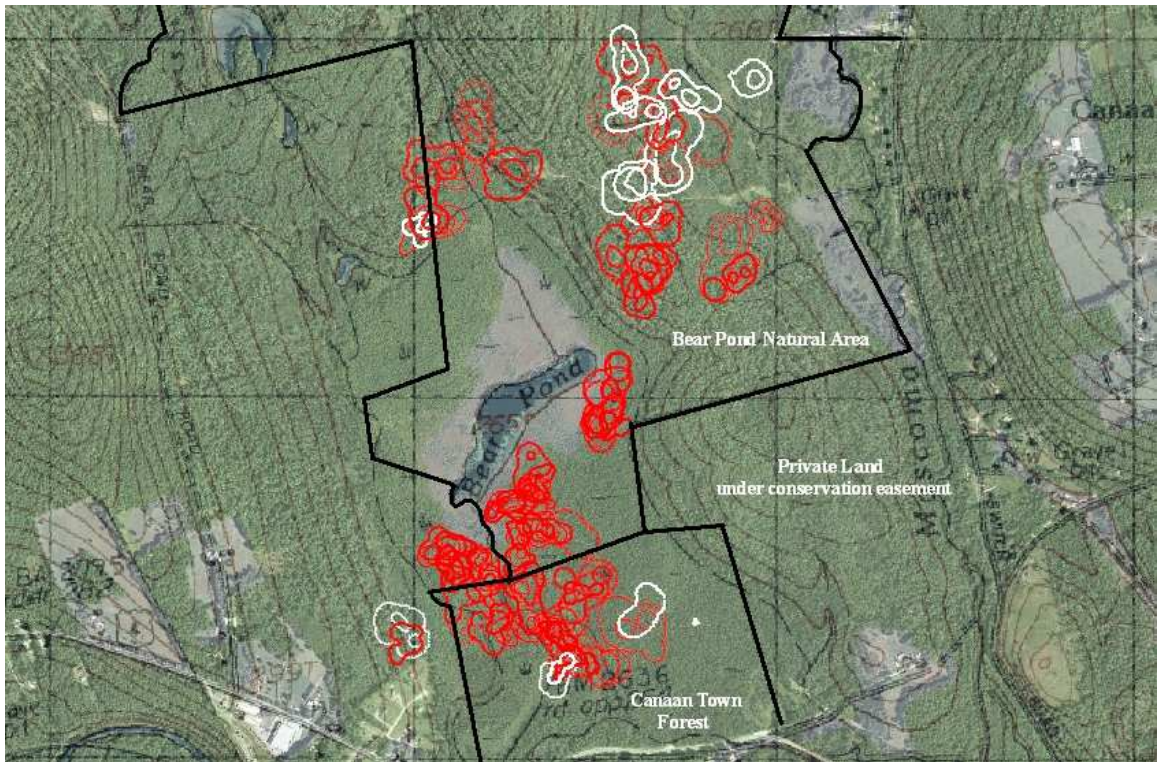


Figure 4.1 Canada warbler territories (95% ADK) and core areas (50% ADK). Only males that have a complete set of six, 30-min observation bouts. Males on the upper plot (BPNA) are shown in blue, male territories on the lower plot (Southern BPNA and CTF) are depicted in red.

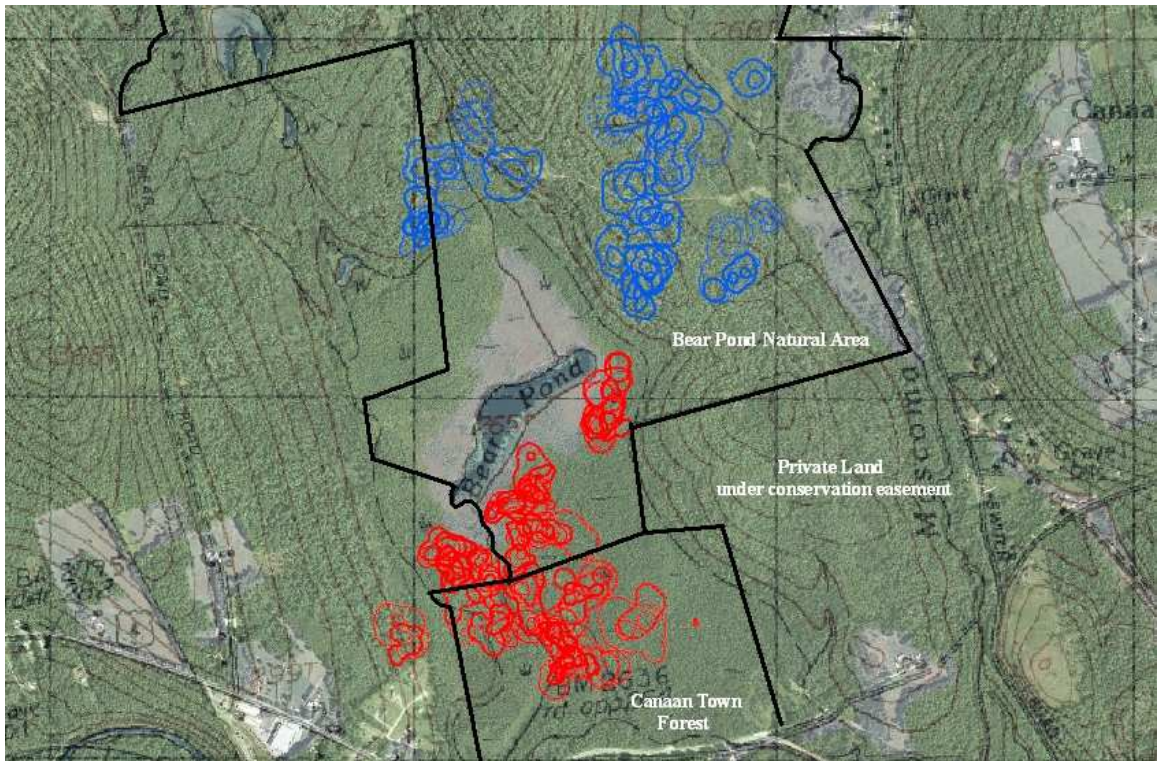


Table 2.1. The average territory (95% ADK) and Core Area (50%) sizes of male Canada warblers from 2003-2006. The territory and core areas are measured in hectares.

	2003	2004	2005	2006
Territory	1.12	0.70	1.17	1.24
Core Area	0.25	0.11	0.19	0.24

Table 2.2. The return rates for male Canada warblers from 2003-2006 in Central New Hampshire. The return rates are males that were banded or breeding in the previous breeding season and returned to the same plot the subsequent year.

Year	Return Rates
2003-2004	0.57 (12 of 21)
2004-2005	0.50 (10 of 20)
2005-2006	0.47 (27 of 57)

Table 2.3. The average territory (95% ADK) and core area (50% ADK) shifts of male Canada warblers in Central New Hampshire.

	2003-2004	2004-2005	2005-2006
Territory	27.55 m	36.89 m	48.43 m
Core Area	26.04 m	30.34 m	51.29 m

Table 2.4. The vegetative habitat characteristics were analysed using Kullback-Leibler information and the Akaike information criterion (AIC) was used to evaluate the models, AICc was used to correct for small sample sizes (Burnham and Anderson 2001). The lowest AIC value indicates the model that best fits the empirical data, therefore the combination of variables included in the model best predict the presence or absence of CAWAs. The model which best predicts the presence of Canada warblers is the sum of all shrubs (>1m <8.0cm dbh).). The variables included the sum of all shrubs (sumshrub, >1m <7.99 cm dbh,), small size class shrubs (<2.5, >1m , < 2.5cm dbh), large size class shrubs (>2.5, >1m, 2.5-7.99cm dbh), average canopy height (canhgt), sum of coniferous (conif) and deciduous (decid) trees, the small size class snags (smsnag, 8-23cm dbh, Anderson 2005), the sum of all snags (sumsnag), number of perch trees (perch), three ground cover types (fern, grass, moss) and three shrub strata density measurements (shrubstrat 3, 1-1.5m, shrubstrat4, 1.5-2m, shrubstrat5, 2-2.5m).

Model	AICc	ΔAICc	Wi	Log_e(L)	k
sumshrub	71.821	0.000	0.381	0	1
shrubstrat 5, perch, can hgt, sumshrub	71.859	0.038	0.374	-0.019	4
sumshrub, perch, canhgt	73.862	2.040	0.137	-1.020	3
<2.5,>2.5	75.551	3.729	0.059	-1.865	2
<2.5, >2.5, canhgt, perch	77.620	5.799	0.021	-2.899	4
perch, canhgt sumsnag, sumshrub	77.901	6.080	0.018	-3.040	4
smsnag, <2.5, >2.5	79.057	7.235	0.010	-3.618	3
fern, grass, moss, <2.5, >2.5	87.895	16.073	0.000	-8.037	5
conif, decid, shrubstrat3,shrubstrat4, shrubstrat5	97.358	25.536	0.000	-12.768	5
Global	104.303	32.481	0.000	-16.241	15

Table 2.5. The number of individual arthropods from each family for territory (Terr.) and non-territory (Non-Terr.) samples. There were 4799 individuals from 54 families. This table is continued on next page as well.

Order	Family/Genus	Common Name	Non-Terr.	Terr.	Total
Araneida	Araneida	Spiders	10	6	16
Coleoptera	Cantharidae	Soldier Beetle	2	3	5
Coleoptera	Cebrionidae	Cebrionid Beetle	0	1	1
Coleoptera	Coccinellidae	Ladybird Beetle	0	1	1
Coleoptera	Curculionidae	Snout Beetle	1	8	9
Coleoptera	Elateridae	Click Beetle	17	39	56
Coleoptera	Helodidae	Marsh Beetle	0	2	2
Coleoptera	Othniidae	False Tiger Beetle	0	1	1
Diptera	Acroceridae	Small Headed Fly	0	1	1
Diptera	Anisopodidae	Wood Gnat	2	3	5
Diptera	Anthomyridae	Anthomyzid Fly	0	4	4
Diptera	Asilidae	Robber Fly	2	2	4
Diptera	Bombyliidae	Bee Fly	0	10	10
Diptera	Chironomidae	Midge	0	2	2
Diptera	Chloropidae	Frit Fly	1	11	12
Diptera	Clusiidae	Clusiid Fly	3	1	4
Diptera	Conopidae	Thick-Headed Fly	15	23	38
Diptera	Culicidae / Aedes	Mosquitoes	78	94	172
Diptera	Curtonotidae	Curtonotid Fly	0	27	27
Diptera	Dolichopodidae	Long-Legged Fly	52	117	169
Diptera	Empididae	Dance Fly	8	1	9
Diptera	Heleomyzidae	Heleomyzid Fly	1	2	3
Diptera	Lauxaniidae	Lauxaniid Flies	89	311	400
Diptera	Muscidae / Fannia	Little House Fly	152	198	350
Diptera	Muscidae / Musca	House Fly	44	95	139
Diptera	Mycetophilidae	Fungus Gnat	472	488	960
Diptera	Otitidae	Picture-winged Fly	0	6	6
Diptera	Pipunculidae	Big Headed Fly	16	43	59
Diptera	Ptychopteridae	Phantom Crane Fly	4	1	5
Diptera	Rhagionidae	Snipe Fly	0	2	2
Diptera	Sciaridae	Dark-Winged Fungus Gnat	63	71	134
Diptera	Stratiomyidae / Ptecticus	Soldier Fly	0	0	0
Diptera	Syrphidae	Syrphid Fly	19	13	32
Diptera	Tabanidae	Deer Fly	11	23	34
Diptera	Tachinidae / Tachinid	Tachinid Fly	0	5	5
Diptera	Therevidae	Stiletto Fly	17	38	55
Diptera	Tipulidae	Crane Fly	16	29	45
Diptera	Unknown spp.		1	3	4
Diptera	Xylophagidae	Xylophagid Fly	0	1	1
Diptera	Xylophagidae / Xylophagus	Xylophagid Fly	0	2	2

Table 2.5 (Cont.)

Order	Family/Genus	Common Name	Non-Terr.	Terr.	Total
Epemeroptera	Epemeroptera spp.	Mayflies	1	0	1
Hemiptera	Pentatomidae	Stink Bug	10	1	11
Hymenoptera	Apidae	Bees	15	14	29
Hymenoptera	Apidae / Nomadini	Cuckoo Bee	4	1	5
Hymenoptera	Apidae / Xylocopinae	Small Carpenter Bee	69	52	121
Hymenoptera	Braconidae	Braconids	53	104	157
Hymenoptera	Cynipidae	Gall Wasp	11	16	27
Hymenoptera	Diapriidae	Diapriids	55	162	217
Hymenoptera	Eulophidae	Eulophids	1	61	62
Hymenoptera	Eurytomidae	Eurytomids or Seed Chalcids	10	13	23
Hymenoptera	Formicidae	Ants	57	54	111
Hymenoptera	Ichneumonidae / Cryptus	Ichneumons	60	33	93
Hymenoptera	Ichneumonidae / Dolichometus	Ichneumons	130	144	274
Hymenoptera	Ichneumonidae / Netelia	Ichneumons	124	216	340
Hymenoptera	Ichneumonidae / Ophion	Ichneumons	25	35	60
Hymenoptera	Pamphilidae	Web-spinning Sawfly	1	0	1
Hymenoptera	Sphecidae	Sphecid Wasp	18	27	45
Hymenoptera	Tenthredinidae / Tenthredo	Common Sawfly	17	30	47
Lepidoptera	Lepidoptera spp.		45	52	97
Plecoptera	Leuctridae	Rolled-Winged Stonefly	10	2	12
Plecoptera	Perlidae	Common Stonefly	129	173	302
TOTALS			1874	2868	4799
Ave./Sample			123.5	239	

Table 3.1 The average territory (95% ADK) and core area (50% ADK) of male Canada warblers. The values are expressed in hectares with the standard error in parenthesis.

	ASY	SY
Territory	1.07 (0.75)	1.3 (0.81)
Core area	0.19 (0.14)	0.23 (0.19)

Table 3.2 Pairing and fledging success of after-second-year (ASY) and second-year (SY) males.

	ASY	SY
Paired	97% (61 of 63)	63% (10 of 16)
Fledged	70% (43 of 61)	75% (6 of 8)

Table 3.3 The habitat characteristics that were sampled on territories of both after-second-year (ASY) males and second-year (SY) males. The mean value (\pm SE) is shown along with Mann Whitney U (MWU) and Wilcoxon W values. The Z value and P values are also shown (significant differences indicated by an asterisk).

Habitat Characteristic	ASY	SY	MWU(Wilcoxon W)	Z(P)
Canopy Height (m)	7.45 (0.26)	8.91 (0.56)	165(1491)	-2.130(0.033)*
Song Posts (0.04 ha)	1.92 (0.10)	2.06 (0.25)	269(1544)	-.555(0.579)
Sum Shrubs	45.20 (2.02)	44.55 (3.10)	291.5(1566.5)	-0.151(0.880)
Deciduous Shrubs (>1m)				
<2.5cm	30.46 (2.98)	22.17 (3.58)	247(313)	-0.331(0.741)
>2.5cm	6.20 (0.96)	5.39 (1.48)	252(318)	-0.238(0.815)
Coniferous Shrubs (>1m)				
<2.5	10.40 (1.09)	8.03 (1.12)	238(304)	-0.506(0.613)
>2.5	4.19 (0.33)	4.00 (0.61)	248.5(314.5)	-0.302(0.763)
Shrub Vertical Density				
0-0.5m	0.88 (0.20)	1.87 (0.48)	177(1452)	-2.269(0.023)*
0.5-1m	1.13 (0.29)	1.73 (0.50)	189(1464)	-2.057(0.040)*
1-1.5m	1.10 (0.21)	1.49 (0.33)	200(1475)	-1.793(0.073)
1.5-2m	0.91(0.13)	1.45 (0.28)	200(1475)	-1.793(0.073)
2-2.5m	0.94 (0.16)	1.71 (0.42)	206(1481)	-1.698(0.090)
Trees				
Sum all size classes				
Small (8-22.9cm DBH)	13.30 (0.82)	16.43 (2.08)	215(1490)	-1.515(0.130)
Medium (23-37.9 cm DBH)	2.34 (0.34)	2.64 (0.55)	254.5(1529.5)	-0.813(0.416)
Coniferous Trees				
Sum all size classes				
Small (8-22.9cm DBH)	6.69 (0.62)	7.33 (1.28)	266.5(1541.5)	-0.597(0.550)
Medium (23-37.9 cm DBH)	0.90 (0.14)	1.08 (0.25)	235(1510)	-1.165(0.244)
Deciduous Trees				
Sum all size classes				
Small (8-22.9cm DBH)	6.51 (0.57)	9.05 (1.24)	192.5(1467.5)	-1.916(0.055)
Medium (23-37.9 cm DBH)	1.32 (0.16)	1.56 (0.51)	295.5(373.5)	-0.80(0.936)
Snags				
Sum of all size classes	1.75 (0.22)	2.69 (0.86)	248(1523)	-0.929(0.353)
Small (8-22.9cm DBH)	1.59 (0.22)	2.48 (0.85)	253.5(1528.5)	-0.831(0.406)
Medium (23-37.9 cm DBH)	0.16 (0.04)	0.20 (0.09)	259.5(1534.5)	-0.845(0.398)

Table 4.1 Habitat Characteristics measured on the upper (BPNA) and Lower (Lower BPNA and CTF) plots. The mean value (\pm SE) is shown along with Mann Whitney U (MWU) and Wilcoxon W values. The Z value and P values are also shown (significance indicated with an asterisk).

Habitat Characteristic	Lower	Upper	MWU (Wilcoxon)	Z-Value (P)
Canopy Height (m)	7.97	8.02	401.5 (1142.5)	-0.79 (0.43)
Song Posts (0.04 ha)	2.02	1.88	406 (706)	-0.74 (0.46)
Sum Shrubs	44.45	26.26	380 (1121)	-1.10 (0.27)
Deciduous Shrubs (>1m)				
<2.5cm	31.87	16.41	144.5 (885.5)	-4.52 (<0.001)*
>2.5cm	3.04	7.48	223 (523)	-3.37 (0.001)*
Coniferous Shrubs (>1m)				
<2.5	3.76	4.08	420.5 (720.5)	-0.514 (0.61)
>2.5	5.78	11.82	234.5 (534.5)	-3.20 (0.001)*
Shrub Vertical Density				
0-0.5m	0.89	1.21	436.5 (1177.5)	0.01 (0.99)
0.5-1m	1.08	1.38	421 (697)	-0.25 (0.805)
1-1.5m	1.3	1.14	391 (1132)	-0.688 (0.49)
1.5-2m	1.53	0.73	247.5 (988.5)	-2.84 (0.005)*
2-2.5m	1.63	0.79	251 (992)	-2.80 (0.005)*

Table 4.2 The percent of after-second-year (ASY) and second-year (SY) males on upper (BPNA) and lower (Southern BPNA and CTF) plot.

	ASY	SY
Lower	57%	38%
Upper	43%	63%
	n=63	n=16

Table 4.3 The pairing and fledging success on the upper (BPNA) and lower (Southern BPNA and CTF) plot.

	Paired	Fledged
Lower	85% (47 of 55)	67% (36 of 54)
Upper	97% (36 of 37)	70% (26 of 37)

Table 4.4 The return rates of male Canada warblers on both plots, upper (BPNA) and lower (Southern BPNA and CTF).

Year	Return Rates	Lower	Upper
2003-2004	0.57 (12 of 21)	0.57 (12 of 21)	-
2004-2005	0.50 (10 of 20)	0.50 (10 of 20)	-
2005-2006	0.47 (27 of 57)	0.52 (13 of 25)	0.44 (14 of 32)

Table 4.5 the average territory shift for the upper and lower plots. Territory (95% ADK) and Core area (50% ADK) shifts are measured in meters.

		2003-2004	2004-2005	2005-2006
Territory	Lower	27.55 m	36.89 m	35.4 m
	Upper	-	-	61.45 m
Core area	Lower	26.04 m	30.34 m	33.49 m
	Upper	-	-	69.08 m