1   Effects of forestry and conspecifics on Canada Warblers

2   *RESEARCH ARTICLE*

3   **Forestry and conspecifics influence Canada Warbler (*Cardellina canadensis*) habitat use**

4   **and reproductive activity in boreal Alberta**

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12   **ABSTRACT**

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14   The Canada Warbler (*Cardellina canadensis*) is a threatened species in Canada due to an

15   annual decline of ~3% annually over the last 50 years. Forestry is potentially a cause of these

16   declines as some studies suggest Canada Warblers prefer old-growth forest. However, some

17   studies suggest Canada Warblers will use harvested areas. Differences in scale between habitat

18   use studies and behavioural phenomena such as conspecific attraction may explain these

19   discrepancies. We quantified multiple orders of habitat use and how this influenced reproductive

20   success to study the response of the Canada Warbler to forestry in Alberta while accounting for

21   conspecific attraction. Point count surveys and tracked individuals where used to understand

22   how density, 2nd and 3rd order habitat use, and probability of pairing and fledging young for male

23   Canada Warblers were influenced by amount, type and age of forest harvest. Forest harvesting

24   had negative effects on density and 2nd order use. Local vegetation structure, forest age within

25   post-harvest stands, or retention of unharvested fragments did not influence use of harvested

26   areas. However, males were more likely to use post-harvest stands in areas close to adjacent

27   unharvested stands and areas near conspecifics (2nd order). Within the home range, intensity of

28   use (3rd order) was highest in unharvested stands, closer to conspecifics, and further from post-

29   harvest-unharvested edges. Lastly, there was no evidence that forestry affected pairing or

30   probability of fledging young, but pairing success was lower in areas with a higher density of

31   Canada Warblers. Our results suggest use of post-harvest stands by Canada Warblers on their

32   boreal breeding grounds is influenced more by conspecifics than by attributes of post-harvest

33   stands themselves. Conservation efforts should prioritize the retention of large tracts of

34   unharvested forest near occupied breeding sites to support high densities of Canada Warblers

35   resulting from the species' clustered breeding distribution.

38

39 INTRODUCTION

40 Conservation of species-at-risk requires the identification of a species habitat requirements and

41 the human activities likely to result in the destruction of that habitat (Fish and Wildlife Service

42 1973, Government of Canada 2011). The Canada Warbler (*Cardellina canadensis*) is a forest

43 songbird considered threatened in Canada (Environment Canada 2016). Forest loss, on both the

44 breeding and wintering grounds, are important drivers of Canada Warbler declines. Degradation

45 of breeding habitat quality by forestry activities may also be a potential threat (DeGraaf et al.

46 1991, Ball et al. 2016, Environment Canada 2016). As a result, the Canadian Recovery Strategy

47 for the Canada Warbler identified the need to determine the amount and characteristics of forest

48 harvesting that can maintain suitable conditions for the species (Environment Canada 2016).

49   Current information on the effects of forestry across the Canada Warblers` breeding

50 range is inconclusive, and sometimes contradictory (reviewed by Reitsma et al. 2010,

51 Environment Canada 2016). Forest harvesting in the boreal forest has been identified as a threat

52 to Canada Warblers by some (Zlonis and Niemi 2014, Ball et al. 2016), while other authors

53 suggest individuals will use old-growth fragments in harvested areas or regenerating stands 11-

54 30 years post-harvest (e.g. Schieck and Hobson 2000, Schieck and Song 2006). Part of this

55 uncertainty in Canada Warblers' use of regenerating forest post-harvest may stem from the fact

56 that various studies have collected data at different spatial scales. To legally designate habitat

57 requirements for the Canada Warbler (Environment Canada 2016), we argue a multi-scale

58 evaluation of habitat requirements is required, as different ecological processes and selection

59 cues may affect habitat associations at different spatial scales (Addicott et al. 1987, Meyer and

60 Thuiller 2006, Lele et al. 2013).

61   For forest songbirds, forest type, amount, stand age, edge, and configuration are

62 important predictors of 2nd order use (i.e. breeding territory placement) and density (i.e. the

63 number of individuals/unit area; MacArthur and MacArthur 1961, Jones 2001, Smith et al.

64 2011). Less is known about 3rd order use (e.g. intensity of use of different patches within home

65 range) in forest songbirds. 3rd order use can only vary within the resource units included in a

66 home range so it may be more strongly influenced by local vegetation features like residuals in

67 harvest blocks than 2nd order use (Meyer and Thuiller 2006). To date most studies of Canada

68 Warbler habitat selection or use have been conducted at the 2nd order level.

69   Although vegetation characteristics are strong predictors of habitat use by forest

70 songbirds, there is growing evidence that social cues are also important (reviewed by Ahlering et

71 al. 2010). Conspecific attraction, a phenomenon where individuals are more likely to use areas

72 near conspecifics despite more or equally suitable vegetation conditions existing elsewhere, may

73 be particularly important for Canada Warblers (Stamps 1988, Ahlering et al. 2010). This species

74 has a short breeding season relative to other migratory songbirds (Flockhart 2010), leaving

75 limited time for individuals to assess habitat quality and search for mates. Settling in areas near

76 conspecifics can reduce search time when deciding where to place territories (Fletcher 2006) and

77 increase mating opportunities (Stamps 1988, Wagner 1998, McKellar et al. 2014). Thus,

78 conspecific attraction should occur more frequently in fragmented forest landscapes where mates

79 can be difficult to locate (Fletcher 2006), which in turn may influence how we perceive Canada

80 Warblers response to forestry activities.

81   In some cases, conspecific attraction may result in some individuals using areas that do

82   not maximize fitness (e.g. human-disturbed landscapes; Beauchamp et al. 1997, Pärt et al. 2007).

83   For example, individuals settling in the periphery of patchily distributed habitat due to

84   conspecific attraction may experience lower breeding success (Nocera et al. 2009). Hence, per

85   capita productivity may not always be correlated with density of breeding individuals (Van

86   Horne 1983, Skagen and Yackel Adams 2011, Hache et al. 2013, Flockhart et al. 2016).

87   Alternatively, suitable habitat may be under-utilized when settlement cues (e.g. conspecific cues)

88   are not available (Gilroy and Sutherland 2007). Conspecific attraction can also result in negative

89   density-dependent effects on breeding success, due to increased resource competition, lower

90   ability to retain mates (Hagan 1996), or higher predation/parasitism rates for individuals in

91   clusters compared to more isolated individuals (Brown 1969, Gilroy and Sutherland 2007). There

92   is a need to understand the importance of vegetation cues and conspecific attraction on habitat

93   use by the Canada Warbler, as resource availability alone may not be sufficient to determine

94   which areas will be used (Campomizzi et al. 2008) and whether or not these areas provide good

95   breeding sites.

96   We quantified the influence of forestry-related factors, local vegetation characteristics,

97   and conspecific attraction on density, hierarchical habitat use, and reproductive activity of

98   Canada Warblers within extensively harvested landscapes in boreal Alberta, Canada.

99   Specifically, we estimated 1) density, 2) use at the point count level (2nd order), 3) intensity of

100   use within home ranges (3rd order), and 4) probability of being paired and fledging young for

101   male Canada Warblers. Based on the vegetation cue hypothesis and associations of Canada

102   Warblers with old-growth forest in boreal Alberta (Schieck et al. 1995, Cooper et al. 1997, Ball

103   et al. 2016), we predicted that forestry-related variables would have negative effects on Canada

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104   Warbler density and habitat use. Based on the orders-of-selection hypothesis, we predicted stand-

105   level vegetation metrics would be more important at the 2nd order, while local vegetation

106   variation would be more important at the 3rd order. Based on previous research on Canada

107   Warbler breeding success in their eastern range (Hallworth et al. 2008a), we predicted that males

108   would adjust home range size to compensate for habitat quality differences and there would be

109   no differences in pairing/probability of fledging young between post-harvest and unharvested

110   stands or age groups. Lastly, based on the conspecific attraction hypothesis we predicted that

111   male Canada Warblers would use areas closer to conspecifics, independent of vegetation cues;

112   that conspecific proximity would explain more of the variation in density and 2nd order use than

113   in 3rd order use; and that males using areas near conspecifics would experience lower probability

114   of pairing and/or fledging young due to competition and crowding effects in a fragmented

115   landscape.

116   **MATERIALS AND METHODS**

117   **Study Area**

118   We conducted this study in three areas near Lesser Slave Lake (55.4313° N, 115.6039°W; LSL),

119   Calling Lake (55.2103° N, 113.1933° W; CL), and Lac La Biche (54.7696° N, 111.9725° W;

120   LLB; Figure 1) in the boreal central mixedwood natural sub-region of northern Alberta, Canada.

121   This sub-region is dominated by aspen (*Populus tremuloides*) and aspen-white spruce (*Picea*

122   *glauca)* mixedwood stands. We selected these study areas based on known presence of Canada

123   Warblers (Ball et al. 2016) in extensively harvested landscapes. The primary land use in these

124   areas was logging for pulp and lumber production, but conventional oil and gas extraction also

125   occurred. Seismic lines and gravel roads were common across the three study areas.

126   **Sampling Design**

127   **Density and 2nd order use.** Using Geographic Information Systems, we pre-selected 132 square

128   survey blocks (17.3 ha each; $n = 53, 35,$ and 44 for LSL, CL, and LLB, respectively; Figure 2)

129   within aspen-dominated stands (Alberta Vegetation Inventory 2008). Blocks represented a

130   gradient of harvest amount (0-100% of survey block harvested) and years since harvesting (0-30

131   years post-harvest; ABMI 2014, Appendix Table 2). A subset of survey blocks included riparian

132   buffers ($n = 44$), isolated forest fragments ($n = 31$) or no harvest ($n = 21$), while the remaining

133   blocks included a portion of one or more contiguous unharvested stands ($n = 36$) expanding into

134   the survey block. Survey blocks were oriented north-south, except for those in riparian areas,

135   which were oriented parallel to the water body (~60 m).

136   From May 27 to June 15, 2014, in the LSL and CL areas, and from June 1 to July 6,

137   2015, in the LLB area, we determined the number of territorial males at point count stations and

138   estimated the total number of males within a 60m buffer around each survey block (hereafter

139   "density"). We achieved this by conducting playback and point count surveys between 0500 and

140   1400 in each survey block. For each survey block, we conducted a single point count (50m

141   radius) at each of four equally-spaced sampling stations (100 m apart) along four 300 m transects

142   (Figure 2), resulting in 16 point counts per survey block with a total of 2,112 point counts across

143   the three study areas. We recorded the total number of territorial males detected by sight or

144   sound at each station using the following protocol: 1) 1 minute silence; 2) 30 seconds with songs

145   of conspecifics; and 3) 1 minute silence. We considered a point count station used if ≥ 1 male was

146   detected (2nd order use). We used this truncated point count method to maximize the number of

147   points sampled (Buskirk and McDonald 1995). The probability of detecting a bird at a point

148   count is affected by: 1) probability that a bird will be detectable (i.e. will sing, or be visibly

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149 present), and 2) probability that the observer will detect a bird that is available (e.g. in different

150 habitat types; Simons et al., 2007, Solymos et al. 2013). Although we did not explicitly assess

151 detection probability, and acknowledge it was not likely 1, we used closely-spaced point count

152 stations and playbacks to increase detection probability by eliciting counter-singing responses

153 (i.e. increasing their visibility and audibility; Kubel and Yahner 2007). We also walked to the

154 location of each male during the point count and recorded GPS locations to ensure males

155 detected were located within the defined survey area. Canada Warbler effective detection radius

156 (EDR: the distance from the sampling point at which as many birds are detected beyond EDR as

157 remained undetected within EDR) is estimated at 60 m (Matsuoka et al. 2012). Thus, we only

158 included males that we detected within a 60 m buffer around each point count location.

159 Furthermore, although detection distance can be lower in regenerating compared to older stands,

160 Schieck (1997) found that observers detected all broadcast vocalizations of songbirds within 50m

161 of the broadcast speaker, regardless of forest age, suggesting that although our absolute detection

162 probability may not be perfect, the relative pattern between harvest treatments is likely

163 comparable.

164

165 **3rd order use.** We used songs of conspecifics and mist-nets to capture territorial males (n = 42),

166 but some could not be captured (hereafter "unbanded"; n = 20). We aged captured males as

167 second-year (SY) or after-second-year (ASY) using molt limits (Pyle 1997), and fitted them with

168 a unique color band combination to identify individuals on subsequent visits. We also tracked

169 unbanded males by relying on spatial location from the previous visit and/or song characteristics,

170 and locations of banded neighbors to identify these individuals (Reitsma et al. 2008, Lankau et

171 al. 2013)

172   We began tracking males 24 hours after capture and conducted weekly tracking bouts per

173   individual for ~6 weeks to delineate home ranges and assess intensity of use of areas within the

174   home range. Surveys were done between 0500 and 1900 (~95% occurred between 0500 and

175   1400). Following the approach used by Barg et al. (2005; see also Hallworth et al. 2008,

176   Reitsma et al. 2008), we recorded the location of each individual every 5 mins within the 30-60

177   min tracking period ("burst"). Barg et al. (2005) suggest that this method is preferable to

178   sequential sampling (e.g. taking one use location per day) for birds with short breeding seasons

179   as it allows the observer to generate a large enough sample size of use locations. Furthermore,

180   because songbirds are able to traverse the length of their territory in a relatively short period,

181   successive locations should be biologically independent (i.e. the bird can traverse the home range

182   within the sampling interval, Barg et al. 2005, Otis and White 1999). We designed daily

183   sampling rotations among males and observers to avoid introducing a temporal or observer bias.

184   If males were not located after three attempted burst sampling bouts, we conducted no further

185   bouts for those males.

186   We were specifically interested in use patterns in and near post-harvest stands. Hence, to

187   determine how much post-harvest forest was used, we tracked 55 males that had been detected

188   <200 m from post-harvest stands on block surveys (n = 23, 14, and 18 for LSL, CL, and LLB,

189   respectively). We also tracked seven birds that had been detected >200 m from post-harvest

190   stands to compare home range sizes and age structure of males using unharvested stands vs.

191   those using post-harvest and unharvested stands. We tracked birds in LSL (*n* = 25) and CL (*n* =

192   16) from May 25 to July 14, 2014, and in LLB (*n*=21) from June 3 to July 18, 2015, obtaining 30

193   location points per male over the season. Due to small sample size of use locations per male, we

194   used 95% minimum convex polygons (MCP) to delineate home range boundaries of each male

195   (ArcGIS 10.2 [ESRI 2012]), rather than Adaptive Kernel Techniques (Seaman 1999). The main

196   disadvantages of using an MCP method is that the researcher cannot distinguish the unused

197   areas, the configuration of used spaces, and it is highly affected by locations on the periphery of

198   the area being used (Barg et al. 2005). To address these issues, we paired our home range

199   delineation with 3rd order use analysis to provide insight into which areas of the home range were

200   used most intensively. We achieved this by overlaying a 10 m $\times$ 10 m grid on home ranges that

201   overlapped post-harvest stands (>0% area harvested; $n = 24$; total of 3,147 cells) and modelling

202   intensity of 3rd order use (i.e. "intensity of use") as the number of use locations within each cell

203   in the home range (Figure 2).

204   **Reproductive activity.** Finding and monitoring nests to assess breeding success is a difficult and

205   time-consuming endeavor (Vickery et al. 1992, Diemer and Nocera 2016). Our objective was to

206   assess reproductive activity of as many males in or near post-harvest stands as possible, we opted

207   to use a reproductive index ranking rather than assessing nesting success and number of young

208   fledged. During each tracking bout, we recorded observations of reproductive activity and ranked

209   each male into one of three categories using a modified version of the Vickery et al. (1992)

210   reproductive index ranking. We considered males paired (rank of 1) if they were observed with a

211   female, building a nest, or with an active nest (i.e. eggs or nestlings). We considered males to

212   have successfully fledged ≥ 1 young (rank of 2) if they were observed with ≥ 1 fledgling (Howlett

213   et al. 2003, Reitsma et al. 2008a, Haché et al. 2013) or observed carrying food to multiple spots

214   within the territory (Flockhart et al. 2016). We considered males unpaired (rank of 0) if we did

215   not detect any evidence of reproductive activity (Bayne 2001, Reitsma et al. 2008a).

216   **Vegetation and conspecific cues.** We obtained forestry variables from the Alberta Biodiversity

217   Monitoring Institute (ABMI) Cutblock layer (2014) and selected variables to represent forestry-

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218   related factors such as presence, amount, and age of post-harvest stands, and presence, size, and

219   edge of unharvested fragments (Appendix Table 3). We used primarily area-based measurements

220   for density models where the survey block was the sampling unit, whereas we used primarily

221   presence and distance-based measurements (i.e. proximity to features) for use models where

222   point count stations (2nd order) and grid cells (3rd order) were the sampling units. We controlled

223   for several confounding environmental variables that were important predictors of Canada

224   Warbler density in Alberta (Ball et al. 2016). Confounding variables included: 1) Hydrography

225   variables, obtained from AltaLis (http://www.altalis.com/products/base/20k_base_features.html),

226   which included rivers (i.e. natural hydrographic features with banks ≥20 m wide), streams (i.e.

227   natural linear hydrographic features with shorelines <20 m wide), and lakes (i.e. bodies of water

228   with a well-defined open water area and shoreline); and 2) Compound topographical index

229   (CTI), a measure of wetness as a function of slope, solar insolation, and terrain wetness, that was

230   developed for northern Alberta (S. Nielsen, unpub. data) using the approach of Gessler et al.

231   (1995). Low CTI values indicated areas with small catchments and steep hills, while high values

232   indicated large catchments and gentle slopes.

233   For each survey block (density), we extracted: 1) percentage of area harvested (0-100%);

234   2) area-weighted age of post-harvest stands (i.e. [sum of area[m^2] of each post-harvest stand

235   within survey block × years since harvested]/survey block area [m^2]); 3) contrast-weighted edge

236   density (CWED, i.e. length of post-harvest-unharvested stand edge × year of harvest); 4)

237   presence of isolated unharvested fragment (0 = absent, 1 = present); 5) amount (m^2) of old-

238   growth (>125 years) aspen-dominated forest within a 1 km buffer around each survey block; 6)

239   distance (m) to the nearest block occupied by ≥1 Canada Warbler; 7) distance (m) to nearest

240   stream, river, and lake; and 9) average CTI.

241   For each point count station (2nd order use), we extracted the same hydrography and CTI

242   variables as well as: 1) presence/absence of post-harvest (post-harvest = 1, unharvested = 0); 2)

243   origin year of stand; 3) distance (m) to post-harvest-unharvested edge; 4) size (m^2) of

244   unharvested fragment (if point was in unharvested stand); and 5) distance (m) to nearest point

245   count station occupied by a male Canada Warbler.

246   To determine what influenced within-home range use (3rd order), the same variables as

247   described for 2nd order use were extracted at the centroid of each 10 x 10 m cell within home

248   ranges, in addition to age of tracked male (SY vs. ASY). We also used these variables to explain

249   variation in reproductive activity in addition to: 1) percent of home range overlapping post-

250   harvest stands; 2) number of use locations within post-harvest stands; 3) density of post-harvest-

251   unharvested edge within home range; and 4) density of males in the survey block.

252   We conducted ground-based local vegetation surveys at a subset of point count stations

253   ($n = 89$) and survey blocks ($n = 49$). For control blocks with no harvesting, we randomly selected

254   one point count station to conduct vegetation surveys, whereas for blocks with both unharvested

255   and post-harvest stands, we randomly selected one point count station for each treatment.

256   Vegetation surveys were also conducted at a subset of grid cells within all home ranges (2-4 per

257   home range, $n = 84$), one at the center of the home range and at three randomly selected cells

258   within the home range. For small home ranges where more vegetation plots would have

259   overlapped, we conducted two vegetation surveys. Surveys consisted of: 1) number of trees (>8

260   cm diameter at breast height); 2) average tree size (cm); 3) percent canopy cover; 4) canopy

261   height (m) within a 11.3 m radius; 5) percent green cover; 6) percent shrub cover; 7) percent

262   downed log cover; 8) number of small shrubs (<2.5 cm in diameter); 9) number of large shrubs

263   (>2.5-8 cm in diameter); and 10) organic litter depth (mm) within a 5 m radius (Martin et al.

264   1997, Hallworth et al. 2008b, Flockhart et al. 2016). We conducted vegetation surveys from mid-

265   July to mid-August.

Statistical Analysis

268   We used negative binomial regression to explain variation in Canada Warbler density. We

269   started by building a baseline model using nuisance and confounding environmental variables

270   (i.e. day of survey, time of day, study area [1 = LSL, 2 = CL, 3 = LLB], observer [$n = 8$], CTI,

271   and distance to lake, river, and stream). We used a backwards step selection process to select

272   variables that resulted in the best model fit based on Akaike's Information Criterion ranking for

273   small sample sizes (AICc). We added other variables to the baseline model using a two-stage

274   approach. First, we tested for effects of forestry-related factors and ranked these models using

275   AICc to determine which combination of forestry and baseline variables resulted in the best

276   model fit. Second, we tested whether adding a variable for conspecific proximity improved the

277   stage 1 model using the same model selection approach. We used α-level $p<0.05$ to determine

278   significance of single variables. We also tested for non-linear effects (squared, quadratic, and

279   cubed). When variables with a quadratic term were included in the top-ranked model, we tested

280   whether a threshold response provided a better fit using package 'segmented' in R (Muggeo

281   2008).

282   We used mixed effect logistic regressions to explain variation in 2nd order use, where

283   survey block ID was added as a random effect, and mixed effect negative binomial regressions

284   with bird ID as a random effect to assess 3rd order use. We used the same model building process

285   as for density, with the addition of a third stage. Using the subset of stations (2nd order) or cells

286   (3rd order) with ground-based local vegetation data, we tested if adding local vegetation

287   variable(s) to the best model from stage 2 improved model fit. In addition, for the subset of

13

288   males where age was known, we tested for age $\times$ presence/absence of post-harvest stand

289   interactions (3rd order) at stage 1.

290   We used ordered logistic regression to analyze reproductive activity. We analyzed

291   probability of pairing (paired vs. unpaired) separately from probability of fledging young

292   (fledged young vs. paired only), as pairing (i.e. attracting a mate) and fledging (i.e. successfully

293   raising $\geq$1 young to fledgling stage) may be driven by different mechanisms (Reitsma et al.

294   2008b). First, we evaluated if 2nd order variables or 3rd order variables influenced probability of

295   pairing (i.e. paired vs. unpaired males) using the same three-stage modelling approach previously

296   described, with the addition of male age as a baseline variable and density of conspecifics as a

297   variable in stage 2. We then used the same modeling approach to test for effects of 2nd and 3rd

298   order variables on the probability of males fledging $\geq$1 young (i.e. fledging young vs. paired

299   only).

300   We used Wilcoxon signed rank to test for differences in home range sizes between males

301   who only used unharvested stands vs. individuals who used both post-harvest and unharvested

302   stands.

303   We analyzed use and density models using the package glmmADMB (Skaug et al. 2011)

304   in R3.1.2 (R Core Team 2014), and reproductive activity models using the ologit command in

305   STATA 13 (Hamilton 2012). We reported standardized regression coefficients (β) $\pm$ SE, test

306   statistic (z), and p-value (p) for each independent variable for the top regression models and test

307   statistic (W) and p-values for the Wilcoxon signed rank test. Lastly, for the top model in each

308   model set, we calculated pseudo r^2 values as a measure of goodness-of-fit using the package

309   MuMIn in R (Barton 2013).

310 **RESULTS**

311 **Density**

312 We detected 96 males on block surveys: 51, 10, and 35, in LSL, CL, and LLB, respectively.

313 Density per block ranged from 0-9 territorial males (mean = 0.75 ± 0.13), but males were only

314 detected on 29% of the survey blocks (38/132). The top-ranked forestry model included a

315 negative cubic effect of percent post-harvest (β = -0.81 ± 0.27; Figure 3A, Supplemental

316 Material Table S1). This model was improved by adding distance to the nearest occupied block

317 (AICc wt = 0.8; Table 1, Supplemental Material Table S1).

318 **2nd Order Use**

319 We detected ≥ 1 territorial male at 91 point count stations (48, 10, and 33 at LSL, CL, and LLB,

320 respectively; 4% of point count stations). The top-ranked forestry model included a presence of

321 post-harvest stands × distance to the nearest edge interaction (β = -3.52 ± 1.13; Table 1,

322 Supplemental Material Table S1) suggesting that when home ranges were in post-harvest stands

323 males used areas closer to unharvested-post-harvest edge rather than the core harvested area

324 (Figure 3B). A non-linear (squared) negative effect of distance to the nearest occupied station (β

325 = -1.45 ± 0.37) improved the model further (Table 1, Supplemental Material Table S1) indicating

326 that 2nd order use decreased with increasing distance to the nearest occupied point count station

327 up to approximately 600 m (±125), after which proximity to conspecifics had no effect (Figure

328 3C). The addition of local vegetation variables did not improve stage 2 models (Supplemental

329 Material Table S1).

330   **3rd Order Use**

331   Average home range size was 0.94 ha (± 0.86). Post-harvest stands were included in the home

332   ranges of 44% (24/55) of males captured < 200 m from a post-harvest stand (i.e. 31/55 males

333   exclusively used unharvested stands). However, the home range of most of these males (15/24)

334   had limited overlap (<20%) with post-harvest stands. Mean size of home ranges that included

335   post-harvest stands (1.27 ha ± 1.16, $n = 24$) was larger than those of home ranges that did not

336   include post-harvest stands (0.72 ha ± 0.90, $n = 38$; $W = 305$, $p < 0.05$).

337   The best model predicting 3rd order use included a positive effect of distance to nearest

338   post-harvest-unharvested edge, suggesting intensity of use increased with distance from edges (β

339    $= 0.61 \pm 0.19$; Table 1). The model was improved by adding proximity to conspecifics (AICc wt

340    $= 0.70$; Supplemental Material Table S1). Males had higher intensity of use in unharvested than

341   post-harvest parts of the home range, and intensity of use in unharvested parts of the home range

342   was higher near conspecifics (post-harvest stands × distance to nearest conspecific interaction; β

343    $= 0.33 \pm 0.17$; Table 1; Figure 3D, Supplemental Material Table S1). No local vegetation

344   variables were significant, nor did they improve upon model stage 2 (Supplemental Material

345   Table S1). We also did not find significant differences in intensity of use of post-harvest stands

346   between male age classes (Supplemental Material Table S1).

347

348   **Reproductive Activity**

349   We tracked 18 ASY, 24 SY, and 20 unbanded males of unknown age. We confirmed pairing and

350   evidence of fledgling ≥1 young for 84% and 69% of males, respectively. For pairing success, the

351   top model only included a negative non-linear (squared) effect density of conspecifics ($\beta = $ -

352   0.82± 0.30; Table 1, Supplemental Material Table S2), indicating that pairing success was higher

353   for males at low and mid-densities (i.e. 1-3 males per block) but decreased at higher densities

354   (Figure 4). Stand-level forestry variables and local vegetation variables did not improve models.

355   For probability of fledging ≥1 young, the best model included 3rd order variables (AICc

356   wt = 0.66; Supplemental Material Table S2). The model was not improved when stand-level

357   forestry variables or proximity to conspecifics were added, but was improved by the addition of

358   average shrub cover (Table 1, Supplemental Material Table S2).

359   **DISCUSSION**

360   **Forestry Effects**

361   Male densities decreased with increasing amounts of harvesting and territorial males were less

362   likely to have home ranges in post-harvest than unharvested stands (2nd order use). This is

363   consistent with other studies in the western boreal (Schieck et al. 1995, Cooper et al. 1997,

364   Schieck and Song 2006, Ball et al. 2016). In western Canada, Canada Warblers tend to be most

365   abundant in old-growth deciduous stands and in stands with increasing canopy height and

366   canopy cover (Hache et al. 2014, Ball et al. 2016). Unharvested old-growth stands (>125 years

367   post-harvest), provide vertical stratification, structural diversity, and higher densities of large

368   trees (Huettmann 2003) which seem to be more important for Canada Warblers than trees typical

369   of younger stands. Although some boreal studies suggest that residual retention in harvested

370   areas or in regenerating stands 11-30 years post-harvest may support some Canada Warblers

371   (Schieck and Hobson 2000, Schieck and Song 2006), we did not find evidence that retention of

372   unharvested fragments (≤ 5 ha) or regeneration of harvested stands (≤ 30 years post-harvest)

373   mitigated effects of forest harvest on density. It is likely that only relatively large fragments will

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374   be occupied (Ball et al. 2016), and that use of fragments is relatively uncommon compared to use

375   of contiguous forest (Schieck and Hobson 2000, Schieck and Song 2006).

376   Our results also suggest that when males are detected in post-harvest stands, their home

377   ranges are located near the edges of adjacent unharvested stands. This is consistent with results

378   from West Virginia, where Canada Warblers used clearcuts in areas closer to edges, whereas this

379   relationship to edge was not observed in areas with heavy partial harvests (i.e. clear-cuts with

380   residual trees plus deferment and shelterwood cuts) or light partial harvests (i.e. single-tree

381   selection and diameter limit cuts; Becker et al. 2012).

382   Males spent less time near the post-harvest – unharvested edges within the home range,

383   suggesting that when males cannot secure their full home range in unharvested stands (e.g. due

384   to competition) males must use both sides of the edge interface to be near adjacent unharvested

385   stands. We also found males in post-harvest stands had larger home range sizes, suggesting that

386   resource availability is lower than in unharvested stands and males must defend larger areas to

387   secure necessary resources (Smith and Shugart 1987, Haché et al. 2013, Newmark and Stanley

388   2016), and Hallworth et al. (2008a) also reported larger home ranges of Canada Warblers in

389   post-harvest stands.

390   **Conspecific Effects**

391   We found higher densities of males closer to survey blocks occupied by conspecifics,

392   irrespective of post-harvest stand attributes. It has been suggested that Canada Warblers might

393   have a clustered breeding distribution (Reitsma et al. 2010, Flockhart 2016), but to our

394   knowledge our study is the first to quantify this spatial distribution for this species.

395   Individual males were more likely to have home ranges near conspecifics, and use

396   unharvested parts of their home ranges near conspecifics more intensively, suggesting that

397   conspecific attraction may be driving the use of post-harvest stands (i.e. males are using areas to

398   be near conspecifics in adjacent unharvested stands). This within home range use pattern also

399   likely reflects the need for greater territorial defense in the unharvested portion of the home

400   range where birds tended to have more neighbors (Lankau et al. 2013). Furthermore, conspecific

401   attraction could explain why previous studies in the boreal region have detected Canada

402   Warblers in post-harvest stands (Schieck and Hobson 2000, Schieck and Song 2006). Hallworth

403   et al. (2008b) also suggested that the proximity of unharvested and post-harvest study sites in

404   New Hampshire may have influenced the use of post-harvest stands by Canada Warblers.

405   We did not find evidence that local vegetation features influenced 2nd order use. One

406   possible explanation of our results is that some males in areas with certain vegetation types (e.g.,

407   earlier arriving males; Hallworth et al. 2008b), whereas conspecific attraction could result in

408   other males using a wider range of vegetation attributes (Nocera et al. 2009). Hence, local

409   vegetation use patterns could be confounded by the effects of conspecific attraction. We also did

410   not find evidence that local vegetation influenced 3rd order use. Other studies have shown that

411   shrub density is an important vegetation feature across the Canada Warbler breeding range

412   (Hallworth et al. 2008b, Chace et al. 2009, Palmer-Ball Jr 2015, Flockhart et al. 2016). Because

413   we included fine-scale vegetation and coarser-grained vegetation metrics in the same models, the

414   effects of the former could be masked fine-scale vegetation could have been masked by the

415   inclusion of the latter. Sample size for our ground-based vegetation surveys was small, which

416   also may limit our ability to detect such effects.

417   Lastly, we did not find a significant difference in the intensity of use (3rd order use) of

418   post-harvest stands between ASY and SY males. Many territorial birds exhibit ideal despotic

419   distribution where dominant individuals (e.g. older males) obtain higher quality home ranges,

420   and experience higher reproductive success (Holmes et al. 1996, Ridley et al. 2004). Conspecific

421   attraction can also sometimes result in younger males using lower quality areas around the

422   periphery of older males' home ranges (Nocera et al. 2009). Our results are more consistent with

423   a variation of an ideal free distribution, where adjustments in home range size can compensate

424   for differences in individuals' ability to obtain high-quality home ranges (Fretwell and Lucas

425   1970, Haché et al. 2013). Hallworth et al. (2008a) also did not find a significant difference in

426   proportion of ASY vs. SY male Canada Warblers in undisturbed vs. second-growth stands.

427

428   **Reproductive Activity**

429   We found no effects of forest harvesting on individual males probability of pairing or fledging

430   young. We might expect these results as most of the males included only low proportions of

431   post-harvest stands within their home range, and adjustments in home range size could result in

432   similar per capita productivity (Fretwell and Lucas 1970; Ridley et al. 2004; Hache et al. 2013).

433   Flockhart et al. (2016) also suggested that Canada Warbler home range size might be a function

434   of habitat quality, where home ranges in high quality habitat are smaller due to pressures from

435   competition and territory defense.

436   We found evidence of a negative non-linear relationship between density and pairing

437   success. However, density did not influence the probability that paired males would fledge

438   young, suggesting that males may experience density-dependent crowding effects on pairing,

439   whereby they are less able to retain mates due to competition (Hagan et al. 1996). Alternatively,

440 observed pairing success could be explained by the presence of hidden leks (Wagner 1998),

441 where unpaired males cluster around paired males to obtain extra-pair copulations with females,

442 resulting in higher densities, but increasing proportions of unpaired males (McKellar et al. 2014).

443 Extra-pair copulations are likely common in Canada Warblers (Reitsma et al. 2010), although

444 empirical studies have not been conducted. Flockhart et al. (2016) found evidence that density

445 affected breeding success of Canada Warblers in Lesser Slave Lake Provincial Park, but they did

446 not distinguish between pairing and probability of fledging young, so whether this resulted from

447 a large number of unpaired males or other density-dependent effects remains unknown.

448   We also found no effect of age on the probability that paired males would fledge young,

449 which is consistent with McKellar et al. (2014) and studies of Canada Warblers from the eastern

450 breeding range (e.g., Reitsma et al. 2008a), although these studies did find that ASY males had

451 higher pairing success than SY males (but see Thériault et al. 2012). Pairing success is often

452 linked to traits that should be positively correlated with male age such as: suitable site selection

453 (Nocera et al. 2009), prior breeding experience with a same mate (McKellar et al. 2014), and

454 females' selection of males with specific physical attributes (e.g. brighter plumage; Rappole

455 1983, Reitsma et al. 2008a). However, if sites from previous years are no longer suitable due to

456 disturbance or if female mates do not survive until the subsequent breeding season, some of these

457 age-related advantages may not be apparent.

458   Average shrub cover (<50 cm in height) improved the model assessing the probability

459 that a paired male would fledge young, but the effect was not significant. Flockhart et al. (2016)

460 found that shrub cover was higher in smaller territories and that smaller territories tended to have

461 lower breeding success. Reitsma et al. (2008a) suggested that although shrub density >1 m in

462   height is an important cue for nest selection, dense cover at lower horizons may prevent the

463   growth of other ground cover features that are important to nesting Canada Warblers.

464   **Management Implications**

465   These results have several implications for prioritizing conservation areas and informing forest

466   management to maintain or recover Canada Warbler breeding populations in western boreal

467   regions. Forest harvesting seems to constitute a threat to breeding habitat as it results in lower

468   use and densities of Canada Warblers than unharvested stands. Post-harvest stand age, local

469   vegetation, presence/size of unharvested fragments, and landscape availability of unharvested

470   stands do not appear to mitigate these effects. Only post-harvest stands near unharvested stands

471   were used, indicating that the core of harvested areas do not constitute usable habitat and Canada

472   Warblers require at least some unharvested stands to support a home range. The use of post-

473   harvest stands by Canada Warblers in Alberta seems to be more strongly influenced by social

474   factors than by attributes of post-harvest stands themselves. Conspecific attraction might also

475   explain why seemingly "suitable" areas of unharvested stands are uninhabited, while similar

476   areas can support very high densities (Reitsma et al. 2010).

477   Hagan et al. (1996) suggest that crowding effects may be greater in small forest patches,

478   emphasizing the importance of protecting large forested areas. We suggest that this management

479   action may be even more important where conspecific attraction leads to crowding in fragments,

480   while other suitable areas remain unoccupied. Hence, protecting large tracts of contiguous

481   unharvested stands near sites occupied by Canada Warblers will be important to provide enough

482   suitable habitat to support high densities, and prevent crowding effects. Experimental

483   manipulations to attract birds to areas in which harvesting is less likely to occur could also be

484   included in long-term conservation planning. Further research into the type and timing of

485   conspecific cues is needed however, and best practices should be adhered to when applying

486   experimental conspecific attraction methods to conservation (Ahlering et al. 2010).

487   Critical habitat designation for species-at-risk is mandated across a species' range and

488   annual cycle, and this information will be important for forest managers in the western boreal,

489   who must protect biodiversity and species-at-risk like the Canada Warbler in the areas they

490   manage. However, cumulative effects of other threats on the breeding grounds, migratory routes,

491   and wintering grounds may contribute to influence population dynamics on the breeding grounds

492   (Sillet et al. 2000, Holmes et al. 2007, Heath et al. 2012). Future studies should address the

493   relative importance of threats across the annual cycle of Canada Warblers and their respective

494   contribution to population regulation.

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843   **Figure Captions**

844   Figure 1. Survey block locations (*n* = 132) in the 3 study areas: Lesser Slave Lake (left), Calling

845   Lake (centre), and Lac La Biche (right), in Alberta, Canada.

846   Figure 2. Example of a territorial male Canada Warbler home range with corresponding 10×10

847   m cells.

848   Figure 3. Predicted density of territorial male Canada Warblers in survey blocks as a function of

849   increasing amount of post-harvest stands (**A**); 2nd order use of post-harvest stands in response to

850   distance (m) to nearest unharvested edge (**B**); 2nd order use of post-harvest stands as a function of

851   increasing distance (m) to the nearest point count station used by a conspecific (**C**); and 3rd order

852   use in harvested areas (solid line) and unharvested areas (dashed line) in response to distance (m)

853   to the nearest conspecific (**D**).

854   Figure 4. Predicted probability of pairing success in male Canada Warblers in response to

855   density of conspecifics.

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866   **TABLES**

867   Table 1. Variables and coefficients for top ranked models predicting: A) Density of males ($n =$

868   132); B) 2nd order use ($n = 2{,}112$); C) 3rd order use ($n = 3{,}147$); D) probability of pairing success

869   ($n = 62$); and E) probability of fledging young ($n = 51$) for Canada Warblers breeding in northern

870   Alberta, Canada. N is the sample size of the model, β is the standardized coefficient, SE is the

871   standard error, z is the test statistic, and P is the p value.

Variables in top models	N	β	SE	z	P
DENSITY					
CUT^3	132	0.81	0.27	-3.06	<0.001
NEAROCC	132	-0.32	0.18	1.66	< 0.1
STUDYAREA	132				
CL:		-1.98	0.54	-3.65	< 0.001
LLB:		1.93	0.57	-3.42	< 0.001
CTI	132	-0.67	0.19	-3.62	<0.001
DISTRIVER	132	-0.32	0.23	-1.39	<0.1
2ND ORDER USE					
IFCUT $\times$ DISTEDGE	2112	-3.52	1.13	-3.11	< 0.005
NEAROCC	2112	-1.45	0.37	-4.31	< 0.001
STUDY AREA	2112				
CL		-1.72	0.49	-3.50	<0.001
LLB		1.10	0.47	-2.40	<0.05
DISTRIVER	2112	-0.35	0.19	-1.82	<0.10
3RD ORDER USE					
IFCUT $\times$ NEAROCC	3147	0.33	0.17	1.93	0.05
DISTEDGE	3147	0.61	0.19	3.13	<0.001

DISTSTREAM	3147	0.28	0.12	2.37	<0.05
PAIRING SUCCESS					
CONSDENSITY^2	62	-0.82	0.30	-2.70	<0.001
PROBABILITY OF FLEDGING YOUNG					
SHRUBCOV	51	-0.99	0.54	-1.83	<0.10
STUDY AREA CL LLB	51	 2.14 1.67	 1.34 1.24	 1.6 1.34	 0.10 0.20
DISTRIVER	51	1.48	0.60	2.47	<0.05

872 * CUT^3 is a cubed term representing the percent of a survey block comprised of post-harvest
873 stands, NEAROCC is the distance to the nearest conspecific, DISTRIVER is the distance (m) to
874 nearest river, IFCUT is the presence/absence (1/0) of post-harvest stands at a point count station,
875 DISTEDGE is the distance (m) to the nearest post-harvest/unharvested edge, DISTSTREAM is
876 the distance (m) to nearest stream, CTI is the average compound topographic index,
877 CONSDENSITY^2 is a squared term representing the number of conspecifics (males) on the
878 survey block. SHRUBCOV is the % shrub cover <50cm height.

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884 **APPENDIX**

885   Table 2. Distribution of survey blocks (17.3 ha, n = 132) by percent post-harvest stands and

886   number of years since harvesting across three study areas (Lesser Slave Lake, Calling Lake, and

887   Lac La Biche).

	Percent post-harvest stands on survey block			
	0-25%	26-50%	51-75%	75-100%
LESSER SLAVE LAKE				
0-10 years	2	3	8	7
11-30 years	1	6	4	2
Unharvested	2	-	-	-
Total	5	9	12	9
CALLING LAKE				
0-10 years	-	1	1	2
11-30 years	2	4	25	13
Unharvested	4	-	-	-
Total	6	5	26	15
LAC LA BICHE				
0-10 years	-	3	4	1
11-30 years	3	11	5	-
Unharvested	18	-	-	-
Total	21	14	9	1
ALL STUDY AREAS				
0-10 years	2	6	13	10

11-30 years	6	21	32	15
Unharvested	24	-	-	-
Total	32	27	45	25

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890 Table 3. List of forestry-related factors used to generate predictions for: A) Density of males ($n =$

891 132); B) 2nd order use ($n = 2,112$); C) 3rd order use ($n = 3,147$); D) Reproductive activity for

892 territorial male Canada Warblers in managed forests in northern Alberta.

Model set	Presence/amount post-harvest stands	Age of post-harvest stands	Edge	Presence/size of unharvested fragment
DENSITY	CUT[3]: % post-harvest stands on survey block (cubed term)	YEAR: represents the area-weighted average year of harvest on the survey block	CWED: a measure of fragmentation-the contrast weighted edge density (unharvested: harvested edge) on the survey block	PATCH represents whether there is an isolated unharvested fragment in the cutblock (1=fragment, 0= no fragment)
2ND ORDER USE	IFCUT represents whether a station	YEAR represents the origin year of	DISTEDGE represents the	PATCH represents the

	is in post-harvest (1) or not (0)	the stand in which the station is located (harvest year for post-harvest, stand origin for unharvested)	distance (m) to the nearest edge (post-harvest-unharvested)	area (m²) of the unharvested patch a station is located in
3RD ORDER USE	IFCUT represents whether a grid cell is in post-harvest (1) or not (0)	YEAR represents the origin year of the stand in which the grid cell is located (harvest year for post-harvest, stand origin for unharvested)	DISTEDGE represents the distance (m) to the nearest post-harvest-unharvested edge	PATCH represents the area (m²) of the unharvested fragment a grid cell is located in
REPRODUCTIVE ACTIVITY	IFCUT represents whether the home range overlaps post-harvest (1) or not (0) PROPCUT is the proportion of	YEARCUT represents the year of harvest of post-harvest stands in the home range	DISTEDGE represents the distance (m) to the nearest post-harvest-unharvested edge	PATCH represents the area (m²) of the unharvested patch a home range overlaps

	home range that overlaps post-harvest, NUMPTSCUT is the number of use locations within post-harvest stands in the home range		EDGEINHR is the length of post-harvest-unhavested edge in a home range	

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