Breeding habitat characteristics of Canada Warblers in central Alberta

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ABSTRACT

Determining habitat attributes used by animals of conservation concern at different spatial scales is a key aspect of developing effective recovery plans. Managers must know whether forest songbirds choose habitat based on selection of specific plant species or on structural features shared by different plant species. Coarse-scale habitat features were measured at point count locations and fine-scale characteristics within and adjacent to breeding territories of Canada Warblers (*Cardellina canadensis* L.) in central Alberta, Canada. Differences in the plant community composition in breeding territories between forest interior and shoreline sites were examined. Breeding success in each breeding territory was estimated through observations of males carrying food. At coarse-scales, Canada Warbler occurrence was positively correlated with shrub density and was higher in deciduous forests. At a fine-scale, woody plant species composition differed significantly between interior and shoreline sites (pseudo-F=32.61, P=0.001), but did not differ between plots located inside and outside bird territories (pseudo-F=1.22, P=0.26). Choke cherry (*Prunus virginiana*) was an indicator species within bird territories, however. Birds with evidence of breeding success had significantly more green alder (*Alnus crispa*) and balsam fir (*Abies balsamea*) in their territories, whereas territories without evidence of breeding success were more likely to have trembling aspen (*Populus tremuloides*), twining honeysuckle (*Lonicera dioica*) and Canada buffaloberry (*Shepherdia canadensis*). The results highlight that Canada Warbler presence is strongly correlated with canopy type and shrub density. There was also evidence that certain shrub and tree species are more abundant at the core of bird territories. These results will help inform critical habitat identification for Canada Warblers in western Canada. Land managers should use forest inventory data sources that include information on shrub density when trying to locate important habitat for Canada Warblers, while being aware that locally, specific plant species may influence Canada Warbler habitat choices and breeding success.

Key words: Canada Warbler, habitat characteristics, breeding territory, coarse-scale habitat, fine-scale habitat, breeding success

RÉSUME

Pour élaborer de bons plans de rétablissement, il faut d'abord pouvoir établir à différentes échelles spatiales les caractéristiques de l'habitat utilisées par les espèces animales menacées. Les aménagistes ont besoin de savoir si les oiseaux chanteurs des forêts choisissent leur habitat en fonction de plantes particulières ou de caractéristiques structurales communes à différentes espèces de plantes. Nous avons donc mesuré les caractéristiques grossières de l'habitat aux sites de dénombrement ainsi que les caractéristiques à l'intérieur et autour des arènes de reproduction de la paruline du Canada (*Cardellina canadensis* L.) dans le Centre de l'Alberta au Canada. Nous nous sommes attardés principalement aux différences de composition des communautés végétales de ces arènes entre les sites boisés et ceux se trouvant en bordure des forêts. On estimait le succès reproducteur dans chaque arène par le nombre d'observations de mâles transportant de la nourriture. Aux échelles grossières, la présence des parulines du Canada augmentait avec la densité des arbustes et était plus élevée dans les forêts de feuillus. À l'échelle plus fine, la composition ligneuse différait significativement entre les sites boisés et ceux se trouvant en bordure des forêts (pseudo-F=32,61, P=0,001), mais ne montrait pas de différence entre les parcelles situées à l'intérieur et en bordure des territoires utilisés par les oiseaux (pseudo-F=1,22, P=0,26). Le cerisier de Virginie (*Prunus virginiana*) s'est avéré être une essence indicatrice dans ces territoires. Les oiseaux qui affichaient un meilleur succès reproducteur se retrouvaient dans des territoires comportant plus d'aulne crispé (*Alnus crispa*) et de sapin baumier (*Abies balsamea*) alors que les territoires ne laissant voir aucun succès reproducteur comportaient le plus souvent du peuplier faux-tremble (*Populus tremuloides*), du chèvrefeuille dioïque (*Lonicera dioica*) et de la shepherdie du Canada (*Shepherdia canadensis*). Les résultats montrent un lien très fort entre la présence de la paruline du Canada, le type de couvert et la densité des arbustes. Il appert de plus que certaines espèces d'arbustes et d'arbres sont plus abondantes au cœur du territoire occupé par les oiseaux. Ces résultats contribueront à documenter les habitats critiques pour la paruline du Canada dans l'Ouest canadien. Les aménagistes du territoire auraient tout avantage à utiliser les données d'inventaire forestier incluant les informations sur la densité des arbustes pour tenter de localiser les habitats propices à la paruline du Canada tout en se rappelant qu'à certains endroits, certaines espèces de plantes spécifiques influenceront directement le choix de l'habitat et le succès reproducteur de la paruline du Canada.

Mots-clés : paruline du Canada, caractéristiques de l'habitat, arènes de reproduction, échelle grossière, échelle fine, succès de reproduction

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Introduction

Defining the critical habitat necessary for the survival or recovery for a species at risk is an important step in developing recovery strategies and is a requirement under Canada's species at risk legislation (Government of Canada 2017). Identifying important habitat attributes for wildlife must consider the hierarchical nature of habitat selection (Johnson 1980, Kristan 2006). First-order habitat selection considers attributes at broad geographic scales amenable to delineating species distributions. Second and third-order habitat selection helps us understand the plant species composition and structure of vegetation where animals place their home range and where within their home range they spend time, respectively (Johnson 1980). Land managers must consider coarse-scale habitat attributes to identify where species of concern might occur and then manage for fine-scale habitat attributes that promote and enhance reproduction and survival for species at risk (Bakermans and Rodewald 2009, Hunt *et al.* 2017).

Generally bird distributions are modeled at coarse scales by remotely sensed land cover and biophysical characteristics such as forest canopy composition, precipitation, slope, and soil moisture (Bayne *et al* 2010). Products from these models include predictive maps of relative abundance or densities of birds (e.g., Thogmartin *et al.* 2004, Ball *et al.* 2016) and are useful to understand how bird populations may be impacted by land use activities (Bayne *et al* 2010). However, the general land cover types used in many models may not provide the spatial resolution necessary to account for fine-scale habitat variables required to develop and implement effective management strategies (Young *et al.* 2005, Hernandez *et al.* 2006). Variation in coarse- and fine-scale habitat requirements for species with large geographic ranges may reduce the accuracy of broad-scale habitat models (Hernandez *et al.* 2006), making it necessary to develop specific conservation plans based on local habitat management units throughout a species range.

An important consideration in identifying fine-scale habitat attributes is whether bird species occupancy is based on a particular species of plant or on structural features that may be shared by many plant species (Rotenberry 1985). Both the physical structure of the vegetation (physiognomy) and plant community composition (floristics) play important roles in the habitat selection of birds (Lee and Rotenberry 2005) that have knock-on effects for survival and reproductive success (Holmes *et al.* 1996, Boves *et al.* 2013, Nemes and Islam 2017). Detailed data on physiognomy and floristics is often collected at bird survey locations (e.g., point counts), monitored breeding territories of birds, or during forestry inventory surveys (e.g., timber cruises). These detailed data provide important breeding habitat features and highlights the amount of variation in both vegetation and structural characteristics of breeding territories at regional and local scales. For example, territories throughout the core breeding range of Swainson's warbler (*Limnothlypis swainsonii*) differed in dominant tree species and habitat variables such as basal area of canopy trees and vine density (Graves 2002). This implies that managing only for physiognomy or floristic attributes may not be sufficient to achieve conservation objectives (Rotenberry 1985, MacFaden and Capen 2002).

The Canada Warbler (*Cardellina canadensis*) is a Neotropical migrant songbird listed as threatened under the Species at Risk Act in Canada, as the population has declined by an estimated rate of 4.5% per year between 1968 and 2007 (COSEWIC 2008, Environment Canada 2016). Habitat loss and degradation on both the wintering and breeding grounds have been identified as potential explanations for the population decline (COSEWIC 2008, Wilson *et al.* 2018). Canada Warblers have a broad breeding distribution, extending from the boreal region of western Canada through to the east coast of Canada and northern-eastern United States (Reitsma *et al.* 2010). Canada Warblers are generally associated with mixed forests with a dense, deciduous shrub layer, and a complex understory (Reitsma *et al.* 2010, Ball *et al.* 2016, Environment Canada 2016, Flockhart *et al.* 2016, Grinde and Niemi 2016).

At a coarse scale, higher densities of Canada Warblers are associated with deciduous and mixed-wood stands with increasing canopy height and canopy cover throughout Canada (Haché *et al.* 2014). Forest type, forest age, soil wetness, and topography are all good predictors of the variation in density of Canada Warblers in Alberta (Alberta Environment and Sustainable Resource Development and Alberta Conservation Association 2014, Ball *et al.* 2016, Hunt *et al.* 2017). However, these coarse-scale analyses are based on remotely sensed variables that have limited resolution to identify understory vegetation structure and composition and may not fully capture the relationship between shrubs and Canada Warbler habitat (Bayne *et al.* 2010, Ball *et al.* 2016). Fine-scale habitat attributes associated with habitat selection, demographics, and reproductive success have been studied in the eastern portions of the breeding range (Hallworth *et al.* 2008a, 2008b; Reitsma *et al.* 2008, Chace *et al.* 2009, Goodnow and Reitsma 2011) but are largely missing from western regions (however see Hunt *et al.* 2017). Detailed information on fine-scale habitat characteristics from the western region is needed to identify critical habitat across the species range, identify suitable management units (Environment Canada 2016), and enhance the ability of land managers to identify and protect critical Canada Warbler habitat.

Our objectives in this study were to identify coarse-scale breeding habitat features based on presence/absence of Canada Warblers and compare the physiognomy and floristics of Canada Warbler breeding territories and their correlation to breeding success between shoreline and interior forest sites at a study area in central Alberta, Canada. Consistent with previous Canada Warbler habitat studies, we predicted that shrub density and a high proportion of deciduous canopy cover would characterize Canada Warbler habitat. If plant community composition also plays a role in the habitat selection of Canada Warblers in this region, we predicted that plant community composition would differ within versus outside breeding territories.

Methods

Study area

The study was conducted in the Lesser Slave Lake Provincial Park (LSLPP; 7 700 ha; 55° 26′ N. 114° 49′ W). The LSLPP is located in the mixed boreal forest region of Alberta, Canada. The western edge of the Park is bordered by Lesser Slave Lake. The southern section contains a sand dune complex and beach ridges along the lakeshore. The elevation ranges from 560 m along the shore to 1020 m at the summit of Marten Mountain, which lies along the east-central boundary of the Park. A highway intersects the Park and there are access roads, hiking trails, utility corridors and a small amount of industrial activity within the Park.

The LSLPP is mainly comprised of mature (> 80 years) or old-growth (> 130 years) mixed boreal forest dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.). The shrub understory (< 8 cm diameter at breast height - dbh) is dominated by tree saplings, willow (*Salix* spp.), green alder (*Alnus crispa* (Ait.) Pursh), beaked hazelnut (*Corylus cornuta* Marsh.), red-osier dogwood (*Cornus stolonifera* L.), Saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt), prickly rose (*Rosa acicularis* Lindl.), low bush-cranberry (*Viburnum edule* (Michx.) Raf.), choke cherry (*Prunus virginiana* L.), and bracted honeysuckle (*Lonicera involucrate* (Richardson) Banks ex Spreng.). The shoreline is characterized by fine sand with emergent vegetation dominated by willow, which is maintained by fluctuating lake levels. Marten Mountain contains areas with vegetation communities associated with the foothills ecoregion with coniferous-dominated forests and the presence of lodgepole pine (*Pinus contorta* Douglas) and understory species such as devil's club (*Oplopanax horridus* (Sm.) Miq.). While much of the forest is of uniform age, differences in understory structure and composition may be caused by other factors such as small scale insect or weather disturbance, topography, microtopography, and soil characteristics.

Avian point counts

Avian point counts were conducted between June 17 and June 27, 2010 at 88 locations throughout the study area. Point count stations were randomly selected within the boundary of the LSLPP with a minimum spacing of 200 m among point count locations. We recorded all Canada Warblers detected during a five min period within a 100 m radius of each point count.

Coarse vegetation surveys

Vegetation structure was measured within approximately 10 m of the centre of each station following the point count (MacFaden and Capen 2002). The average canopy height, shrub height (shrubs and tree sapling stems > 50 cm height and < 8 cm dbh), and ground vegetation height (herbaceous species and grasses) were estimated after Hallworth *et al.* 2008a and Chace *et al.* 2009. Canopy closure was scaled to nearest continuous canopy cover values of 87.5%, 62.5%, 37.5%, and 12.5% coverage. Canopy composition was estimated by determining the amount of canopy coverage provided by each tree species to the nearest 10%, and the canopy was assessed as deciduous, coniferous, or shrub dominated. The percent-cover of the shrub and herbaceous layers was estimated to the nearest 10%. Coarse woody debris was classified on an ordinate scale as low (1: < 10% estimated ground cover), medium (2: 10% -50% estimated ground cover), or high (3: > 50% estimated ground cover), and this was considered as a linear variable in statistical models. The ground slope (degrees) was measured at the centre of each station.

Territory mapping

Male Canada Warblers were tracked with fitted radio-transmitters between June 11 and June 30 in 2012 (n = 16) and 2013 (n = 15) to estimate the size of breeding territories. Tracking locations were grouped into two broad categories: shoreline sites (hereafter shoreline) in forested areas within 700 m of Lesser Slave Lake and interior sites (hereafter interior) located in the central area of the LSLPP (> 2 km from the shoreline) which included a major creek complex and Marten Mountain. Canada Warblers were detected in higher abundances in these interior and shoreline areas during point counts, indicating that they contain important characteristics for breeding habitat. While these forests are in close proximity to each other, the variation in topography and other landscape features have strong influences on the vegetation composition within each forested area.

A 0.31 g radio-transmitter (Model LB-2X; Holohil Systems Ltd., Carp, ON, Canada) was attached to each captured male after being banded with a numbered aluminum band and two celluloid colour bands. After an approximate 24 h adjustment period, males were tracked by honing on the birds position using an H-Yagi antenna (Telonics, Inc., Mesa, AZ, USA) and R-1000 radio-transceiver (Communication Specialists, Inc., Orange, CA, USA). Each male was tracked over four to six days from 05:00 until 13:00 to attempt to collect a minimum of 40 total location points. Daily tracking bouts consisted of rotating through the marked males within an area to obtain approximately 10 location points for each male per day. Observers continued to re-sight males during normal tracking bouts if radio-transmitters were confirmed to have failed or fell off prematurely (n=3). See Flockhart *et al.* (2016) for a more detailed description of these methods.

Estimating breeding success

Time constraints prevented nest searching and monitoring. Observations of males carrying food were used to determine if an active nest at some stage of the nesting cycle was in the territory because they provision incubating females, nestlings, and fledglings (Reitsma *et al.* 2010). Provisioning males were deemed as having evidence of breeding success although we did not know the outcome of the nests. This method of estimating breeding success should be viewed with some caution. Male singing decreases during provisioning (Krikun *personal observation*), which can make it difficult to locate males carrying food in dense shrub areas. If a nest had failed, the timing of our dedicated provisioning searches may have occurred before the young of the second nest hatched. However, we think late re-nesting attempts are limited given that Canada Warblers have one of the shortest breeding season windows (Flockhart 2007). All observations of provisioning males were recorded during regular tracking bouts. Males that were not recorded carrying food were revisited for a dedicated one hour observation session after June 30. Given the short breeding season of Canada Warblers at the study site, our observations fall within the expected period when males would be feeding nestlings or fledglings (Flockhart 2010).

Territory vegetation sampling

Territory boundaries were estimated using 95% minimum convex polygons (MCP, Hallworth *et al.* 2008b), and identified the core area of each territory using 95% kernel density estimators (KDE), with least-squares cross-validation as the smoothing parameter (Barg *et al.* 2005), in the *adehabitat* package in R (Calenge 2006). All location points recorded for each male were used to define territories. Vegetation plots were sampled within territories (n = 149; 71 interior and 78 shoreline) of 31 males from July 23 to August 15 in 2012 and 2013. Each territory contained three (n = 4) or five (n = 27) circular (11.3 m radius = 0.04 ha) vegetation sampling plots depending on the size and configuration of the territory. One plot was centred based on the coordinates that corresponded with the peak of the latitudinal and longitudinal kernel density curves derived from the KDE, which represented the core area of the territory. The remaining vegetation plots were arranged within the MCP boundary so that the diameter of each plot remained within the territory boundary and did not overlap with another vegetation plot. The habitat differences surrounding each Canada Warbler territory were investigated by sampling outside territory plots. For each territory, an additional three vegetation plots were established (n = 93; 45 interior and 48 shoreline) approximately 25 m outside of the MCP boundary at bearings 0°, 120°, and 240° from the core area of the territory. The 25 m distance was selected to detect if local vegetation composition within a used stand influences habitat selection. All trees > 8 cm dbh were identified to species and counted within the 11.3 m radius circle. In a 5-m radius of the centre of each vegetation plot, all shrubs and saplings (> 50 cm height, < 8 cm dbh at 10 cm height) were identified and counted.

Statistical analysis

1. Vegetation structure analysis

Generalized linear models with a binomial error distribution were used to determine the probability of Canada Warbler presence using canopy, shrub, and ground level data collected during point counts. Nine *a priori* models based on previous research were used as well as personal observations about the vegetation attributes characteristic of the presence of Canada Warblers near the study area (Table 1). As a ground nesting species, we tested if an increase in shrub density and ground-level elements, explained Canada Warbler presence by offering more nesting locations or improved nest concealment, which could result in higher reproductive success (Goodnow and Reitsma 2011). The dominant canopy type has a large effect on the development and diversity of the understory layer and the structural features of the canopy can influence conditions that promote shrub development, such as light penetration and temperature (Macdonald and Fenniak 2007). The variation in slope from the elevational differences within the LSLPP can influence soil moisture or other conditions that could affect canopy or shrub development (Hart and Chen 2006) and also create more undercuts that could provide additional nesting locations.

Table 1. Model parameters of coarse-scale habitat attributes used to explain Canada Warbler (CAWA) presence in the Lesser Slave Lake Provincial Park. Variables considered were dominant canopy type (DomCan), canopy height (CanHgt), canopy closure (CanClose), shrub density (ShrubDen), herbaceous density (HerbDen), coarse woody debris (CWD), and slope (Slope).

Model	Explanation	Variables	Reference
1	Dominant canopy type and structure determines CAWA presence	DomCan, CanHgt, CanClose	Haché *et al.* 2014
2	Dominant canopy type alone determines CAWA presence	DomCan	Observational
3	CAWA density is highest in dense understory	ShrubDen	Hallworth *et al.* 2008a
4	Canopy type influence on shrub density with highest CAWA density in dense understory	DomCan, ShrubDen	Observational
5	CAWA density responds similarly to habitat variables of CAWA in eastern hardwood forests	CanHgt, ShrubDen, HerbDen	Chace *et al.* 2009
6	Warbler density responds similarly to habitat variables of CAWA in eastern hardwood forests	CanHgt, ShrubDen	Chace *et al.* 2009
7	Ground cover, nest concealment and nesting opportunities	ShrubDen, HerbDen, CWD	Goodnow and Reitsma 2011
8	Slope and canopy type influence ground microclimate conditions	Slope, DomCan	Ball *et al.* 2016
9	Slope influences shrub establishment	Slope, ShrubDen, HerbDen	Ball *et al.* 2016

Table 2. Models that explain presence of Canada Warblers in Lesser Slave Lake Provincial Park, Alberta. Presented for each model are the number of model parameters (K), Akaike Information Criterion corrected for small sample size (AICc), the difference between the model AICc and that of the model with the lowest AICc (ΔAICc), model likelihood (l_i), model weight (w_i), and model log-likelihood (LL). Variables considered were dominant canopy type (DomCan), canopy height (CanHgt), canopy closure (CanClose), shrub density (UnderDen), herbaceous density (HerbDen), coarse woody debris (CWD), and slope (Slope).

Model	K	AICc	ΔAICc	l_i	w_i	LL
ShrubDen + DomCan	4	88.01	0.00	1.00	0.52	-39.76
Slope + DomCan	4	90.59	2.59	0.27	0.14	-41.05
DomCan	3	90.67	2.66	0.26	0.14	-42.19
ShrubDen + HerbDen+ Slope	4	91.23	3.23	0.20	0.10	-41.38
ShrubDen	2	93.63	5.62	0.06	0.03	-44.74
DomCan + CanHgt + CanClose	5	94.32	6.31	0.03	0.02	-41.79
ShrubDen + CanHgt	3	94.94	6.93	0.03	0.02	-44.33
ShrubDen + HerbDen + CWD	4	95.12	7.11	0.03	0.01	-43.32
ShrubDen + CanHgt + HerbDen	4	95.34	7.33	0.03	0.01	-43.43

Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c) was used to evaluate our candidate model set (Burnham *et al.* 2011). Models were ranked based on the difference in AIC_c compared to the model with the lowest AIC_c (ΔAIC_c). Due to model selection uncertainty, model-averaging was used to calculate parameter estimates of all variables from the candidate model set. The predicted relationship between the probability of presence and those explanatory variables where the 95% CI did not overlap zero were considered statistically significant. All statistical modelling was done in R 3.1.2 (R Development Core Team 2014).

2. Plant community analysis

PERMANOVA (permutational ANOVA; Anderson 2001, Anderson *et al.* 2008) was used to test for differences in woody plant species composition between vegetation sampling plots of interior versus shoreline sites, plots within bird territories versus outside bird territories, plots in the core areas of bird territories versus outside, and plots within the territories of individual birds versus without evidence of breeding success. PERMANOVA is a multivariate analysis of variance performed on a resemblance matrix, with *P*-values calculated via permutation. A resemblance matrix for all plots was calculated using the Bray-Curtis similarity metric on the square root transformed stem densities of all trees and shrubs. Because of the strong differences in plant community composition between shoreline and interior sites, the PERMANOVA tests were repeated for territory versus non-territory, and with evidence of breeding success versus without evidence of breeding success for plots in each site type separately.

Even if overall plant composition did not vary between the compared vegetation plot types, certain shrub or tree species may be significantly more frequent and/or abundant in certain plot types. Indicator species analysis (Dufrêne and Legendre 1997) was used to determine which plant species were indicators of site type (shoreline versus interior), bird territory status (within a bird territory versus outside any bird territory), territory cores (core of territory versus outside territory), and breeding success. Indicator species analysis is a technique that combines relative abundance and relative frequency of occurrence of a species in different site types and uses permutation to test for significant differences (Dufrêne and Legendre 1997). Non-metric multidimensional scaling (NMDS) was used to visualize differences between plot types. For all analyses, one vegetation plot was removed that was centred on an oil well pad and hence was devoid of trees and shrubs. The program PRIMER was used for PERMANOVA tests (Clarke and Gorley 2006), PC-ORD for indicator species analysis (McCune and Mefford 2011), and the *vegan* package in R for NMDS ordination.

Results

Canada Warbler presence

A total of 27 Canada Warblers were found at 20 of the 88 point count locations (Table S1). The most stringent model to predict occurrence using coarse structural attributes found Canada Warbler presence increased with shrub density and varied between canopy types (Table 2). Deciduous-dominated canopies had a higher probability of presence (Fig. 1), and larger model averaged parameter estimates compared to coniferous-dominated canopies (-1.43 ± 0.66 vs -3.38 ± 0.99, respectively; Table 3). The second most parsimonious model included slope (Table 2) but the parameter estimate overlapped zero (Table 3).

Plant community analysis

Shoreline and interior plots differed significantly in overall woody plant community composition (pseudo-F = 32.61, P= 0.001; Fig. 2). Indicator species of interior sites included balsam fir (*Abies balsamea* (L.) Mill.), green alder, Saskatoon berry, white birch, beaked hazelnut, bracted honeysuckle, pin cherry (*Prunus pensylvanica* L.f.), and wild red raspberry (*Rubus idaeus* L.) (Table S2). Indicators of shoreline sites were red-osier dogwood, twining honeysuckle, white spruce, balsam poplar, trembling aspen, prickly rose, willow, and Canada buffaloberry (Table S2).

Overall woody plant species composition did not differ significantly within versus outside Canada Warbler territories across interior and shoreline (pseudo-F = 1.22, P = 0.26), or for

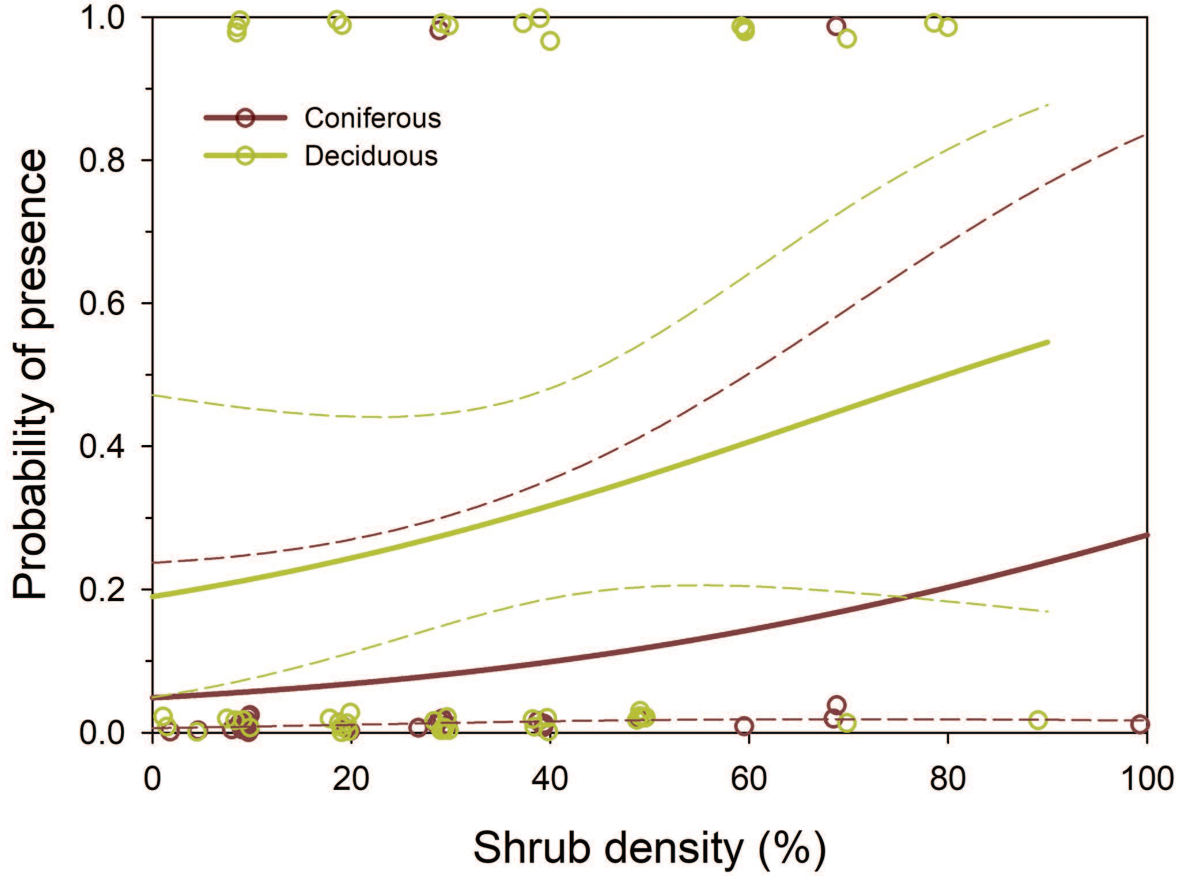

Fig. 1. Predicted probability of presence (solid lines) and 95% confidence interval (dashed lines) of Canada Warblers and percent shrub density in Lesser Slave Lake Provincial Park, Alberta. The predicted probability of Canada Warbler presence varied depending on whether a location was dominated by coniferous (red line) or deciduous (yellow line) canopy structure. The plotted range of shrub density was the minimum and maximum observed values for each canopy type while all other predictor variables were held constant at their mean observed value. The points are the observed presence-absence data.

interior and shoreline plots separately (interior pseudo-F = 0.87, $P = 0.51$; shoreline pseudo-F = 1.25, $P = 0.23$). However, indicator species analysis showed plots within bird territories were more likely to contain choke cherry (44% of plots within bird territories had choke cherry, with a mean of 7.8 stems per plot (SD = 16.39), whereas only 23% of plots outside bird territories had choke cherry, with a mean of 3.7 stems per plot (SD=11.10); Table S2). There were no indicator species of within-territory plots for interior sites (Table S3), but trembling aspen was an indicator of within-territory plots in shoreline sites (93% of plots within bird territories had trembling aspen with a mean of 18.4 stems per plot (SD=13.43), whereas only 66% of plots outside bird territories had trembling aspen, with a mean of 12.6 stems per plot (SD=12.97); Table S4). The woody plant composition of core area plots did not significantly differ from plots outside bird territories across all sites (pseudo- t = 1.05, $P = 0.37$) or when interior and shoreline

Table 3. Model-averaged parameter estimates, unconditional standard error and 95% confidence interval of variables to explain Canada Warbler presence in the Lesser Slave Lake Provincial Park

Variable	Estimate	SE	95% CI
Slope	0.055	0.034	-0.012 – 0.123
Canopy – Deciduous	-1.43	0.66	-2.74 – -0.13
Canopy – Coniferous	-3.38	0.99	-5.32 – -1.43
Canopy – Shrub	-0.78	1.02	-2.77 – 1.21
Understory density	0.027	0.012	0.003 – 0.052
Canopy height	0.029	0.035	-0.040 – 0.098
Herbaceous density	0.021	0.018	-0.015 – 0.056
Coarse woody debris	-0.31	0.40	-1.10 – 0.47
Canopy Closure	0.004	0.015	-0.026 – 0.034

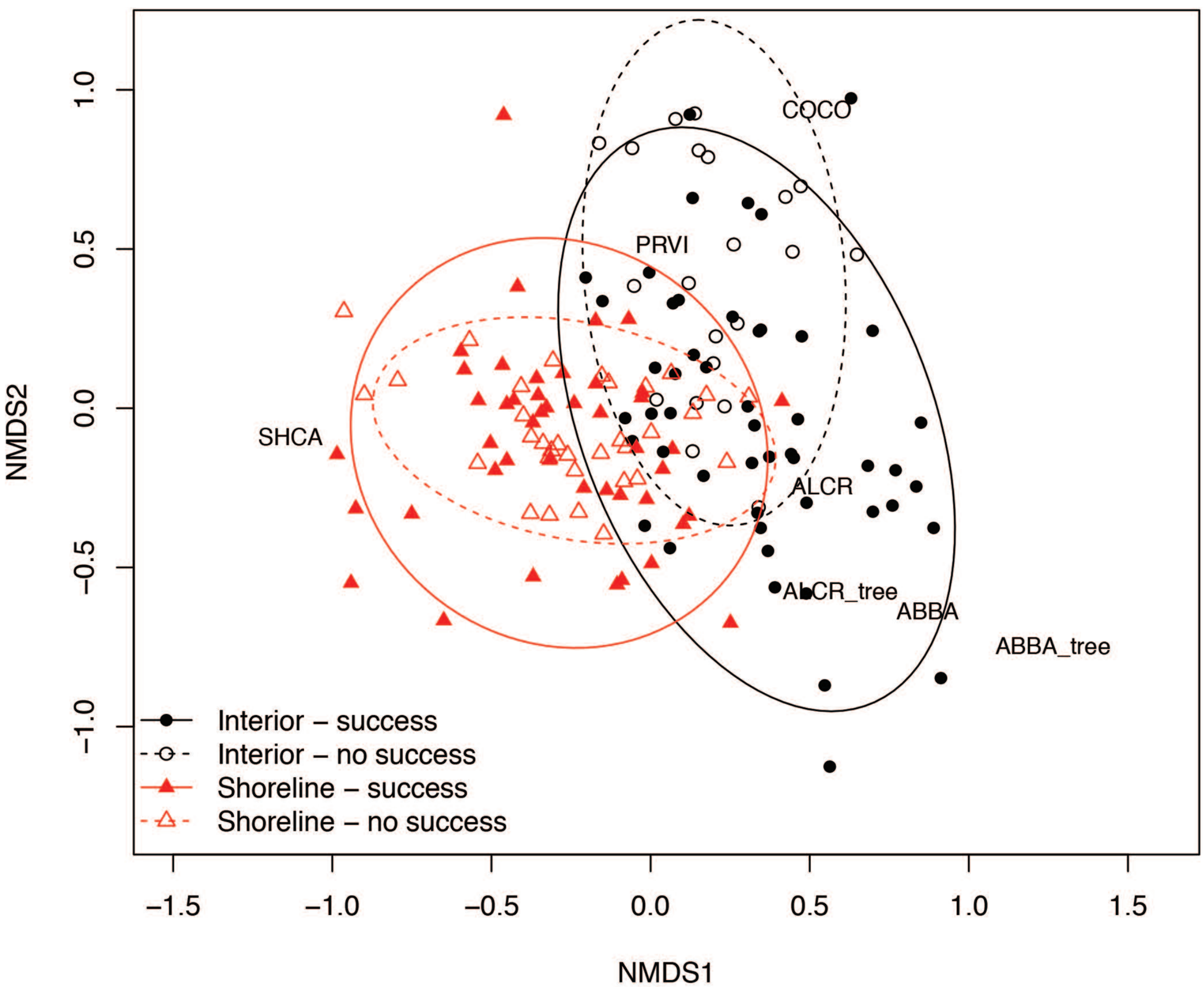

Fig. 2. Non-metric multidimensional scaling ordination of all 149 vegetation plots located within a bird territory (i.e., excluding plots surveyed outside bird territories) in woody plant species space. Symbols indicate plots in different site types ("interior" or "shoreline"), and in the territories of birds with or without evidence of nesting success ("success" or "no success"). Ellipses are the 90% confidence intervals of the multivariate distribution of each group. Select indicator species mentioned in the text are indicated: ABBA = balsam fir (shrub), ABBA_tree = balsam fir (tree), ALCR = green alder (shrub), ALCR_tree = green alder (tree), COCO = beaked hazelnut, PRVI = chokecherry, SHCA = Canada buffaloberry. Stress in three dimensions is 16.38.

plots were analyzed separately (interior: pseudo-t = 0.72, P =0.85; shoreline: pseudo-t =1.06, P =0.32). However, Saskatoon berry and choke cherry were indicators of plots at the centre of bird territories compared to plots outside territories in interior and shoreline sites pooled (Table S2), and Saskatoon berry and lowbush cranberry were indicators of central-territory plots in the shoreline area (Table S4).

There was a significant difference in woody plant composition between plots within territories that had evidence of breeding success (n = 19) versus territories without evidence of breeding success (n = 12, pseudo-F = 2.29, P = 0.008). This result may be driven by the interior sites which, when analyzed alone, showed a strong difference (pseudo-F = 6.37, P = 0.001; Fig. 2), whereas composition of woody plants near the shoreline was not strongly correlated with breeding success (pseudo-F = 1.76, P = 0.05). Across all sites, green alder and balsam fir were found in more plots and in significantly higher abundance within territories of birds with evidence of breeding success (Table S2). Plots in territories without evidence of breeding success across all site types were more likely to have trembling aspen, twining honeysuckle, and Canada buffaloberry in higher densities (Table S2). Significant indicators of interior plots in territories of birds with breeding success were green alder and balsam fir, with beaked hazelnut, choke cherry, snowberry, and balsam poplar indicators of plots in territories with no evidence of breeding success (Table S3). In shoreline plots with evidence of breeding success, significant indicators were choke cherry and balsam poplar, while plots in territories without evidence of breeding success had higher frequency and abundance of Saskatoon berry, twining honeysuckle, and bracted honeysuckle (Table S4).

Discussion

As expected, Canada Warbler presence in the Lesser Slave Lake Provincial Park was best explained by deciduous canopy cover and a high shrub density. Occurrences of Canada Warblers increased with increasing shrub density in different canopy types, but the probability of presence was higher in deciduous-dominated than coniferous-dominated canopies. High shrub density alone was not as strong at explaining Canada Warbler presence. These results indicate that there is an important relationship between the shrub and canopy layers for Canada Warbler habitat.

These results are consistent with previous studies reporting that deciduous canopy cover is associated with higher Canada Warbler densities in Alberta (Ball *et al.* 2016) and western Canada (Haché *et al.* 2014). High shrub density was also reported as an important variable in Canada Warbler habitat selection in eastern regions (Hallworth *el al.* 2008a, Chace *et al.* 2009), suggesting that it is an important habitat feature throughout their breeding range. In western regions, higher abundances of Canada Warblers have been detected in older aged, contiguous, and unharvested forests compared to fragmented or postharvest stands (Hunt *et al.* 2017). Deciduous forests contain the highest abundance of shrub species in this region (Chávez and Macdonald 2010), and older forests develop understory communities that are heavily influenced by canopy cover, tree abundance, soil dynamics, site history, and neighbouring landscape effects (Hart and Chen 2006, Macdonald and Fenniak 2007, Kumar *et al.* 2017). Overall understory density can be higher in stands regenerating from clearcuts or low retention harvesting eight years postharvest compared to unharvested stands, but grass species accounted for much of this cover (Craig and Macdonald 2009). Grass was considered as herbaceous density in our models and was not a strong characteristic in explaining Canada Warbler presence. Postharvest stands may also contain high densities of tall, rapidly colonizing, shade-intolerant, deciduous species (Hart and Chen 2006, Kumar *et al.* 2017), which may limit the development of other ground cover elements important for Canada Warbler nesting (Reitsma *et al.* 2008). It can take up to 20 years before the effects of post-disturbance understory cover begin to decrease (Hart and Chen 2006).

Given the structural similarities but strong vegetation composition differences between the forest interior and the lakeshore, any associations of Canada Warbler habitat with specific plant species seem to depend on the local community composition. Off-territory woody species composition was similar to within-territory composition, but choke cherry was an indicator of plots within bird territories across both site types. This could simply reflect an association of this species with a specific vegetation structure, i.e., plots with higher shrub density tend to have greater abundance of choke cherry (R. Krikun, J. McCune, D.T.T. Flockhart, and E. Bayne, unpublished data). However, the abundance of beaked hazelnut is also associated with areas of high shrub density, yet it was not an indicator of in *vs.* out of bird territories. Therefore, it is possible that birds select territories, not only based on high shrub density, but also some other characteristic that is correlated with or caused by higher frequencies and densities of choke cherry. For example, high abundance of choke cherry may provide a high shrub density while also maintaining or promoting ground attributes required for nesting opportunities, such as elements of the herbaceous layer that could increase nest concealment. There were also a few species that characterized core areas of a territory when compared with areas outside a territory. These included choke cherry, Saskatoon, and lowbush cranberry. Further observational or experimental tests are needed to determine what traits of these species may be affecting habitat choice by Canada Warblers, or whether their frequency and abundance is correlated with other important habitat characteristic such as prey abundance (Smith and Shugart 1987).

Several plant species differ significantly in frequency and/or abundance, depending on whether or not evidence of breeding success had been observed. Interestingly, two of these indicators were inconsistent between the two site types: while plots in the shoreline area where males were observed carrying food were indicated by balsam poplar and choke cherry, these species were associated with a lack of such provisioning evidence in interior sites.

The Canada Warbler is a ground nesting species that builds an open cup nest. Therefore, nest concealment may be an important factor in habitat selection as nest success has been shown to be positively influenced by shrub density and vegetation cover (Goodnow and Reitsma 2011, Hunt *et al.* 2017). Predators are a primary factor in nest mortality (Martin and Roper 1988, Bayne and Hobson 2002), and may have other indirect effects on Canada Warbler breeding success that influence singing and foraging behaviour (Flockhart *et al.* 2016). Past studies have found that vegetation structure plays a more important role in nest concealment than floristics for ground nests, which includes Canada Warblers (Rangen *et al.* 1999, Reitsma *et al.* 2008). Our results suggest that shrub species identity has a correlation with breeding success but these effects may depend on vegetation community context. This study was unable to determine what these indirect effects might be, or what traits of the plant species explain variation in breeding success. It is possible that the structural complexity resulting from high heterogeneity is important for breeding success since indicators of breeding evidence included both early and late-successional species, deciduous shrubs and trees and a conifer. The role of shrub species in breeding success may be confounded by other site factors however. For example, territory size was shown to have a direct effect on Canada Warbler breeding success but was influenced by factors that included shrub cover, conspecific density, and presence of predators (Flockhart *et al.* 2016).

Conclusion

This study confirms that identification and prioritization of conservation areas for Canada Warblers in the western boreal forest should focus on older-aged deciduous stands greater than 80 years that contain dense understory (Ball *et al.* 2016). This should involve the use of remote sensing to detect the amount of shrub cover (Vierling *et al.* 2008), or include shrub density data from ground surveys with canopy information provided by forest inventory sources (Bayne *et al.* 2010).

These results support previous recommendations that large tracks of contiguous unharvested forests be maintained in areas with high densities of Canada Warblers (Hunt *et al.* 2017), given Canada Warbler habitat association with both shrub density and older-aged deciduous forests.

The variation in woody species composition between site types makes it difficult to suggest specific plant indicators to identify Canada Warbler habitat through ground surveys. It is recommended that land managers recognize that higher frequencies and abundances of choke cherry, and perhaps Saskatoon and lowbush cranberry, have a higher association with Canada Warblers, but these associations are not exclusive. Therefore, full site context that includes both coarse- and fine-scale habitat features should be considered when identifying critical Canada Warbler habitats. Future studies can improve the understanding of the shrub density levels selected by Canada Warblers by examining if a threshold response exists between the amount of shrub cover available and Canada Warbler presence. A more nuanced understanding of vegetation structure and composition may contribute to learning how to promote breeding success in terms of nesting and post-fledging habitat and how to determine if the specific indicator species of breeding success are also indicative of higher quality habitat. These results suggest that Canada Warblers can select for a variety of habitats, provided that canopy and understory cover requirements are met, but specific plant species may influence habitat selection and breeding success.

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