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Long-term changes in boreal forest occupancy within regenerating harvest units

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ABSTRACT

Many observational and short-term experimental studies have examined how boreal bird communities respond to forest harvesting. However, there are virtually no longitudinal studies that have assessed long-term effects of forest harvesting on boreal birds. The Calling Lake Fragmentation Study is a long-term experiment in northern Alberta's boreal forest, established in 1993. We have 24 years of avian point count data (1993–2016) from this study site, giving us the opportunity to study how the boreal songbird community has responded over 23 years to forest regeneration after harvesting. We ran multi-season occupancy models of 51 species surveyed at 72 stations (8 stations per 40-ha sampling area) within 3 unharvested forest sites, 3 harvest units that were cut in 1984 and treated to enhance conifer survival, and 3 harvest units that were cut in 1994 and left untreated to regenerate naturally. Eight of 21 species associated with older boreal forests (≥60–80 years old) used harvest units 23–33 years post-harvest. Eleven of 16 species associated with shrublands or younger forests used harvest units, before declining as harvest units regenerated, while four of 16 such species increased their probability of occupying harvest units over the monitoring period. Increased occupancy by 5 Neotropical migrants and 2 short-distance migrants was associated with increased El Nino weather events preceding a given breeding season. We also found evidence that increased occupancy of 3 species within harvest units was preceded by and correlated with increased occupancy by those species in unharvested forests, while occupancy of 4 species in unharvested forests was preceded by and correlated with increased occupancy within harvest units. Our results indicate the importance of unharvested forests for some boreal songbird species, the utility of longitudinal studies with controls for assessing changes in occupancy due to forest regeneration in harvest units versus factors operating at larger spatial scales, and the potential of harvest units to serve as habitat for boreal birds up to 33 years post-harvest.

1. Introduction

In Canada's boreal forest, forestry removes and creates habitat for different species of birds, depending on the preferred forest age-class (Drapeau et al., 2000; Schieck and Song, 2006) and stand type used by each species (Westworth and Telfer, 1993; Kirk et al., 1996; Kirk and Hobson, 2001). Understanding how such alterations affect boreal bird communities at different temporal and spatial scales is a key element of sustainable forest management (Niemi et al., 1998). Most reports of age and stand type preferences by boreal birds come from short-term studies that compare different stand types (Westworth and Telfer, 1993; Kirk et al., 1996; Kirk and Hobson, 2001), stand origins (e.g. clearcut vs. burns, Schieck and Song, 2006; Huggard et al., 2014), forest age-classes (Drapeau et al., 2000), or characteristics of species that use recently harvested areas (Larue et al., 1995; Norton and Hannon, 1997). Fewer longitudinal studies of boreal bird communities exist (e.g. Glennon, 2014), particularly ones that monitor post-harvest succession directly.

Longitudinal studies are valuable for many reasons. The dynamics of forest bird populations – both species capable of using harvested areas and those preferring unharvested forests – are influenced over time scales longer than a single year (Kirk et al., 1996; Niemi et al., 1998). Forest managers are interested in knowing when harvested and regenerating forest stands become suitable for boreal forest birds, how this suitability compares to older, unharvested forests, and for how long recently harvested areas provide suitable habitat for birds that prefer younger forest. If species occupancy within harvested and unharvested forests primarily reflects differences in vegetation composition and

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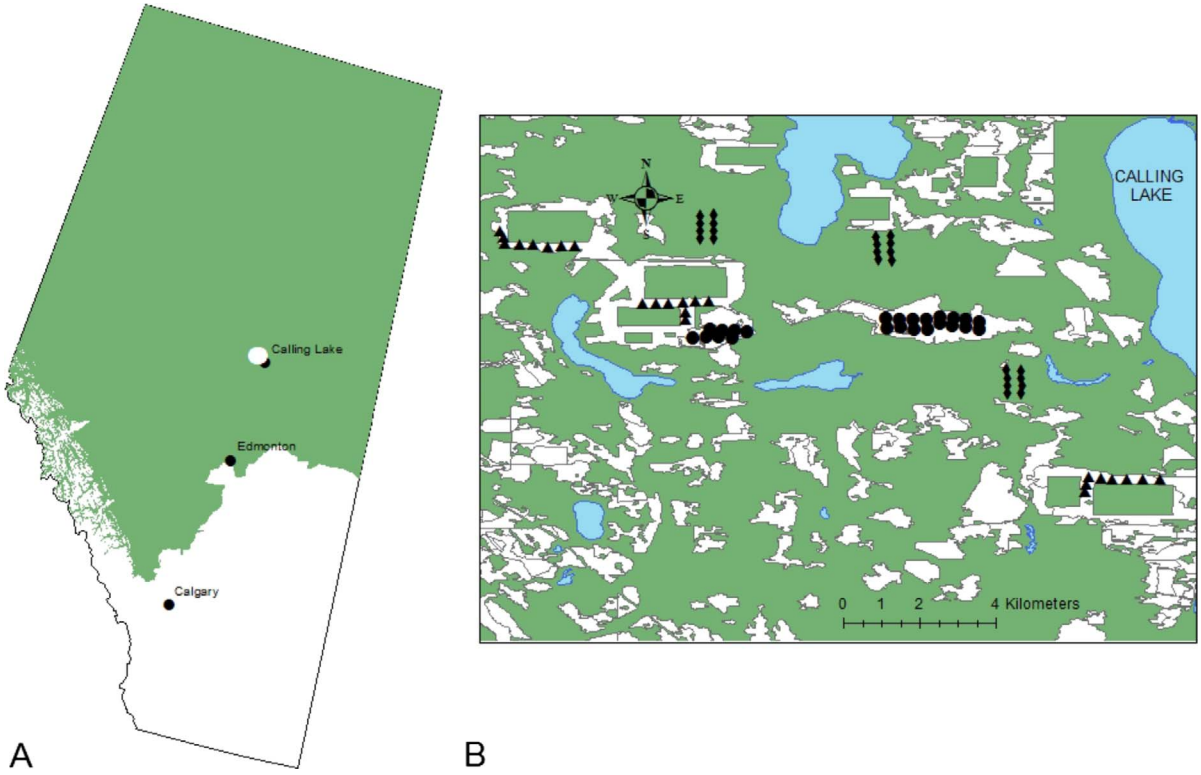

Fig. 1. Map of study area at Calling Lake, Alberta, Canada, indicating (A) location in the boreal forest (boreal zone map: Natural Resources Canada from Brandt (2009)), and (B) experimental design, where white patches indicate harvested areas and blue indicates lakes. Black diamonds = stations in unharvested forests serving as control sites; black triangles = stations within harvest sites cut in 1994 ("untreated harvest units"); black circles = stations within harvest sites cut in 1984 and treated to enhance conifer establishment ("treated harvest units").

structure associated with forest age (Brassard and Chen, 2010), then local patterns in occupancy over time should be independent among regenerating and unharvested forests. However, if density-dependent processes affect habitat selection, then perception of the relative value of regenerating forest stands may be influenced by correlated patterns of avian response.

When sites subjected to one or more forest management treatments are compared to untreated control sites over time, changes attributable to the treatments can be distinguished from those related to other population drivers. Nevertheless, factors affecting regional abundance can mask treatment effects in the short-term. For example, following years in which a species experiences high productivity in unharvested forests, harvested sites may be occupied due to saturation of preferred habitats (Niemi et al., 1998). Changes in boreal bird occupancy might also be associated with regional outbreaks of arthropod prey that make stand types differentially suitable over time (e.g. spruce budworm) (Kirk et al., 1996; Niemi et al., 1998; Venier and Holmes, 2010). More broadly, weather events on non-breeding grounds, such as those associated with El Niño conditions, may influence return rates of Neotropical and short-distance migrants, through effects on plant and insect productivity, and resultant winter food supply and overwinter survival of birds (Sillett et al., 2000; Jaksic, 2001; Nott et al., 2002). Carry-over effects from wintering ground processes may be common, but their effects on habitat use by birds on the breeding grounds are poorly understood because of limited longitudinal studies of different habitats, and limited knowledge of the wintering locations of many boreal birds. Depending on where the birds overwinter, years with strong El Niño conditions may be associated with drier wintering grounds, with lower plant and insect productivity, fewer winter food supplies and lower return rates (Sillett et al., 2000), or wetter wintering grounds, with greater food supplies and higher return rates (Nott et al., 2002). Clearer signals of habitat preference may be apparent in the breeding season following years of poorer wintering conditions and lower return rates, with lower occupancy rates in less preferred site types. Conversely, higher return rates associated with more favourable winter conditions may result in greater saturation of less suitable habitat types.

In this paper, we examine the long-term occupancy patterns of the breeding bird community in an experimental study in the boreal mixedwood forests of northern Alberta, Canada (Schmiegelow and Hannon, 1993; Schmiegelow et al., 1997). Our focus is on the successional trajectory of the post-harvest bird community in regenerating forests following clearcut logging. Harvest treatments were implemented in 1984 and 1994, and harvested sites and unharvested controls were surveyed annually from 1993 to 2016, providing a 33-year study window in this naturally dynamic system. The spatial and temporal extent of the design allow harvest treatment effects to be clearly distinguished from other local, regional, and range-wide influences on site occupancy by boreal birds during the breeding season.

We had three primary objectives: (1) describe breeding season occupancy patterns of individual boreal bird species and species guilds over a 23-year period, and up to 33 years post-harvest, within three forest site types: (a) harvest units cut in 1984 and treated to enhance conifer establishment; (b) harvest units cut in 1994 and left to regenerate naturally, and (c) unharvested control sites; (2) explore the potential influence of range-wide weather events during the non-breeding season on species occupancy patterns during the breeding season in different boreal forest site types; (3) examine breeding season occupancy over time in different site types for concurrent increases or decreases suggestive of regional influences on occupancy patterns.

2. Methods

2.1. Study area

The Calling Lake Fragmentation Project is located near Calling Lake (55°10′47″N 113°16′21″W), in northern Alberta, Canada (Schmiegelow