RESEARCH ARTICLE

Forestry and conspecifics influence Canada Warbler (*Cardellina canadensis*) habitat use and reproductive activity in boreal Alberta, Canada

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ABSTRACT
The Canada Warbler (*Cardellina canadensis*) is a threatened species in Canada due to an annual decline of ~3% over the last 50 yr. Some studies suggest that Canada Warblers prefer old-growth forest and that forestry practices may reduce suitable habitat, while other research indicates that the species will also use harvested areas. Differences in scale between habitat use studies and behavioral phenomena such as conspecific attraction may explain this discrepancy. We examined how Canada Warblers responded to forestry and conspecifics in Alberta, Canada. We used point counts, burst sampling, and behavioral observations to determine how the density, home range placement (second-order habitat use), within-home-range space use (third-order habitat use), and probability of pairing and fledging young of male Canada Warblers were influenced by postharvest conditions (i.e. amount, age [$\leq$ 30 yr postharvest], and retention of unharvested fragments) and conspecifics. Male density was 86% lower in postharvest than in unharvested stands. However, males were 16.6 times more likely to place their home ranges in postharvest stands within 100 m of unharvested stands than 300 m into harvested areas, and 3 times more likely to place their home ranges 100 m from conspecifics than 300 m away. Within-home-range space use was 1.1 times higher 50 m from conspecifics than 350 m away, and 2.6 times higher 300 m from an edge than 100 m away. Use of harvested areas did not affect reproductive activity, but the probability of pairing was 1.8 times higher for males in low-density (2 males per 17.3 ha) than in high-density areas (7 males per 17.3 ha). Our results suggest that Canada Warbler use of postharvest stands on the boreal breeding grounds is more heavily influenced by conspecifics than by postharvest conditions. Because Canada Warbler territories are clustered, conservation efforts should prioritize the retention of large tracts of unharvested forest near occupied breeding sites.

Keywords: boreal forest, species at risk, conservation, conspecific attraction, forest management, habitat use, songbird

Les pratiques forestières et les congénères influencent l'utilisation de l'habitat et l'activité reproductive chez *Cardellina canadensis* dans la forêt boréale de l'Alberta

RÉSUMÉ
Cardellina canadensis est une espèce menacée au Canada en raison des déclins annuels de ses populations de l'ordre de ~3 % au cours des 50 dernières années. Certaines études suggèrent que cette espèce préfère les vieilles forêts et que les pratiques forestières peuvent réduire la quantité d'habitat propice, alors que d'autres recherches indiquent qu'elle utilise également les zones récoltées. Des différences d'échelle entre les études sur l'utilisation de l'habitat et les phénomènes comportementaux tels que l'attraction conspécifique peuvent expliquer cette divergence. Nous avons examiné comment C. canadensis répondait aux pratiques forestières et aux congénères en Alberta, au Canada. Nous avons utilisé les points d'écoute, l'échantillonnage de salve et des observations comportementales afin de déterminer comment la densité, le placement du domaine vital (utilisation de l'habitat de 2e ordre), au sein de l'utilisation de l'espace du domaine vital (utilisation de l'habitat de 3e ordre), et la probabilité d'appariement et d'envol des jeunes pour les mâles de C. canadensis étaient influencés par les conditions post-récolte (i.e. quantité, âge [$\leq$ 30 ans après la récolte], rétention de fragments non récoltés) et les congénères. La densité des mâles était 86 % plus faible dans les peuplements post-récolte que dans les peuplements non récoltés. Cependant, les mâles étaient 16,6 fois plus susceptibles de placer leur domaine vital dans les peuplements post-récolte dans un rayon de 100 m des peuplements non récoltés qu'à 300 m à l'intérieur des zones récoltées, et trois fois plus susceptibles de placer leur domaine vital à 100 m de leurs congénères qu'à 300 m d'eux. À l'intérieur des domaines vitaux, l'utilisation de l'espace était 1,1 fois plus élevée à 50 m des congénères qu'à 350 m, et 2,6 fois plus élevées à 300 m d'une lisière qu'à 100 m. L'utilisation des zones récoltées n'a pas affecté l'activité reproductive, mais la probabilité d'appariement était 1,8 fois plus élevée pour les mâles dans les zones à faible densité (i.e. deux mâles/17,3 ha) que dans les zones à forte densité (i.e. sept

mâles/17,3 ha). Nos résultats suggèrent que l'utilisation des peuplements post-récolte par C. canadensis sur les sites de reproduction en forêt boréale est davantage influencée par les congénères que par les conditions post-récolte. Puisque les territoires de C. canadensis sont groupés, les efforts de conservation devraient prioriser la rétention de grandes étendues de forêt non récoltée près des sites de reproduction occupés.

Mots-clés: forêt boréale, espèce en péril, conservation, attraction conspécifique, gestion de la forêt, utilisation de l'habitat, oiseau chanteur

INTRODUCTION

The conservation of species at risk requires the identification of species' habitat requirements and the human activities likely to result in the destruction of those habitats (USFWS 1973, Government of Canada 2011). The Canada Warbler (*Cardellina canadensis*) is a forest songbird considered threatened in Canada (Environment Canada 2016). Forest loss, on both the breeding and wintering grounds, may be an important driver of Canada Warbler declines (McDermott and Rodewald 2014, Ball et al. 2016). Degradation of breeding habitat quality by forestry activities is another potential threat (Ball et al. 2016, Grinde and Niemi 2016). As a result, the Canadian Recovery Strategy for the Canada Warbler has identified the need to determine the amount and characteristics of forest harvesting that can maintain suitable conditions for the species (Environment Canada 2016).

Current information on the effects of forestry on Canada Warblers across the breeding range is inconclusive, and sometimes contradictory (reviewed by Reitsma et al. 2009, Environment Canada 2016). Boreal forest harvesting has been identified as a threat to Canada Warblers by some researchers (Zlonis and Niemi 2014, Ball et al. 2016), while other authors have suggested that birds will use old-growth fragments in harvested areas or regenerating stands 11–30 yr postharvest (e.g., Schieck and Hobson 2000, Schieck and Song 2006). Part of this uncertainty surrounding Canada Warblers' use of postharvest stands may stem from data having been collected at different spatial scales. To legally designate habitat requirements for the Canada Warbler (i.e. critical habitat; Government of Canada 2011, Environment Canada 2016), we argue that a multiscale evaluation of habitat requirements is needed, as different ecological processes and selection cues may affect habitat associations at different spatial scales (Meyer and Thuiller 2006, Lele et al. 2013, Grinde and Niemi 2016).

For forest songbirds, forest type, amount, stand age, edge, and configuration are important predictors of second-order habitat use (i.e. breeding territory placement) and density (i.e. the number of individuals per unit area; MacArthur and MacArthur 1961, Johnson 1980, Jones 2001, Smith et al. 2011). Less is known about third-order habitat use (e.g., the intensity of use of different patches within a home range; Johnson 1980) by forest songbirds (but see Marzluff et al. 2004). Third-order habitat use can only vary within the resource units included in a home range, so it may be more strongly influenced by local vegetation features (e.g., understory density) than second-order use (Johnson 1980, Meyer and Thuiller 2006). To date, most studies of Canada Warbler habitat selection or use have been conducted at the second-order level.

Although vegetation characteristics are strong predictors of habitat use by forest songbirds, there is growing evidence that social cues are also important (reviewed by Ahlering et al. 2010). Conspecific attraction, a phenomenon whereby individuals are more likely to use areas near conspecifics, despite more or equally suitable vegetation conditions existing elsewhere (Stamps 1988, Ahlering et al. 2010), may be particularly important for Canada Warblers. This species has a short breeding season relative to other migratory songbirds (Flockhart 2007), leaving limited time for individuals to assess habitat quality and search for mates. Settling in areas near conspecifics can reduce search time when deciding where to place territories (Fletcher 2006) and can increase mating opportunities (Stamps 1988, Wagner 1998, McKellar et al. 2014). Thus, conspecific attraction should occur more frequently in fragmented forest landscapes, where mates can be difficult to locate (Fletcher 2006), which in turn may influence how we perceive Canada Warblers' responses to forestry activities.

In some cases, conspecific attraction may result in some individuals using areas that do not maximize fitness (Beauchamp et al. 1997, Pärt et al. 2007). For example, individuals that settle on the periphery of patchily distributed habitat due to conspecific attraction may experience lower breeding success (Nocera et al. 2009). Hence, per capita productivity may not always be correlated with the density of breeding individuals (Van Horne 1983, Skagen and Yackel Adams 2011, Flockhart et al. 2016). Alternatively, suitable habitat may be underutilized when settlement cues (e.g., conspecific cues) are not available (Gilroy and Sutherland 2007). Conspecific attraction can also result in negative density-dependent effects on breeding success, due to increased resource competition, lower ability to retain mates (Hagan et al. 1996, Szymkowiak et al. 2016), or higher predation or parasitism rates for individuals in clusters compared with isolated individuals (Brown 1969, Gilroy and Sutherland 2007). There is a need to understand the importance of

vegetation cues and conspecific attraction on habitat use by the Canada Warbler, as resource availability alone may not be sufficient to determine which areas will be used (Campomizzi et al. 2008, Cunningham et al. 2016) and whether or not those areas provide suitable breeding sites.

We quantified the influence of postharvest conditions, local vegetation characteristics, and conspecific attraction on the density, hierarchical habitat use, and reproductive activity of male Canada Warblers within extensively harvested landscapes in boreal Alberta, Canada. Specifically, we estimated (1) density, (2) home range placement (second-order habitat use), (3) within-home-range space use (third-order habitat use), and (4) the probability of pairing and fledging young. Based on the vegetation cue hypothesis and the association of Canada Warblers with old-growth forest in boreal Alberta (Schieck et al. 1995, Cooper et al. 1997, Ball et al. 2016), we predicted that increased harvesting (presence and area) would have negative effects on Canada Warbler density and habitat use, whereas time since harvest and the retention of large unharvested fragments would have positive effects. Based on the orders-of-selection hypothesis, we predicted that postharvest condition (stand-level vegetation) would be more important at the second-order level of habitat use, while local vegetation variation would be more important at the third-order level. Based on previous research on the breeding success of Canada Warblers in the eastern portion of their range (Hallworth et al. 2008a), we predicted that males would adjust home range sizes to compensate for habitat quality differences, resulting in no differences in the probabilities of pairing or fledging young between postharvest and unharvested stands or between bird age groups (second-year vs. after-second-year birds). Lastly, based on the conspecific attraction hypothesis, we predicted that male Canada Warblers in our fragmented study landscape would use areas closer to conspecifics independently of vegetation cues, that conspecific proximity would explain more variation in density and second-order habitat use than third-order habitat use, and that increased density would reduce the probability of males pairing and fledgling young.

METHODS

Study Area

We worked in 3 areas, near Lesser Slave Lake (55.4313°N, 115.6039°W), Calling Lake (55.2103°N, 113.1933°W), and Lac La Biche (54.7696°N, 111.9725°W; Figure 1), in the Boreal Central Mixedwood Natural Subregion of northern Alberta, Canada. This subregion is dominated by quaking aspen (*Populus tremuloides*) and quaking aspen–white spruce (*Picea glauca*) mixedwood stands. We selected these study areas based on known presence of Canada Warblers in extensively harvested landscapes (Ball et al.

2016). The primary land use in these areas was logging for pulp and lumber production, but conventional oil and gas extraction also occurred. Seismic lines and gravel roads were common across the 3 study areas.

Sampling Design

Density and second-order habitat use. Using Geographic Information Systems (GIS), we preselected 132 square survey blocks (17.3 ha each; Figure 2; $n = 53$, 35, and 44 for the Lesser Slave Lake, Calling Lake, and Lac La Biche study areas, respectively) within aspen-dominated stands (Alberta Environment and Parks 2008). Blocks represented a gradient of harvest amount (0–100% of survey block harvested) and years since harvest (0–30 yr postharvest; Appendix Table 2). Data were provided by the Alberta Biodiversity Monitoring Institute (ABMI, Edmonton, Alberta, Canada; http://www.abmi.ca/). A subset of survey blocks included riparian buffers ($n = 44$), isolated forest fragments ($n = 31$), or no harvest ($n = 21$), while the remaining blocks included a portion of ≥ 1 contiguous unharvested stands ($n = 36$) expanding into the survey block. Survey blocks were oriented north–south, except for those in riparian areas, which were oriented parallel to and ~60 m away from the water body.

From May 27 to June 15, 2014, in the Lesser Slave Lake and Calling Lake areas, and from June 1 to July 6, 2015, in the Lac La Biche area, we determined the number of territorial males at point count stations and estimated the total number of males within a 60 m buffer around each survey block (hereafter, "density") using playback and point count surveys between 0500 and 1400 hours. In each survey block, we conducted a single point count (50-m radius) at each of 4 equally spaced sampling stations (100 m apart) along 4 300-m transects (Figure 2), resulting in 16 point counts per survey block, with a total of 2,112 point counts across the 3 study areas. We recorded the total number of territorial males detected by sight or sound at each station using the following protocol: (1) 1 min silence; (2) 30 s of songs of conspecifics; and (3) 1 min silence. We considered a point count station used if ≥ 1 male was detected (second-order use). We used this truncated point count method to maximize the number of points that we could sample (Buskirk and McDonald 1995). The probability of detecting a bird at a point count is affected by (1) the probability that a bird will be detectable (i.e. will sing or be visibly present), and (2) the probability that an observer will detect a bird that is present (e.g., in different habitat types; Simons et al. 2007, Sólymos et al. 2013). Although we did not explicitly assess detection probability, and acknowledge that it was likely not 1.0, we used closely spaced point count stations and song playback to increase detection probability by eliciting countersinging responses (i.e. to increase visibility and audibility; Kubel and Yahner 2007). We also walked to the location of each male
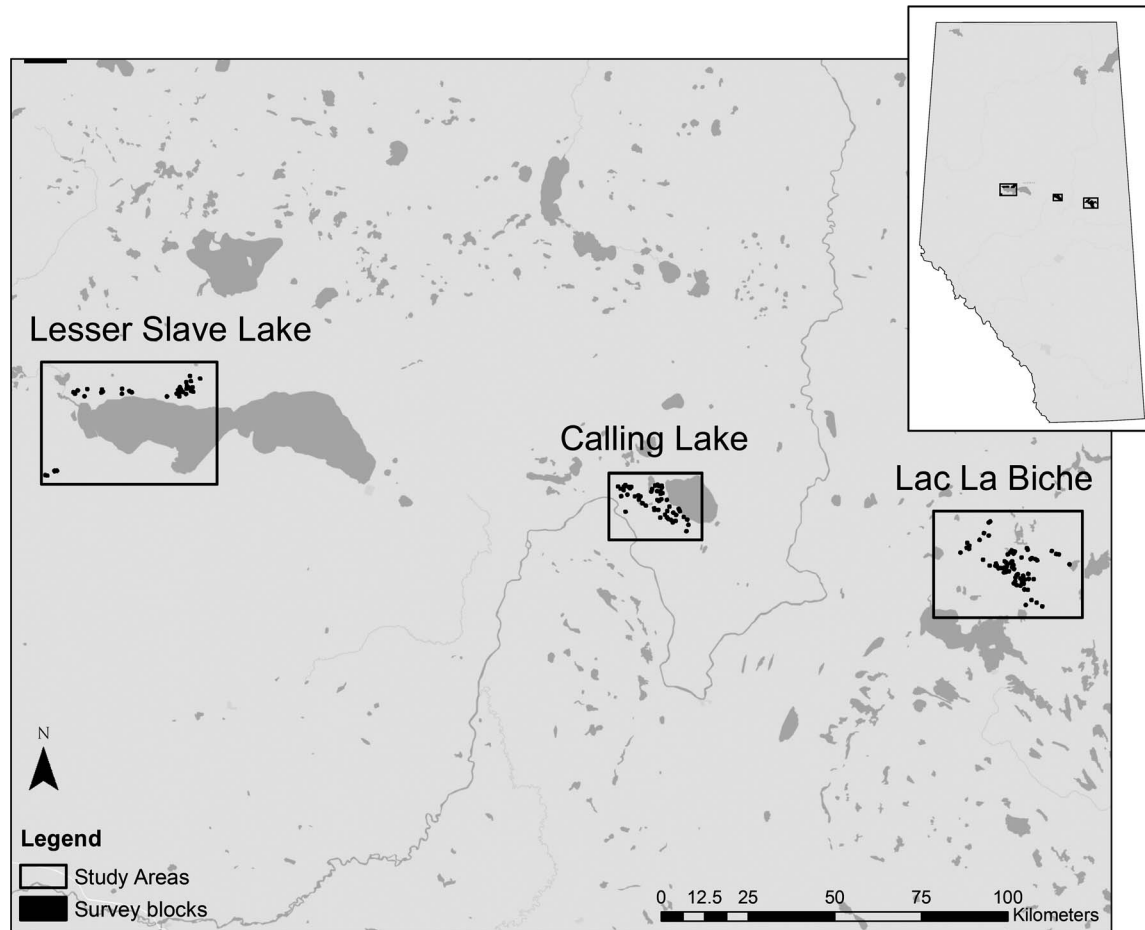
FIGURE 1. Survey block locations (17.3 ha each, $n = 132$) in the 3 study areas used to examine the responses (density, habitat use, and reproductive activity) of Canada Warblers to forestry and conspecifics in Alberta, Canada.
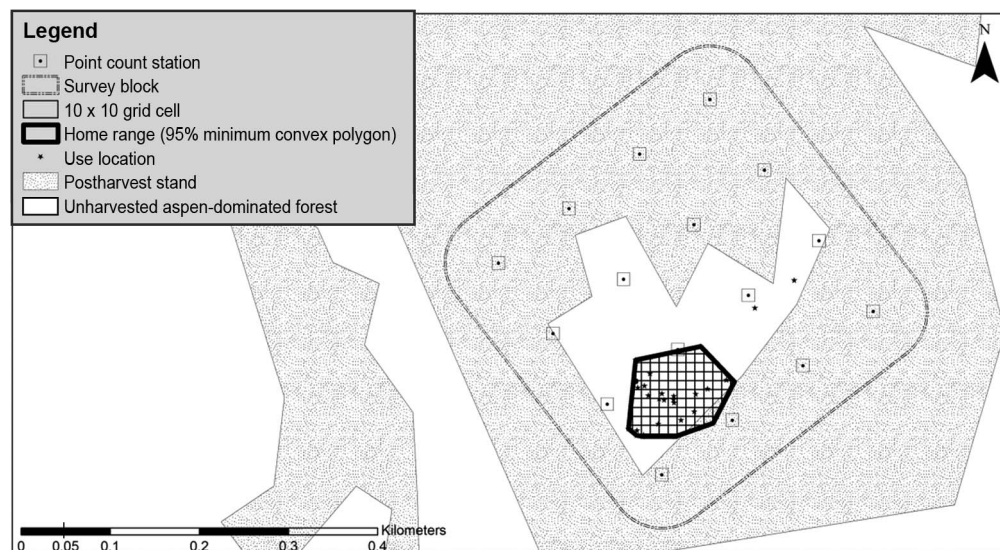

FIGURE 2. Example of a survey block (17.3 ha) where playback point counts were conducted in aspen-dominated forest in Alberta, Canada, within which a territorial male Canada Warbler home range overlaps postharvest stands. Corresponding 10×10 m grid cells overlaid on the home range were used to quantify within-home-range space use.

detected during a point count and recorded the GPS location, to ensure that detected males were located within the defined survey area. Canada Warbler effective detection radius (EDR: the distance from the sampling point at which observers detect as many birds beyond the EDR as remain undetected within the EDR) is estimated at 60 m (Matsuoka et al. 2012). Thus, we only included males that we detected within a 60-m buffer around each point count location. Furthermore, although detection distance can be lower in regenerating compared with older stands, Schieck (1997) found that observers detected all broadcast vocalizations of songbirds within 50 m of the broadcast speaker, regardless of forest age, suggesting that, although our absolute detection probability probably was not perfect, the relative pattern between harvest treatments was likely comparable.

Third-order habitat use. We used songs of conspecifics and mist nets to capture territorial males ($n = 42$), but some could not be captured (hereafter, "unbanded"; $n = 20$). We aged captured males as second-year (SY) or after-second-year (ASY) using molt limits (Pyle 1997), and fitted them with a unique color band combination to identify individuals on subsequent visits. We also tracked unbanded males by relying on spatial location from the previous visit and/or song characteristics, along with locations of banded neighbors, to identify these individuals (Reitsma et al. 2008, Lankau et al. 2013).

We began tracking males 24 hr after capture and conducted weekly tracking bouts of each individual for ∼6 weeks to delineate home ranges and to assess space use within the home range. We followed birds between 0500 and 1900 hours (∼95% of tracking sessions occurred between 0500 and 1400 hours). Following the approach used by Barg et al. (2005; see also Hallworth et al. 2008a, Reitsma et al. 2008), we recorded the location of each individual every 5 min within the 30–60 min tracking period ("burst"). Barg et al. (2005) suggested that this method is preferable to sequential sampling (e.g., taking one use location per day) for birds with short breeding seasons as it allows the observer to generate a large enough sample size of use locations. Furthermore, because a songbird is able to traverse the length of its territory within this sampling interval, successive locations should be biologically independent (Otis and White 1999, Barg et al. 2005). We designed daily sampling rotations among males and observers to avoid introducing a temporal or observer bias. If males were not located after 3 attempted burst sampling bouts, we conducted no further bouts for those males.

We were specifically interested in habitat use patterns in and near postharvest stands. Hence, to determine how much postharvest forest was used, we tracked 55 males that had been detected <200 m from postharvest stands during block surveys ($n = 23$, 14, and 18 males for Lesser Slave Lake, Calling Lake, and Lac La Biche, respectively). We also tracked 7 birds that had been detected >200 m from postharvest stands to compare home range sizes and age structure of males using unharvested stands only vs. those using both postharvest and unharvested stands. We tracked birds in the Lesser Slave Lake ($n = 25$) and Calling Lake ($n = 16$) areas from May 25 to July 14, 2014, and in the Lac La Biche ($n = 21$) study area from June 3 to July 18, 2015, obtaining 30 location points per male over the season. Due to the small sample size ($n = 30$), we used 95% minimum convex polygons (MCP) to delineate the home range boundaries of each male (ArcGIS 10.2, ESRI, Redlands, California, USA), rather than adaptive kernel techniques (Seaman et al. 1999). The main disadvantages of using an MCP method are that the researcher cannot distinguish unused areas, the configuration of used spaces, or the influence of peripheral locations (Barg et al. 2005). To address these issues, we overlaid a 10 m × 10 m grid on home ranges that overlapped postharvest stands (>0% area harvested; $n = 24$; total of 3,147 grid cells) and calculated within-home-range space use (third-order habitat use) as the number of use locations within each grid cell in the home range (Figure 2).

Reproductive activity. We used reproductive index ranking to assess reproductive activity (Vickery et al. 1992, Diemer and Nocera 2016). During each tracking bout, we recorded observations of reproductive activity and classified each male into 1 of 3 categories using a modified version of the Vickery et al. (1992) reproductive index rank. We considered males paired (rank = 1) if they were observed with a female, building a nest, or with an active nest (i.e. eggs or nestlings). We considered males to have successfully fledged ≥1 young (rank = 2) if they were observed with ≥1 fledgling (Howlett and Stutchbury 2003, Reitsma et al. 2008, Haché et al. 2013) or were observed carrying food to multiple spots within the territory (Flockhart et al. 2016). We considered males unpaired (rank = 0) if we did not detect any evidence of reproductive activity (Bayne and Hobson 2001, Reitsma et al. 2008).

Vegetation and conspecific cues. We obtained forestry variables from the Alberta Biodiversity Monitoring Institute Cutblock layer for 2014 and selected variables to represent postharvest condition, such as presence, amount, and age of postharvest stands, and presence, size, and edge of unharvested fragments (Figure 3, Appendix Table 3). We used primarily area-based measurements for density models for which the survey block was the sampling unit; we used primarily presence and distance-based measurements (i.e. proximity to features) for habitat use models for which point count stations (second-order use) and grid cells (third-order use) were the sampling units. We controlled for the following 2 confounding environmental variables, which are important predictors of Canada Warbler density in Alberta (Ball et al. 2016): (1)
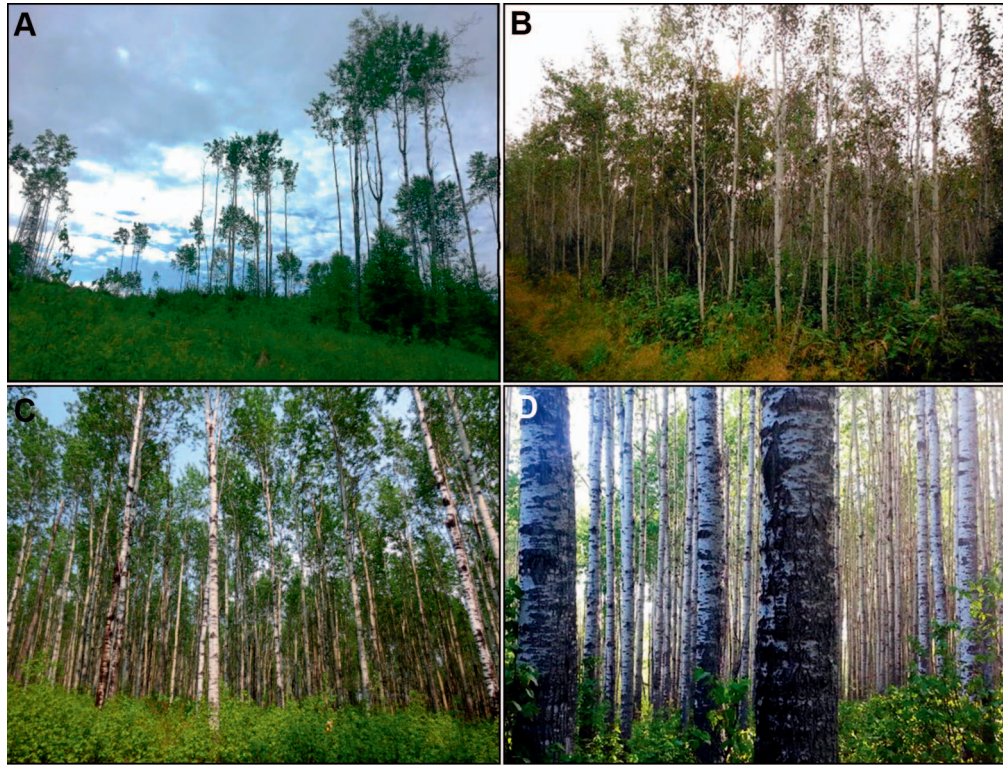
FIGURE 3. Examples of postharvest and unharvested conditions in aspen-dominated stands in Alberta, Canada, including: (**A**) <5 yr postharvest with retained unharvested fragments; (**B**) 5–10 yr postharvest; (**C**) 11–30 yr postharvest (photo credit: Kiirsti Owen); and (**D**) >75-yr-old unharvested stand.

hydrographic variables (AltaLIS; http://www.altalis.com/products/base/20k_base_features.html) such as rivers (i.e. natural hydrographic features ≥20 m wide with defined banks), streams (i.e. natural linear hydrographic features <20 m wide with obvious shorelines), and lakes (i.e. bodies of water with a well-defined open water area and shoreline); and (2) the compound topographical index (CTI), a measure of wetness as a function of slope, solar insolation, and terrain wetness (Gessler et al. 1995) developed for northern Alberta (S. Nielsen, University of Alberta; species.abmi.ca). Low CTI values indicate areas with small catchments and steep hills, while high values indicate large catchments and gentle slopes.

For each survey block (density), we extracted: (1) the percentage of area harvested (0–100%); (2) the area-weighted age of postharvest stands (i.e. the sum of [area {m^2} of a postharvest stand within a survey block × years since harvest]/survey block area {m^2}); (3) contrast-weighted edge density (CWED; i.e. the length of postharvest–unharvested stand edge × year of harvest); (4) the presence of isolated unharvested fragment(s) (0 = absent, 1 = present); (5) the amount (m^2) of old-growth (>125 yr) aspen-dominated forest within a 1-km buffer around each survey block; (6) the distance (m) to the nearest block occupied by ≥1 Canada Warbler; (7) the distance (m) to the nearest stream, river, and lake; and (8) average CTI.

For each point count station (second-order habitat use), we extracted the same hydrographic and CTI variables as well as: (1) presence vs. absence of postharvest stand (postharvest = 1, unharvested = 0); (2) origin year of stand; (3) distance (m) to postharvest–unharvested edge; (4) size (m^2) of unharvested fragment (if point was in unharvested stand); and (5) distance (m) to nearest point count station occupied by a conspecific.

To determine what factors influenced within-home-range space use (third-order habitat use), we extracted the same variables as described for second-order use at the centroid of each 10 × 10 m grid cell within the home range, in addition to the age of the tracked male (SY vs. ASY). We also used these variables to explain variation in reproductive activity, in addition to: (1) the percent of the home range overlapping postharvest stands; (2) the number of use locations within postharvest stands; (3) the density of postharvest–unharvested edge within the home range; and (4) the density of males in the survey block.

We conducted ground-based local vegetation surveys at a subset of point count stations ($n = 89$) and survey blocks ($n = 49$) from mid-July to mid-August. For blocks with no

harvesting, we randomly selected one point count station at which to conduct vegetation surveys. For blocks with both unharvested and postharvest stands, we randomly selected one point count station for each treatment. Vegetation surveys were also conducted in a subset of grid cells within all home ranges (2–4 per home range, $n = 84$), one at the center of the home range and a further 2 (for small home ranges) or 3 in randomly selected grid cells within the home range. We measured: (1) the number of trees (>8 cm diameter at breast height [dbh]); (2) average tree size (dbh [cm]); (3) percent canopy cover; (4) canopy height (m) within an 11.3-m radius; (5) percent green cover (live ground cover); (6) percent shrub cover; (7) percent downed log cover; (8) number of small shrubs (<2.5 cm stem diameter); (9) number of large shrubs ($>2.5–8$ cm stem diameter); and (10) organic litter depth (mm) within a 5-m radius (Martin et al. 1997, Hallworth et al. 2008b, Flockhart et al. 2016).

Statistical Analysis

We used negative binomial regression to examine variation in Canada Warbler density. We started by building a baseline model using nuisance and confounding environmental variables (i.e. day of survey, time of day, study area [1 = Lesser Slave Lake, 2 = Calling Lake, 3 = Lac La Biche], observer [$n = 8$], CTI, and distance to lake, river, and stream). We used a backward step selection process to select the nuisance and confounding variables that resulted in the best model fit based on Akaike's information criterion corrected for small sample sizes (AIC_c). We then added other variables to the resulting baseline model using a 2-stage approach. First, we tested for effects of postharvest conditions and ranked these models using AIC_c to determine which combination of forestry and baseline variables resulted in the best model fit. Second, we tested whether adding a variable for conspecific proximity improved the stage 1 model using the same model selection approach. We used an α-level of $P < 0.05$ to determine the significance of single variables. We also tested for nonlinear effects (squared, quadratic, and cubed). When variables with a quadratic term were included in the top-ranked model, we tested whether a threshold response provided a better fit using package segmented (Muggeo 2008) in R (R Core Team 2014).

We used mixed effects logistic regression, in which survey block ID was added as a random effect, to explain variation in second-order habitat use, and mixed effects negative binomial regression with bird ID as a random effect to assess third-order habitat use. We used the same model building process as we used for density, with the addition of a third stage. Using the subset of point count stations (second-order use) or grid cells (third-order use) with ground-based local vegetation data, we tested whether adding local vegetation variable(s) to the best model from stage 2 improved model fit. In addition, for the subset of known-age males, we tested for age*presence vs. absence of postharvest stand interactions (third-order use) at stage 1.

We used ordered logistic regression to analyze reproductive activity. We analyzed the probability of pairing (paired vs. unpaired) separately from the probability of fledging young (successfully fledged young vs. paired only), as pairing (i.e. attracting a mate) and fledging young (i.e. successfully raising ≥ 1 young to the fledgling stage) may be driven by different mechanisms (Reitsma et al. 2008). First, we evaluated whether second-order variables or third-order variables influenced the probability of pairing using the same 3-stage modeling approach previously described, with the addition of male age as a baseline variable and the density of conspecifics as a variable in stage 2. We then used the same modeling approach to test for effects of second- and third-order variables on the probability of males fledging ≥ 1 young.

We used a Wilcoxon signed rank test to test for differences in home range sizes between males who only used unharvested stands vs. individuals who used both postharvest and unharvested stands.

We analyzed use and density models using package glmmADMB (Skaug et al. 2011) in R 3.1.2 (R Core Team 2014) and reproductive activity models using the ologit command in STATA 13 (Hamilton 2012). We report the standardized regression coefficient (β) $\pm$ SE, test statistic (z), and P-value (P) for each independent variable for each top regression model, and the test statistic (W) and P-value for the Wilcoxon signed rank test. For the top model in each model set, we calculated pseudo r^2 values as a measure of goodness-of-fit using package MuMIn in R (Bartoń 2013).

RESULTS

Density

We detected 96 males during block surveys: 51 in the Lesser Slave Lake study area, 10 in the Calling Lake area, and 35 at Lac La Biche. Density per block ranged from 0 to 9 territorial males (mean = 0.75 $\pm$ 0.13), but males were detected in only 29% of the survey blocks (38/132). The top-ranked forestry model (Supplemental Material Table S1) included a negative cubic effect of percent postharvest stands ($\beta = -0.81 \pm 0.27$; Figure 4A, Table 1), indicating a steeper decline in density between unharvested and moderately harvested blocks than between moderately and highly harvested blocks. This model was improved by adding distance to the nearest occupied block ($\beta = -0.32 \pm 0.18$; model weight = 0.77; Table 1, Supplemental Material Table S1), but this effect was not significant.
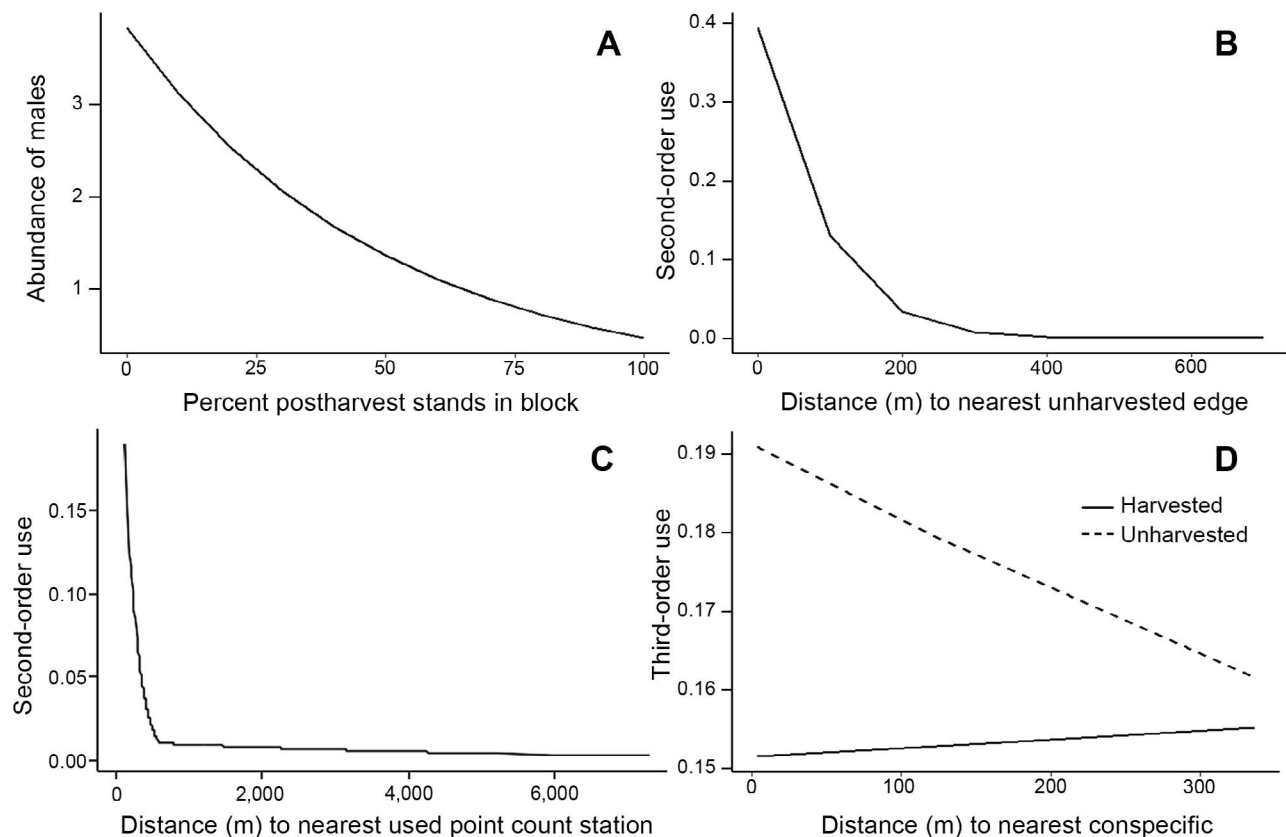
FIGURE 4. Predicted (**A**) density in survey blocks as a function of increasing amounts of postharvest stands; (**B**) second-order use of postharvest stands in response to distance (m) to the nearest unharvested edge; (**C**) second-order use of postharvest stands as a function of increasing distance (m) to the nearest point count station used by a conspecific; and (**D**) third-order use in harvested areas (solid line) and unharvested areas (dashed line) in response to distance (m) to the nearest conspecific for territorial male Canada Warblers in Alberta, Canada.

Second-order Use

We detected $\geq$1 territorial male at 91 (4%) point count stations (48 at Lesser Slave Lake, 10 at Calling Lake, and 33 at Lac La Biche). The top-ranked forestry model included a presence of postharvest stands*distance to the nearest edge interaction ($\beta = -3.52 \pm 1.13$; Table 1, Supplemental Material Table S1) suggesting that males were more likely to place their home ranges in postharvest stands that were close to adjacent unharvested stands than in core harvested areas (Figure 4B). A nonlinear (squared) negative effect of distance to the nearest occupied point count station ($\beta = -1.45 \pm 0.37$; Table 1) improved the model further (Supplemental Material Table S1), indicating that second-order habitat use decreased with increasing distance to the nearest occupied point count station up to $\sim$600 m ($\pm$ 125 m SE), after which proximity to conspecifics had no effect (Figure 4C). The addition of local vegetation variables did not improve stage 2 models (Supplemental Material Table S1).

Third-order Use

Average home range size was 0.94 ± 0.11 ha. Postharvest stands were included in the home ranges of 44% (24/55) of males captured <200 m from a postharvest stand (i.e. 31/55 males exclusively used unharvested stands). However, the home ranges of most of these males (15/24) had limited overlap (<20%) with postharvest stands. The mean size of home ranges that included postharvest stands (1.27 $\pm$ 0.22 ha, $n = 24$) was larger than that of home ranges that did not include postharvest stands (0.72 $\pm$ 0.08 ha, $n = 38$; $W = 305$, $P < 0.05$).

The best model predicting third-order habitat use included a positive effect of distance to the nearest postharvest–unharvested edge (Supplemental Material Table S1), suggesting that space use within the home range increased with distance from an edge ($\beta = 0.61 \pm 0.19$; Table 1). The model was improved by adding an interaction between postharvest stand presence and proximity to conspecifics ($\beta = 0.33 \pm 0.17$, model weight = 0.70; Supplemental Material Table S1). Space use by

TABLE 1. Variables and coefficients from top-ranked models (Supplemental Material Table S1 and S2) predicting: (**A**) the density of males ($n = 132$); (**B**) second-order use ($n = 2,112$); (**C**) third-order use ($n = 3,147$); (**D**) the probability of pairing success ($n = 62$); and (**E**) the probability of fledging young ($n = 51$) for Canada Warblers breeding in northern Alberta, Canada. N is the sample size of the model, β is the standardized coefficient, SE is the standard error, z is the test statistic, and P is the P-value.

Variables in top models [§]	N	β	SE	z	P
(**A**) Density of males					
CUT[3]	132	−0.81	0.27	−3.06	<0.001
NEAROCC	132	−0.32	0.18	1.66	0.08
STUDYAREA, CL	132	−2.11	0.54	−3.65	<0.001
STUDYAREA, LLB	132	1.98	0.57	−3.42	<0.001
CTI	132	−0.67	0.19	−3.62	<0.001
DISTRIVER	132	−0.32	0.23	−1.39	0.06
(**B**) Second-order use					
IFCUT*DISTEDGE	2,112	−3.52	1.13	−3.11	<0.005
NEAROCC	2,112	−1.45	0.37	−4.31	<0.001
STUDYAREA, CL	2,112	−1.72	0.49	−3.50	<0.001
STUDYAREA, LLB	2,112	−1.10	0.47	−2.40	0.02
DISTRIVER	2,112	−0.35	0.19	−1.82	0.07
(**C**) Third-order use					
IFCUT*NEAROCC	3,147	0.33	0.17	1.93	0.05
DISTEDGE	3,147	0.61	0.19	3.13	<0.001
DISTSTREAM	3,147	0.28	0.12	2.37	0.02
STUDYAREA, CL	3,147	0.58	0.27	2.12	0.04
STUDYAREA, LLB	3,147	0.83	0.43	1.94	0.05
(**D**) Pairing success					
CONSDENSITY[2]	62	−0.82	0.30	−2.70	<0.001
(**E**) Probability of fledging young					
SHRUBCOV	51	−0.99	0.54	−1.83	0.07
STUDYAREA, CL	51	2.14	1.34	1.60	0.10
STUDYAREA, LLB	51	1.67	1.24	1.34	0.20
DISTRIVER	51	1.48	0.60	2.47	0.01

[§] CUT[3] is a cubed term representing the percent of a survey block comprised of postharvest stands, NEAROCC is the distance to the nearest conspecific, DISTRIVER is the distance (m) to the nearest river, IFCUT is the presence or absence (coded as 1 or 0) of a postharvest stand at a point count station, DISTEDGE is the distance (m) to the nearest postharvest or unharvested edge, DISTSTREAM is the distance (m) to the nearest stream, CTI is the average compound topographic index, CONSDENSITY[2] is a squared term representing the number of conspecifics (males) in the survey block, and SHRUBCOV is the percent shrub cover <50 cm in height. CL is the Calling Lake study area, and LLB is the Lac La Biche study area.

males was higher in unharvested than in postharvest parts of the home range, and space use in unharvested parts of the home range was 1.1 times higher near conspecifics (<50 m) than farther from conspecifics (350 m). In contrast, space use in postharvest stands was not affected by proximity to conspecifics (Table 1, Figure 4D, Supplemental Material Table S1). No local vegetation variables were significant, nor did they improve upon model stage 2 (Supplemental Material Table S1). We also did not find significant differences in within-home-range space use of postharvest stands between male age classes (Supplemental Material Table S1).

Reproductive Activity

We tracked 18 ASY males, 24 SY males, and 20 unbanded males of unknown age. We confirmed pairing for 84% of males and evidence of fledging ≥1 young for 69% of males. For pairing success, the top model included only a negative nonlinear (squared) effect of the density of conspecifics (β

$= −0.82 ± 0.30$; Table 1, Supplemental Material Table S2), indicating that pairing success was higher for males at low and mid densities (i.e. 1–3 males per block) than at high densities (Figure 5). Stand-level forestry variables and local vegetation variables did not improve models. For the probability of fledging ≥1 young, inclusion of average shrub cover improved upon the baseline model (β $= −0.99 ± 0.54$; Table 1, Supplemental Material Table S2), but this single variable was not significant. The model was not improved when proximity to conspecifics or stand-level forestry variables were added.

DISCUSSION

Forestry Effects

Male Canada Warbler densities decreased with increasing amounts of harvesting, and territorial males were less likely to have home ranges in postharvest than in unharvested stands (second-order habitat use). These
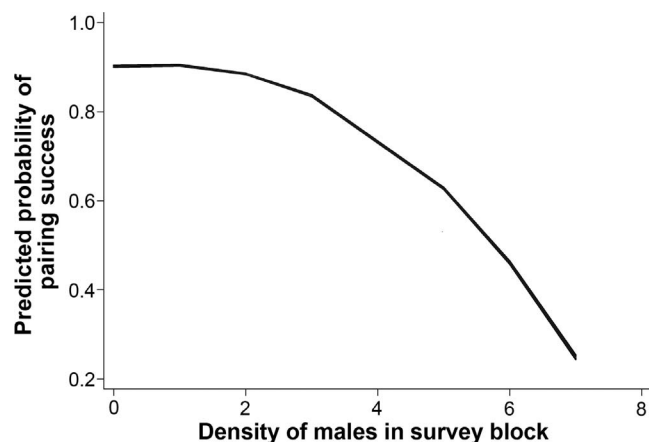
FIGURE 5. Predicted probability of pairing success of male Canada Warblers in response to the density of conspecifics in Alberta, Canada.

findings are consistent with the results of other studies in the western boreal forest (Schieck et al. 1995, Cooper et al. 1997, Schieck and Song 2006, Ball et al. 2016). In this region, Canada Warblers tend to be most abundant in old-growth deciduous stands and in stands with increasing canopy height and canopy cover (Haché et al. 2014, Ball et al. 2016). Unharvested old-growth stands (>125 yr postharvest) provide vertical stratification, structural diversity, and high densities of large trees (Huettmann 2003), which seem to be more important to Canada Warblers than vegetation conditions typical of younger stands. Although some boreal studies have suggested that residual retention of unharvested fragments in harvested areas or in regenerating stands 11–30 yr postharvest may support some Canada Warblers (Schieck and Hobson 2000, Schieck and Song 2006), we did not find evidence that retention of unharvested fragments (≤5 ha) or regeneration of harvested stands (≤30 yr postharvest) mitigated the effects of forest harvest on warbler density. It is likely that only relatively large fragments will be occupied (Ball et al. 2016), and that use of fragments is relatively uncommon compared with use of contiguous forest (Schieck and Hobson 2000, Schieck and Song 2006).

Our results also suggest that when males do occur in postharvest stands, their home ranges are located near the edges of adjacent unharvested stands. This is consistent with results from West Virginia, USA, where Canada Warblers used clear-cuts in areas closer to, rather than farther from, edges, whereas this relationship with edges was not observed in areas with heavy partial harvests (i.e. clear-cuts with residual trees plus deferment and shelter-wood cuts) or light partial harvests (i.e. single-tree selection and diameter-limit cuts; Becker et al. 2012).

Males spent more time in areas farther from, rather than closer to, the postharvest–unharvested edges within their

home ranges, suggesting that when males cannot secure their full home ranges in unharvested stands (e.g., due to competition), they must use both sides of the edge interface to be near adjacent unharvested stands. We also found that males who used postharvest stands had larger home range sizes, suggesting that resource availability is lower in postharvest than in unharvested stands and therefore that males must defend larger areas in postharvest stands to secure necessary resources (Smith and Shugart 1987, Haché et al. 2013, Newmark and Stanley 2016). Hallworth et al. (2008a) also reported larger home ranges of Canada Warblers in postharvest stands.

Conspecific Effects
We found higher densities of males close to survey blocks occupied by conspecifics, irrespective of postharvest stand attributes. Our results lend further support to the hypothesis that Canada Warblers have a clustered breeding dispersion (Reitsma et al. 2009, Flockhart et al. 2016). Individual males were more likely to have home ranges near conspecifics, and used unharvested parts of their home ranges near conspecifics more intensively. Conspecific attraction may be driving the use of postharvest stands where conspecifics are present in adjacent unharvested stands. This within-home-range use pattern also likely reflects the need for greater territorial defense in the unharvested portion of the home range, where birds tended to have more neighbors (Lankau et al. 2013). Furthermore, conspecific attraction could explain why previous studies in the boreal forest region have detected Canada Warblers in postharvest stands (Schieck and Hobson 2000, Schieck and Song 2006). Hallworth et al. (2008b) also suggested that the proximity of unharvested and postharvest study sites in New Hampshire, USA, might have influenced the use of postharvest stands by Canada Warblers.

We did not find evidence that local vegetation features influenced second-order habitat use. One possible explanation is that some males (e.g., earlier-arriving males; Hallworth et al. 2008b) select areas based on vegetation cues, whereas other males, who select areas based on conspecific cues, might use a wider range of vegetation attributes (Nocera et al. 2009). Hence, conspecific attraction could confound local vegetation use patterns. We also did not find evidence that local vegetation influenced third-order habitat use. Other studies have shown that shrub density is an important vegetation feature across the Canada Warbler breeding range (Palmer-Ball 1996, Hallworth et al. 2008b, Chace et al. 2009, Flockhart et al. 2016). Because we included fine-scale and coarse-grained vegetation metrics in the same models, the inclusion of the latter could have masked the effects of the former. Sample size for our ground-based vegetation

surveys was small, which also may have limited our ability to detect such effects.

Finally, we did not find a significant difference in the within-home-range space use (third-order use) of post-harvest stands between ASY and SY males. Many territorial birds exhibit ideal despotic distributions, in which dominant individuals (e.g., older males) obtain higher-quality home ranges and experience higher reproductive success (Holmes et al. 1996, Ridley et al. 2004) than subordinate individuals. Conspecific attraction can also sometimes result in younger males using lower-quality areas around the periphery of older males' home ranges (Nocera et al. 2009). Our results are more consistent with a variation of an ideal free distribution, in which adjustments in home range size can compensate for differences in individual ability to obtain a high-quality home range (Fretwell and Lucas 1970, Haché et al. 2013). Hallworth et al. (2008a) also did not find a significant difference in the proportions of ASY vs. SY male Canada Warblers in undisturbed vs. second-growth stands.

Reproductive Activity

We found no effects of forest harvesting on the probability of a male Canada Warbler pairing or fledging young. These results are not surprising because most males included only low proportions of postharvest stands within their home ranges. Adjustments in home range size can also result in similar per capita productivity (Fretwell and Lucas 1970, Ridley et al. 2004, Haché et al. 2013). Flockhart et al. (2016) suggested that Canada Warbler home range size might be a function of habitat quality, whereby home ranges in high-quality habitat are smaller due to pressures from competition and territory defense.

We found evidence of a negative nonlinear relationship between density and pairing success. However, density did not influence the probability that paired males would fledge young. Males may experience negative density-dependent crowding effects on pairing, whereby they are less able to attract or retain a mate due to competition (Hagan et al. 1996, Szymkowiak et al. 2016). Alternatively, observed pairing success could be explained by the presence of hidden leks (Wagner 1998), where unpaired males cluster around paired males to obtain extrapair copulations with females, resulting in higher densities but increasing proportions of unpaired males (McKellar et al. 2014). Extrapair copulations are likely common in Canada Warblers (Reitsma et al. 2009), although empirical studies have not been conducted. Flockhart et al. (2016) found evidence that density affected the breeding success of Canada Warblers in Lesser Slave Lake Provincial Park, but they did not distinguish between pairing and the probability of fledging young, so whether this finding resulted from a large number of unpaired males or other density-dependent effects remains unknown.

Male age also did not affect the probability of pairing or fledging young. The latter result is consistent with the findings of McKellar et al. (2014) and studies of Canada Warblers from the eastern portion of the breeding range (e.g., Reitsma et al. 2008). Pairing success is often linked to traits that should be positively correlated with male age, such as suitable site selection (Nocera et al. 2009), prior breeding experience with the same mate (McKellar et al. 2014), and females' selection of males with specific physical attributes (e.g., brighter plumage; Rappole 1983, Reitsma et al. 2008). However, if sites from previous years are no longer suitable due to disturbance, or if female mates do not survive until the subsequent breeding season, some of these age-related advantages may not be apparent.

Average shrub cover (of shrubs <50 cm in height) improved the model assessing the probability that a paired male would fledge young, but the (negative) effect was not significant. Flockhart et al. (2016) found that shrub cover was higher in smaller territories and that smaller territories tended to have lower breeding success. Reitsma et al. (2008) suggested that, although the density of shrubs >1 m in height is an important cue for nest site selection, dense cover at low horizons may prevent the growth of other ground cover features that are important to nesting Canada Warblers.

Management Implications

These results have several implications for prioritizing conservation areas and informing forest management to maintain or recover Canada Warbler breeding populations in western boreal regions. Forest harvesting seems to constitute a threat to breeding habitat as it results in lower use and densities of Canada Warblers than in unharvested stands. Postharvest stand age, local vegetation, presence and size of unharvested fragments, and landscape availability of unharvested stands do not appear to mitigate these effects. Postharvest stands near unharvested stands are much more likely to be used, indicating that the cores of harvested areas constitute less usable habitat and that Canada Warblers require at least some unharvested stands to support a home range. The use of postharvest stands by Canada Warblers in Alberta seems to be more strongly influenced by social factors than by the attributes of postharvest stands themselves. Conspecific attraction might also explain why seemingly suitable areas of unharvested stands are uninhabited, while similar areas can support very high densities (Reitsma et al. 2009). Conspecific attraction is likely important for other boreal birds, and could confound current knowledge about use or lack of use of harvested areas (Thériault et al. 2012). In scenarios in which intensive behavioral observations are not possible, incorporating proximity to undisturbed habitat and to conspecifics could provide valuable

information when prioritizing areas for boreal songbird conservation.

Hagan et al. (1996) suggested that crowding effects may be greater in small forest patches, emphasizing the importance of protecting large forested areas. We suggest that this management action may be even more important where conspecific attraction leads to crowding in fragments while other suitable areas remain unoccupied. Hence, protecting large tracts of contiguous unharvested stands near sites occupied by Canada Warblers will be important to provide enough suitable habitat to support high densities and prevent crowding effects. Long-term conservation efforts could include the use of playback experiments (i.e. vocalizations of conspecifics) during territory establishment (or during the postfledging period) to attract birds to suitable breeding areas (e.g., Albrecht-Mallinger and Bulluck 2016) where harvesting is less likely to occur. However, further research into the type and timing of conspecific cues used by Canada Warblers is necessary prior to using experimental conspecific attraction methods (Ahlering et al. 2010).

Critical habitat identification for species at risk in Canada is mandated (Government of Canada 2011). The results from our study will be important to land managers in the western boreal region that need to consider the protection of biodiversity and species at risk in land use planning. However, cumulative and carryover effects from other threats on the breeding and wintering grounds and along migratory routes may contribute to influence population dynamics on the breeding grounds (Norris et al. 2004, Holmes 2007, Rockwell et al. 2012). Future studies should address the relative importance of other threats across the annual cycle of Canada Warblers to inform international conservation planning.

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APPENDIX TABLE 2. Distribution of survey blocks (17.3 ha, $n = 132$) by percent postharvest stands (0–100% harvested) and number of years since harvest (<30 yr) across 3 study areas (Lesser Slave Lake, Calling Lake, and Lac La Biche) used to examine the responses (density, habitat use, and reproductive success) of Canada Warblers to forestry and conspecifics in Alberta, Canada. Percent postharvest stand categories >0 are not applicable (NA) to survey blocks that were completely unharvested. Values are zero where no survey blocks of that type (i.e. % postharvest stand and year of harvest) were sampled.

| | Percent postharvest stands in survey block | | | |
	0–25%	26–50%	51–75%	75–100%
Lesser Slave Lake				
0–10 yr	2	3	8	7
11–30 yr	1	6	4	2
Unharvested	2	NA	NA	NA
Total	5	9	12	9
Calling Lake				
0–10 yr	0	1	1	2
11–30 yr	2	4	25	13
Unharvested	4	NA	NA	NA
Total	6	5	26	15
Lac La Biche				
0–10 yr	0	3	4	1
11–30 yr	3	11	5	0
Unharvested	18	NA	NA	NA
Total	21	14	9	1
All study areas				
0–10 yr	2	6	13	10
11–30 yr	6	21	32	15
Unharvested	24	NA	NA	NA
Total	32	27	45	25

APPENDIX TABLE 3. List of postharvest conditions used to generate predictions for: (**A**) the density of males ($n = 132$); (**B**) second-order use ($n = 2{,}112$); (**C**) third-order use ($n = 3{,}147$); and (**D**) reproductive activity for territorial male Canada Warblers in managed forests in northern Alberta, Canada.

Model set	Presence and/or amount of postharvest stands	Age of postharvest stands	Edge	Presence and/or size of unharvested fragment
(**A**) Density	CUT³: Percent postharvest stands in survey block (cubed term)	YEAR: Represents the area-weighted average year of harvest in the survey block	CWED: A measure of fragmentation—the contrast-weighted edge density postharvest–unharvested edge in the survey block	PATCH: Represents whether there is an isolated, unharvested fragment in the cut block (1 = fragment, 0 = no fragment)
(**B**) Second-order use	IFCUT: Represents whether a point count station is in a postharvest stand (1) or not (0)	YEAR: Represents the origin year of the stand in which the point count station is located (harvest year for postharvest, stand origin for unharvested)	DISTEDGE: Represents the distance (m) to the nearest postharvest–unharvested edge	PATCH: Represents the area (m²) of the unharvested fragment in which a point count station is located
(**C**) Third-order use	IFCUT: Represents whether a grid cell is in a postharvest stand (1) or not (0)	YEAR: Represents the origin year of the stand in which the grid cell is located (harvest year for postharvest, stand origin for unharvested)	DISTEDGE: Represents the distance (m) to the nearest postharvest–unharvested edge	PATCH: Represents the area (m²) of the unharvested fragment in which a grid cell is located
(**D**) Reproductive activity	IFCUT: Represents whether the home range overlaps a postharvest stand (1) or not (0). PROPCUT: The proportion of the home range that overlaps a postharvest stand. NUMPTSCUT: The number of use locations within postharvest stands in the home range	YEARCUT: Represents the year of harvest of postharvest stands in the home range	DISTEDGE: Represents the distance (m) to the nearest postharvest–unharvested edge. EDGEINHR: The length of postharvest–unharvested edge in a home range	PATCH: Represents the area (m²) of the unharvested fragment that a home range overlaps