



# Canada warbler (*Wilsonia canadensis*) breeding ecology in young forest stands compared to a red maple (*Acer rubrum*) swamp

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## Abstract

Individuals within a species occur in different habitat types often with differences in reproductive output. The Canada warbler (*Wilsonia canadensis*) is an example of such a species as it occurs in several different types of forest habitats, including clear-cuts regenerating after timber harvest and stands of varying ages with dense subcanopy layers. We examined whether Canada warbler breeding ecology differed between a red maple (*Acer rubrum*) swamp with a thick, naturally-occurring understory and a 20-year-old partial cut with low retention. We mapped male territories on each plot in 2005 and 2006 to determine differences in habitat, territory size, site fidelity, and reproductive success. The results showed little difference in most vegetative characteristics. Overall stem density, number of song perches, and canopy height were similar for both plots. However, we observed differences in species composition, size class of shrubs and trees, and moss ground cover between the two forest types. We also found that individual males used 40–50% less area in the red maple swamp compared to the second-growth plot. These differences did not appear to influence site fidelity or the proportion of males fledging at least one young, measures that were relatively high on both plots. The results of this study are significant for Canada warbler conservation because they demonstrate that suitable habitats for the species can be created through specific harvest strategies. Such timber management strategies may help to reverse the significant decline the species has experienced over the past 40 years in the northeastern United States.

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## 1. Introduction

The gradient of breeding habitat suitable for a given bird species in the northeastern United States has been the focus of several studies (Rodenhouse and Holmes, 1992; Holmes et al., 1996; Hunt, 1996). Different individuals of the same species will utilize a variety of habitat types during the breeding season as long as the species' needs are met. Measuring reproductive performance within different habitats for a single species provides a better understanding of each habitat's bird conservation value. In the northeastern United States early-successional species will use naturally-occurring habitats, but also human-altered habitats such as those created by forest management practices (DeGraaf and Yamasaki, 2003). Clear-cuts, selective harvesting and strip cutting all influence bird

communities in different ways (Norton and Hannon, 1997). Costello et al. (2000) found that clear-cutting provides habitat for a more diverse group of early-successional species than group selection. Substantial changes in habitat structure result from clear-cutting, which removes all trees from an area at one time, and partial cutting with low retention, which retains up to 20% of the trees in a harvest area. These changes alter avian species composition, in turn. Clear-cuts and heavy partial cuts can benefit early-successional forest-dwelling species by providing suitable breeding habitat. However, they may cause declines in forest-interior birds because these species require large stands of intact forest (Robinson and Robinson, 1999; Harrison et al., 2005).

The type of habitat used during the breeding season by a particular species, or by specific individuals within populations, has been shown to affect the reproductive output of forest warblers, such as the black-throated blue warbler (*Dendroica caerulescens*, Holmes et al., 1996), and the American redstart (*Setophaga ruticilla*, Hunt, 1996). Forest management has the

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potential to simulate naturally-occurring forest with high stem densities. For disturbance-dependent species, more management strategies that approximate historical ranges of variation among habitat conditions need implementation (DeGraaf and Yamasaki, 2003). Creation of high-quality habitat could be a useful tool in managing for early to mid-successional bird species of conservation concern. Studies comparing reproductive success among managed and unmanaged habitats are needed to measure performance and to determine whether particular management strategies provide good breeding habitat.

Canada warblers (*Wilsonia canadensis*) breed throughout the northeastern United States in both natural and human-altered habitats (Webb et al., 1977), including forested wetlands (Golet et al., 2001), regenerating harvest zones (Hagan et al., 1997), and older forests in which high winds, ice storms, or insect outbreaks have disturbed the canopy (Hall, 1984; Faccio, 2003; Crawford and Jennings, 1989). Common features include high shrub density and emergent trees that serve as song perches (Kendeigh, 1945; Titterington et al., 1979; Hallworth unpublished data). Canada Warblers responded favorably to timber removal after 5+ years in several studies summarized by Lambert and Faccio (2005). However, all of these studies relied strictly on census results, which provide an incomplete, and potentially misleading index of habitat quality compared to measures of reproductive success (Van Horne, 1983; Vickery et al., 1992).

Canada warblers arrive in New Hampshire prior to complete leaf-out (Hallworth, personal observation), and are establishing territories based more on shrub stem (<8.0 cm dbh) density rather than species composition (Hagan and Meehan, 2002; Ueland, 2004; Anderson, 2005). Some harvesting strategies create large, dense, mixed deciduous/coniferous stands that are usable by Canada warblers. The species shows preference for such habitats for foraging and breeding and has been shown to occur there in greater abundances, especially if some trees remained unharvested serving as song perches (Titterington et al., 1979; Sodhi and Paszkowski, 1995; Hagan and Meehan, 2002). Although large early-successional stands may provide greater areas of suitable breeding habitat for this species, they have been documented responding to smaller disturbances such as canopy gaps created by natural disturbances, such as wind throw and ice storms (Faccio, 2003).

In New Hampshire, Canada warblers have declined by an average of 4.6% per year over the past 40 years (Sauer et al., 2005). Being a Neotropical–Nearctic migratory bird, the Canada warbler is susceptible to declines induced by changes in habitat throughout its life history, including its wintering grounds in South America and its breeding grounds in North America, as well as habitat used during migration between the two. The North American Bird Conservation Initiative has designated this species as a highest priority landbird in Conservation Region 14 (Atlantic Northern Forest) for both conservation and research (Therres, 1999; Dettmers, 2003; Rich et al., 2004; Lambert and Faccio, 2005), yet it has remained essentially unstudied at the population level. By measuring the reproductive success of marked individuals in

populations inhabiting both naturally dense forest stands and young stands following timber harvest, we can assess the viability of creating suitable habitat for the Canada warbler.

This study focused on age ratios, territory sizes, reproductive success, and return rates between an area that was intensively harvested in 1985 with 5–15% of trees (mostly red maple) left standing and an adjoining red maple swamp with a naturally dense understory. Both sites feature canopy trees emerging from a dominant, subcanopy layer. We compared reproductive success among marked male Canada warblers in these two habitat types to assess whether timber harvest practices may address the decline of the Canada warbler.

## 2. Methods

### 2.1. Study site

This study was conducted in 2005 and 2006 on the Canaan Town Forest (40 ha) and the Bear Pond Natural Area (BPNA) (363 ha) in Canaan, New Hampshire (43.667, –72.068, see Fig. 1). Canaan is >85% forested and the study area is within a forest-dominated landscape. A residential development bounds the southwest corner of the study area, but all other directions from the study area are contiguous forest. The red maple swamp (encompassing the Canaan Town Forest and southern BPNA) is an approximately 40 ha wetland dominated by red maple (*Acer rubrum*), balsam fir (*Abies balsamea*), and red spruce (*Picea rubens*), interspersed with small patches of mixed, deciduous/coniferous upland forest. The understory (2.5–7.99 cm dbh) is dominated by black alder (*Ilex verticillata*), large-leaved holly (*Ilex montana*) and balsam fir (Ueland, 2004), and the ground cover is comprised of mosses, ferns, grasses, and forbs with patchy areas of standing water (see Van de Poll, 2006 for species list). Several low-gradient drainages meander through

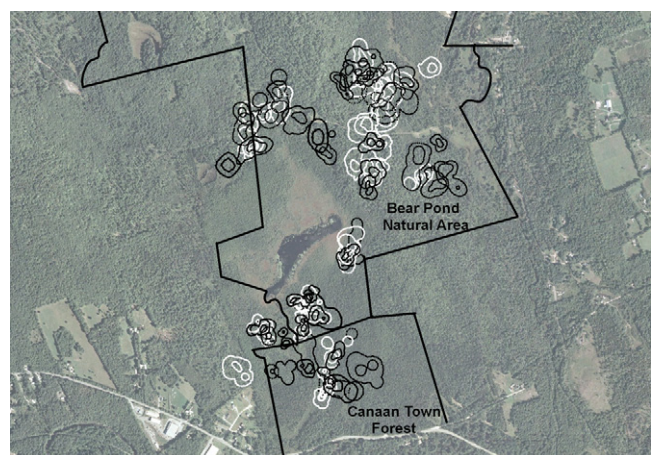


Fig. 1. Male Canada warbler territories on both Canaan Town Forest (red maple swamp, south of Bear Pond) and the Bear Pond Natural Area (second-growth plot, north of Bear Pond). Territories were mapped in 2005 and 2006 and each shows a core area and home range. Territories in black are from 2005 and territories in white are from 2006. Individuals did not occur in areas between and surrounding territories. The red maple swamp is mostly one contour ranging from 80 to 81 m elevation. The second-growth plot has slightly greater relief ranging from 81 to 89 m elevation.

this plot forming standing water throughout the breeding season. This plot has little topographic relief with predominantly hydric soils and high densities of hydrophilic plants.

The second-growth plot (all within BPNA) is a mixed deciduous/coniferous upland forest encompassing an area of approximately 43 ha with greater topographic relief. When it was intensively harvested in 1985, many residual trees (5–15% depending upon the area within the plot) of lower commercial value were left standing. The trees (>8.0 cm dbh) of the second-growth plot are predominantly red maple, balsam fir, eastern hemlock (*Tsuga canadensis*), red spruce, and big-toothed aspen (*Populus grandidentata*). This plot has a greater density of coniferous species within the subcanopy layers. Like in the red maple swamp, the ground cover is dominated by ferns and mosses with greater amounts of leaf litter and little to no standing water.

## 2.2. Field methods

### 2.2.1. Mapping territories and determining pairing status and reproductive success

For both years (2005 and 2006) territorial males were captured with the aid of an audio lure, aged (Rappole, 1983; Pyle, 1997), and color-banded. Male territories were mapped from 26 May to 10 July each year using handheld GPS (accuracy 3–10 m depending upon topography and stem densities) and recording locations at 5-min intervals. Each male was followed for six 30-min periods for a minimum of 42 location points. Location data were only used if males were positively identified by color combinations or all locations were within the territory boundaries of previous and subsequent 30 min observation periods. Pairing was determined if a female was repeatedly detected within a male's territory, and a male was considered reproductively successful if at least one fledgling was detected (Howlett and Stutchbury, 2003). Adaptive Kernel (ADK) was used to calculate the territory boundaries (95% ADK) and the core territory areas (50% ADK) of each individual with a complete set of six 30-min observation periods (Barg et al., 2005). Territory boundaries and sizes were calculated using CALHOME home range analysis program (Kie et al., 1994). The territory (Kolmogorov–Smirnov stat = 0.156, d.f. = 69,  $P < 0.001$ ) and core area (Kolmogorov–Smirnov stat = 0.180, d.f. = 69,  $P < 0.001$ ) 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.

### 2.2.2. Vegetation sampling

We used minimum convex polygons (MCP), calculated by CALHOME (Kie et al., 1994), to delineate male territories for the purposes of vegetation analysis. Of the 69 total males with complete sets of 30-min observations, a subset of 27 males in the red maple swamp and 20 males on the second-growth plot were randomly selected for vegetation measurements. Due to documented shifting of territory configurations and changes in territory sizes for returning males, each individual territorial male was treated as an independent sample. All vegetation

characteristics were quantified using a modification of the Breeding Biology Research and Monitoring (BBIRD) protocol (Martin and Conway, 1994). A total of 16 habitat variables within established territories were measured to compare the two plots (Table 1). Each territory had a set of four 11.3-m radius (0.04 ha) vegetation plots located within MCPs that encompassed all observation points within a territory. The first plot was placed at the polygon's center and peripheral plots were at bearings of 0, 120, and 240° 30 m from the center. If a plot contained fewer than two observation points or was more than 50% outside of the polygon, it was shifted the least distance possible, so that it: (a) did not overlap with another plot; (b) remained more than 50% within the polygon and (c) included the maximum number of observations of the territorial male possible.

The number of song perch trees in each plot was quantified. A song perch tree was any tree that emerged at least 3 m above the surrounding canopy and at least 5 m distance in all directions from other emergent trees. Mosses, grasses, and ferns were the only relevant ground cover categories quantified as determined by previous analyses (Anderson, 2005; Ueland, 2004). The density of the shrub strata was quantified using a pole (2.5 m long and 2.5 cm 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. For analysis, the four plots on each territory were averaged to best approximate the habitat in the area sampled.

### 2.2.3. Prey abundance

We used malaise traps to obtain an index of prey abundance on Canada warbler territories compared to non-territory locations during two sample periods (31 May–18 June and 27 June–10 July 2006). A total of eight locations were sampled, four in red maple swamp territories, and four in second-growth territories. Each location was sampled once per sample period. A single sample consisted of all arthropods captured in the malaise trap for an entire photoperiod (sunrise to sunset). Territory locations were generated using a random number generator. All sampling occurred during fair weather.

## 2.3. Data analysis

Mann–Whitney  $U$  was used to analyze differences in vegetation characteristics. Wilcoxon  $W$  was used to analyze the differences in territory sizes. Prey abundance was compared between the two plots using a two-factor ANOVA. Chi-square analyses were used to compare age ratios, pairing and fledging success, and return rates between the red maple swamp and the second-growth plot.

## 3. Results

Sixty-nine male territories had a complete set of six 30-min. observation bouts, 56 after second year (ASY) and 13-second year (SY) males, over the two years. Two additional males of

Table 1  
Habitat characteristics measured on the second-growth plot (BPNA) and the red maple swamp (lower BPNA and CTF)

Habitat characteristic	R.M. swamp	Second growth	MWU	Z-value (P)
Canopy height (m)	7.97 ( $\pm 1.87$ )	8.02 ( $\pm 1.88$ )	401.5	-0.79 (0.43)
Song posts (mean/0.04 ha) <sup>a</sup>	2.02 (0.89)	1.88 (1.07)	406	-0.74 (0.46)
Sum shrubs	44.45 (15.84)	26.26 (22.48)	380	-1.10 (0.27)
Deciduous shrubs (>1 m)				
<2.5 cm (mean/0.00785 ha) <sup>b</sup>	31.87 (11.32)	16.41 (9.27)	144.5	-4.52 (<0.001)*
>2.5 cm	3.04 (1.70)	7.48 (7.09)	223	-3.37 (0.001)*
Coniferous shrubs (>1 m)				
<2.5 cm (mean/0.00785 ha) <sup>b</sup>	3.76 (1.87)	4.08 (2.61)	420.5	-0.51 (0.61)
>2.5 cm	5.78 (4.82)	11.82 (7.52)	234.5	-3.20 (0.001)*
Coniferous trees				
Sum all size classes (stems/0.04 ha)	10.65 (4.66)	6.43 (3.45)	218	-3.44 (0.001)*
Coniferous 8–22.9 cm dbh	9.39 (4.99)	5.77 (3.29)	229	-3.28 (0.001)*
Coniferous 23–27.9 cm dbh	1.25 (2.43)	0.90 (0.85)	455.5	-0.007 (0.99)
Coniferous >38 cm dbh	0.01 (0.05)	0.06 (0.16)	426.5	-0.90 (0.37)
Deciduous trees				
Sum all size classes (stems/0.04 ha)	7.80 (5.34)	9.23 (3.70)	380	-1.10 (0.27)
Deciduous 8–22.9 cm dbh	6.97 (5.32)	7.20 (3.55)	390	-0.95 (0.34)
Deciduous 23–37.9 cm dbh	0.83 (1.19)	1.74 (1.26)	212.5	-3.53 (0.001)*
Deciduous >38 cm dbh	0.45 (0.16)	0.02 (0.07)	440.5	-0.53 (0.60)
Snags				
Sum all size classes (stems/0.04 ha)	2.15 (2.02)	1.57 (1.42)	384.5	-1.04 (0.30)
Snags 8–22.9 cm dbh	1.98 (1.95)	1.38 (1.33)	376.5	-1.15 (0.25)
Snags 23–27.9 cm dbh	0.15 (0.28)	0.18 (0.29)	413.5	-0.72 (0.47)
Snags >38 cm dbh	0.02 (0.07)	0.00 (0.02)	429	-1.05 (0.29)
Shrub foliar density (1 m radius)				
0–0.5 m (touches/interval)	0.89 (0.19)	1.21 (0.18)	436.5	0.01 (0.99)
0.5–1 m	1.08 (0.05)	1.38 (0.37)	421	-0.25 (0.805)
1–1.5 m	1.30 (0.45)	1.14 (0.55)	391	-0.69 (0.49)
1.5–2 m	1.53 (0.96)	0.73 (0.30)	247.5	-2.84 (0.005)*
2–2.5 m	1.63 (0.72)	0.79 (0.20)	251	-2.80 (0.005)*
Ground cover (%/0.00785 ha)				
Fern	19.47 (19.01)	19.60 (21.30)	5592	-1.74 (0.08)
Grass	7.71 (14.56)	6.53 (10.16)	6407.5	-0.12 (0.90)
Moss	21.08 (25.54)	12.41 (20.70)	2317.5	-8.21 (<0.001)*

The mean value ( $\pm$ S.E.) is shown along with Mann–Whitney *U* (MWU), *Z* value and *P* values. Significant values are indicated with an asterisk.

<sup>a</sup> Area of 11.3 m radius.

<sup>b</sup> Area of 5 m radius.

unknown age had complete sets, but were not used for age comparisons. Over 91% (63 of 69) of the males were uniquely color-banded to identify individuals in the field. Eighty-five percent of male territory-holders in the red maple swamp were ASY, whereas 78% on the second-growth plot were ASYs. This difference was not statistically significant ( $\chi^2 = 1.09$ , d.f. = 1,  $P > 0.05$ ).

We found no significant difference between the reproductive performance of males in the red maple swamp compared to the second-growth plot. There were higher rates of pairing on the second-growth plot (36 of 37 males) compared to the red maple swamp (28 of 32 males), but the difference was not significant ( $\chi^2 = 2.45$ , d.f. = 1,  $P > 0.05$ ). There was also no significant difference in fledging at least one young between the second-growth plot (26 of 36 males) and the red maple swamp (21 of 28 males,  $\chi^2 = 0.17$ , d.f. = 1,  $P > 0.05$ ). In 2006, the return rate of 44% on the second-growth plot was not significantly different

from the return rate of 52% in the red maple swamp ( $\chi^2 = 0.38$ , d.f. = 1,  $P > 0.05$ ).

The average territory (95% ADK) size for all males was significantly smaller in the red maple swamp (0.88 ha  $\pm$  0.10 S.E.) compared to the second-growth plot (1.50 ha  $\pm$  0.121, Wilcoxon  $W = 1936$ ,  $Z = -4.95$ ,  $P < 0.001$ ). The average core area (50% ADK) was also significantly smaller in the red maple swamp (0.15  $\pm$  0.02) than it was on the second-growth plot (0.29  $\pm$  0.03, 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 in the red maple swamp (territory = 0.876 ha  $\pm$  0.11 core area = 0.154 ha  $\pm$  0.02) compared to the second-growth plot (territory = 1.425 ha  $\pm$  0.12, core area = 0.265 ha  $\pm$  0.03). The territory (Wilcoxon  $W = 32$ ,  $Z = -1.68$ ,  $P = 0.093$ ) size of SYs did not differ between the two plots (red maple swamp = 0.885 ha  $\pm$  0.51, second-growth =



1.614 ha  $\pm$  0.99) but the core area (Wilcoxon  $W = 29$ ,  $Z = -2.07$ ,  $P = 0.039$ ) was significantly smaller in red maple swamp (0.125 ha  $\pm$  0.04) compared to the second-growth plot (0.317 ha  $\pm$  0.07).

Nine of 27 habitat variables we measured were significantly different between the two plots (see Table 1). The average total number of shrubs within territories was not significantly different between the two study areas but there were nearly double the number of small size class (<2.5 cm dbh) deciduous shrubs in the red maple swamp and more deciduous and coniferous shrubs of the larger size class (>2.5 < 8.0 cm dbh) on the second-growth plot. The average density of the shrub foliage in the upper two strata (1.5–2 m, 2–2.5 m) was greater in the red maple swamp. Coniferous trees of all size classes were more abundant on the second-growth plot, but conifers of the smallest size class (>8.0 < 23 cm dbh) were more abundant in the red maple swamp. Deciduous trees of the medium-size class (>22.9 < 38 cm dbh) were more abundant on the second-growth plot. Only one component of ground cover, moss, was much more abundant in the red maple swamp.

We collected a total of 4799 individual insects from 54 families in malaise trap samples. Analysis was restricted to 1590 individuals of 41 families because we removed taxa considered to be unlikely prey for Canada warblers, for example, fungus gnats (Diptera, Mycetophilidae) and many hymenopterans. The prey abundance was not significantly different among red maple swamp and second-growth territory and non-territory sampling stations ( $F = 1.234$ , d.f. = 3,  $P = 0.299$ ). The average captures per sampling period was highest for territories in the red maple swamp but the variance was also highest (26.5 individuals per sample,  $\pm 49.5$ ). Arthropod abundance was patchy in all sample categories (average in non-territories near red maple swamp =  $12.1 \pm 25.9$ , second-growth territories =  $18.1 \pm 32.3$ , second-growth non-territories =  $15.7 \pm 28.2$ ). Prey abundance did not change from early to later in the breeding season ( $F = 0.84$ , d.f. = 3,  $P = 0.47$ ).

#### 4. Discussion

Territory and core area sizes were significantly smaller for males in the red maple swamp, suggesting higher quality habitat. However, this did not translate to higher fitness in terms of pairing success or male ability to fledge at least one young.

In comparing the different habitat types on the second-growth plot and red maple swamp, similar vegetation characteristics were found, but also some important differences. The two plots were similar in number of song perches, canopy height, and the total number of shrubs. However, the two plots differed in shrub species composition. Specifically, the number of coniferous and deciduous stems differed between the plots, as did the stem densities within each of the two size classes for both coniferous and deciduous shrubs. This indicates that the species composition of the shrub layer plays a relatively minor role in Canada warbler reproductive performance and demographic composition. However, overall shrub stem density is critical to breeding Canada warblers. Other differences in habitat characteristics result from a combination

of differing hydrology and age of forest stands. The red maple swamp had almost twice the moss ground cover owing to the wetter conditions in the swamp, which may increase the amount of the most concealed nesting substrate (Hallworth, personal observation). The greater abundance of medium-sized deciduous trees on the second-growth plot is due to its successional age and likely contributes to its value to Canada warblers as breeding habitat.

The differences in the sizes of territories and core areas between the two plots suggest the potential for greater resource availability in the red maple swamp. We did not detect a difference in invertebrate prey abundance, however, this may have been due to small sample sizes. Although, the averages and standard errors across samples were similar. A possible explanation for smaller territories in the red maple swamp is the need for males to patrol territories efficiently. Larger territories in thicker vegetative cover may make it more difficult to detect intruders. The red maple swamp had nearly twice the density of small diameter deciduous stems than the second-growth plot (small stems <2.5 cm dbh: red maple swamp = 31.87 within 5 m radius, second-growth = 16.41), and these densities were two to four times that of the larger diameter shrub stems (>2.5 cm: red maple swamp = 3.04, second-growth = 7.48).

Commercial and residential development in the northeastern United States has placed red maple swamps and other forested wetlands at risk (Golet et al., 1993). In order to slow the decline of Canada Warblers in the region, a greater emphasis should be placed on the preservation of these natural habitats. Conservation of natural habitats is important because they will remain useful to the species indefinitely. Alternatively, suitable habitat can be temporarily created through timber harvest.

The Canada warbler population has been declining at 2.7% per year throughout its breeding range and in New Hampshire at 4.6% annually since 1966 (Sauer et al., 2005). Regeneration of former agricultural land to forest over the last century may be contributing to this decline (Litvaitis, 1993). Several community-level studies from the northeastern United States indicate regenerating forests are most suitable for Canada warblers 6–20 years post-harvest (Titterton et al., 1979; DeGraaf, 1985; Hagan et al., 1997). When the understory grows above 6 m, the stand declines in suitability for the Canada warbler (Hagan and Meehan, 2002). Forest management practices that create early-successional stands increase the areas in which Canada warblers can breed successfully for a number of years.

This study is based upon one plot in each of two distinct habitats used by breeding Canada warblers, but the number of territorial males is sufficiently high to suggest potential management strategies aimed at reversing this species' decline. The data from this local area strongly suggest that silvicultural practices creating a dense understory and leaving residual trees for perch sites will enhance Canada warbler breeding habitat. Canada warbler habitat that is created by logging is ephemeral at the stand level, but could be maintained at the landscape level by the rotation of partial and/or clear-cut harvests (Lambert and Faccio, 2005). DeGraaf and Yamasaki (2003) indicate that Canada warblers first appear approximately 5 years post-cut, are common 10 years later, and remain present until subsequent

cutting if residual stems remain. If such practices can be implemented at the landscape scale, then Canada warbler recruitment may increase within the Northeast region where the population is currently in decline. Such a strategy should aim to balance benefits to early-successional species with effects on forest-interior wildlife, water quality, and other ecological attributes. Future investigations of productivity-area thresholds for Canada warblers in managed forests would help land stewards evaluate the tradeoffs.

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## References

- Anderson, E.A., 2005. Habitat characteristics of paired and unpaired male Canada Warblers (*Wilsonia canadensis*) in a forested wetland in Canaan, NH. M.Ed. Thesis, Plymouth State University, Plymouth, NH.
- Barg, J.J., Jones, J., Robertson, R.J., 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. *J. Anim. Ecol.* 74, 139–149.
- Costello, C.A., Yamasaki, M., Pekins, P.J., Leak, W.B., Neefus, C.D., 2000. Songbird response to group selection harvest and clearcuts in a New Hampshire northern hardwood forest. *Forest Ecol. Manage.* 127, 41–54.
- Crawford, H.S., Jennings, D.T., 1989. Predation by birds on spruce budworm *Choristoneura fumiferana*: functional, numerical, and total responses. *Ecology* 70, 152–163.
- DeGraaf, R.M., 1985. Breeding bird assemblages in New England northern hardwoods. In: Regan, R.J., Capen, D.E. (Eds.), *Conference Proceedings Johnson State College on The Impact of Timber Management Practices on Nongame Birds in Vermont*, Johnson, pp. 5–22.
- DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecol. Manage.* 185, 179–181.
- Dettmers, R., 2003. Priority Bird Species in Bird Conservation Region 14. North American Bird Conservation Initiative, Arlington, VA.
- Faccio, S.D., 2003. Effects of ice storm-created gaps on forest breeding bird communities in central Vermont. *Forest Ecol. Manage.* 186, 133–145.
- Golet, F.C., Calhoun, A.J.K., DeRagon, W.R., Lowry, D.J., Gold, A.J., 1993. Ecology of red maple swamps in the glaciated northeast: a community profile. Biological Report 12, U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA.
- Golet, F.C., Wang, Y., Merrow, J.S., DeRagon, W.R., 2001. Relationships between habitat and landscape features and the avian community of red maple swamps in southern Rhode Island. *Wilson Bull.* 113, 217–227.
- Hall, G.A., 1984. Population decline of Neotropical migrants in an Appalachian forest. *Amer. Birds* 18, 14–18.
- Hagan, J.M., Meehan, A.L., 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. *Forest Sci.* 48, 231–242.
- Hagan, J.M., McKinley, P.S., Meehan, A.L., Grove, S.L., 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *J. Wildl. Manage.* 61, 718–735.
- Harrison, R.B., Schmiegelow, F.K.A., Naidoo, R., 2005. Stand-level response of breeding forest Songbirds to multiple levels of partial-cut harvest in four boreal forest types. *Can. J. For. Res.* 35, 1553–1567.
- Holmes, R.T., Marra, P.P., Sherry, T.W., 1996. Habitat specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *J. Anim. Ecol.* 65 (2), 183–195.
- Howlett, J.S., Stutchbury, B.J.M., 2003. Determinants of between-season site, territory, and mate fidelity in Hooded warblers (*Wilsonia citrina*). *Auk* 120 (2), 457–465.
- Hunt, P.D., 1996. Habitat selection by American redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. *Auk* 113 (4), 875–888.
- Kendeigh, S.C., 1945. Community selection by birds on the Helderberg plateau of New York. *Auk* 62, 418–436.
- Kie, J.G., Baldwin, J.A., Evans, C.J., 1994. CALHOME Home range analysis program. United States Forest Service, Pacific Southwest Research Station, California Department of Fish and Game.
- Lambert, J.D., Faccio, S.D., 2005. Canada Warbler: population status, habitat use, and stewardship guidelines for Northeastern forests. VINS Technical Report 05-04. Vermont Institute of Natural Science, Woodstock, VT.
- Litvaitis, J.A., 1993. Response of early-successional vertebrates to historic changes in land use. *Conserv. Biol.* 7, 866–873.
- Martin, T.E., Conway, C.J., 1994. Breeding Bird (BBIRD) field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
- Norton, M.R., Hannon, S.J., 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Can. J. For. Res.* 27, 44–53.
- Pyle, P., 1997. Identification Guide to North American Birds, part I Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- Rappole, J.H., 1983. Analysis of plumage variation in the Canada warbler. *J. Field Ornithol.* 54 (2), 152–159.
- Rich, T.D., Beardmore, C.J., Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Inigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S., Will, T.C., 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, NY.
- Robinson, W.D., Robinson, S.K., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conserv. Biol.* 13, 58–66.
- Rodenhouse, N.L., Holmes, R.T., 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. *Ecology* 73 (1), 357–372.
- Sauer, J.R., Hines, J.E., Fallon, J., 2005. The North American Breeding Bird Survey, Results and Analysis 1966–2004, Version 2005.2. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Sodhi, N.S., Paszkowski, C.A., 1995. Habitat use and foraging behavior of four parulid warblers in a second growth forest. *J. Field Ornithol.* 66 (2), 227–288.
- Therres, G.D., 1999. Wildlife species of conservation concern in the Northeastern United States. *Northeast Wildl.* 54, 93–100.
- Titterton, R.W., Crawford, H.S., Burgason, B.N., 1979. Songbird response to commercial clear-cutting in Maine spruce-fir forests. *J. Wildl. Manage.* 43, 602–609.
- Ueland, A., 2004. Habitat selection of Canada warblers (*Wilsonia canadensis*) in a forested wetland in Canaan, NH. M.Ed. Thesis, Plymouth State University, Plymouth, NH.
- Webb, W.L., Behrend, D.F., Saisorn, B., 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildl. Monogr.* 91, 1–35.
- Van de Poll, R., 2006. Final report on a partial natural resources inventory of the Bear Pond Natural Area. In: Reitsma, L. (Ed.), *Natural Resource Inventory of the Bear Pond Natural Area 2003–2005*. Canaan, NH, pp. 8–38.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47, 893–901.
- Vickery, P.D., Hunter, M.L., Wells, J.V., 1992. Is density an indicator of breeding success? *Auk* 109, 706–710.