Effects of energy development on habitat use of an avian peatland specialist and generalist at multiple spatial scales

by

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Abstract

With the persistent demand for petroleum energy products, the energy development footprint in northern Alberta continues to expand, perforating habitat in the boreal forest. Modern *in situ*, or below ground, bitumen extraction techniques have broadened the extent of accessible reserves and are creating a different type of footprint than conventional surface mining. Development of exploratory vegetation clearings, including 3-dimensional seismic lines (hereafter "seismic"), winter roads, and well sites, as well as permanent infrastructure, such as roads, pipelines, extraction wells, and industrial facilities, creates an expansive network of small-scale disturbances that alter biological communities, including songbirds. Additional work is needed to understand how different development features influence species-specific habitat use and selection for songbirds, especially in peatland habitats that are less-well understood.

Here I examined the influence of different *in situ* oil sands development feature types on habitat use and selection of a conifer generalist, Dark-eyed Junco (*Junco hyemalis*), and peatland specialist, Palm Warbler (*Setophaga palmarum*), songbird at multiple spatial scales within peatland habitats. Specifically, the objectives of this study were to: (1) identify the relative effects of different *in situ* development and habitat features on landscape-level avian occurrence and local-scale habitat selection for songbirds with different habitat niche breadths; and (2) understand potential behavioural mechanisms affecting species-specific responses to *in situ* developments on individual territory placement and within-territory habitat selection. I used point counts to sample Dark-eyed Junco and Palm Warbler occurrence at 157 peatland sites located across a range of development feature types and intensities. I also examined territory-level (2nd order) and within-territory (3rd order) habitat selection by conducting behavioural observations within 11, 25-hectare sites. I modelled occurrence (presence-absence) for each species using binomial logistic regression; and modelled territory and within-territory selection using generalized linear mixed effect models to compare used to available locations for 80-82 individuals of each species. Permanent polygonal and linear features influenced occurrence for both species, whereas exploratory features did not, suggesting that permanent development features have a greater impact on avian populations. Both species avoided permanent (e.g. polygonal or linear) or larger exploratory features (e.g. well sites) at the territory scale, but relative use of development features was greater for Dark-eyed Juncos than Palm Warblers. At the within-territory scale, Dark-eyed Juncos avoided permanent features and well sites for singing but were more likely to sing by wide linear features in areas with taller vegetation, relative to locations with shorter vegetation. Juncos were more likely to forage on or near all features except seismic, but relative intensity of use for some features was greater in areas near higher productivity vegetation. Palm Warblers avoided singing by well sites but selected singing locations near wide linear features in areas with taller vegetation. Palm Warblers avoided foraging on or near well features across all habitat productivity levels but selected seismic features only in low productivity habitats.

Our results show that avian responses to different development features are complex, with species-specific responses that vary for different behaviours and local habitat characteristics. Use, selection, and avoidance of different development features varies with spatial scale, and even small, 2-3 m wide seismic features can influence avian behaviours. I recommend pairing fine-scale behavioural studies with coarse-scale avian monitoring to increase understanding of the mechanisms driving species-specific responses to different development feature types and inform landscape management decisions.

Preface

This thesis is an original work by Thea Carpenter using data collected in collaboration with Environment and Climate Change Canada (ECCC), the Oil Sands Monitoring Program (OSM) and Matrix Solutions Inc. (Matrix). This project was enabled by Dr. C. Lisa Mahon of ECCC who provided funding through ECCC and the OSM program, conceptualized the study design, participated in data collection, and provided guidance on all aspects of the study. Chapter II uses data provided by Jonah Keim of Matrix Environmental Solutions. This project was co-supervised by Dr. Scott Nielsen and Dr. Erin Bayne, who provided academic resources and guidance on analysis and writing. Thea was involved in all aspects of the project including assisting with project design, developing methods, data collection, analysis, and writing. Chapter 2 and 3 will be submitted for publication.

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Chapter 1: Background

Oil sands development in northern Alberta

The boreal forest region in Canada is becoming increasingly perforated by resource development activities, including agriculture, forestry, and energy resource extraction. Although agriculture and forestry currently comprise the greatest total human footprint in terms of area, anthropogenic features associated with oil and gas development are steadily increasing and are estimated to have a greater relative impact (i.e. response per equivalent area) on some wildlife populations (Sólymos et al. 2015). In Canada, the highest intensity energy extraction occurs within the oil sands region of northern Alberta, where the total estimated energy footprint has increased 1.5 times between 1999-2016, from approximately 2131 km^2 to 3211 km^2 (ABMI 2018). Comprising of the Cold Lake, Athabasca, and Peace River Oil Sand Areas, the total oil sands area is approximately 14 million hectares (140 000 km^2) and, of this, currently 58% or 8.2 million hectares are under lease (Alberta Government 2017a).

The phrases 'tar sands' or 'oil sands', frequently used to describe the energy extraction in Alberta, refer to the type of oil deposits commonly found in the region. Unlike conventional crude oil, that flows freely, the oil deposits in northern Alberta are primarily in the form of bitumen, a semi-solid substance that must be heated or diluted before it will flow. Additionally, approximately 97% of the bitumen deposits are located greater than 75 m below the earth's surface, making them accessible only by *in situ*, or below-ground, extraction methods (Alberta Energy 2017). Recent advent of the economically feasible steam-assisted gravity drainage (SAGD) technique, whereby precise directional drilling is used to inject high-pressure steam into the viscous substrate to mobilize the bitumen for removal, has initiated a rapid expansion of small-scale anthropogenic features within the region (Jordaan et al. 2009, Rosa et al. 2017).

In situ energy extraction involves various types of development features for locating, extracting, processing, and transporting bitumen, including both exploratory and permanent features. In the exploration phase of development, surface vegetation is cleared to enable the access of seismic machinery for sub-surface mapping of the substrate composition. These long, straight vegetation clearings, historically approximately 5-8 m wide, but now more commonly 2-3 m wide, are systematically spaced across the landscape to provide access for equipment that identifies potential reservoir locations using seismic analyses (Lee & Boutin 2006, Schneider & Dyer 2006). Precise directional drilling involves spacing these linear features, hereafter 'seismic' lines, at intervals of approximately 50-100 m in a dense grid pattern to facilitate detailed three-dimensional reservoir delineation (Dabros et al. 2018). In high potential areas, an exploratory well is drilled to confirm the presence of a reservoir, which requires additional larger features, including 5-20 m wide linear winter roads and 50 by 80 m wide exploratory well sites. An exploratory well may be further developed, if oil is proven, or be capped and left undeveloped if oil is not proven. Although individually these features are relatively small in extent, they are widely distributed across the region and may take upwards of 30-100 years to regenerate naturally (MacFarlane 2003, Lee & Boutin 2006, Van Rensen et al. 2015).

Where productive bitumen deposits are located, the extraction and processing phase leads to development of additional permanent linear infrastructure, including gravel roads, pipelines, or transmission lines approximately 25-60 m wide, polygonal extraction well sites approximately 150 by 200 m wide, and larger central processing facilities. Cumulatively, the anthropogenic footprint from oil and gas development creates wide-scale habitat perforation, contributes upwards of 353,000 km of anthropogenic edge, and has no natural analogue (Pickell et al. 2013, 2014). Beyond the direct loss of habitat for some species, these anthropogenically derived habitat changes can alter the spatial configuration of habitat patches, increase the amount of early successional vegetation, modify the structural variability of vegetation, and affect ecological relationships in plant and wildlife communities (Linke et al. 2008, Venier et al. 2014, Pattison et al. 2016, Riva et al. 2019).

In addition to structural changes, vegetation clearings associated with exploratory or permanent development features alter local habitat conditions both within and adjacent to features including the amount of light, wind speed, soil compaction, and moisture retention (Stern et al. 2018, Dabros et al. 2018). These changes may benefit some species, by facilitating movement (Riva et al. 2018a, Roberts et al. 2018) or increasing food resource accessibility, while simultaneously degrading habitat connectivity, resource availability, or refuge from predators for other species (Toews et al. 2018). Opposing benefits and losses for individual species can alter population dynamics, such as predator-prey relationships, and shift community structure (Fisher & Burton 2018, Riva et al. 2018b, Mahon et al. 2019). Linear features, for example, are considered the ultimate cause of population declines for threatened woodland boreal caribou species (*Rangifer tarrandus caribou*), due to both direct and indirect impacts on gray wolf (*Canus lupus*) predator populations (Hebblewhite 2017). Gray wolves can capitalize on linear features as movement corridors, which facilitates increased movement rates, greater access into caribou habitat, and higher encounter rates with caribou prey species (Dickie et al. 2017). The regenerating habitat created by linear seismic clearings also positively influences abundance of alternative white-tailed deer (*Odoicoleus virginianus*) prey populations, thus indirectly facilitating increases in gray wolf population numbers and further enhancing the impacts on caribou species (Hebblewhite 2017). Predicting and managing the influence of development features on complex ecological relationships, such as these, is crucial to understanding changes in biological diversity and implementing sustainable resource practices.

Avian responses to small scale development features

For avian populations, direct and indirect impacts of energy development features can lead to population declines and changes in community composition. Documented sources of direct mortality include collisions with infrastructure or vehicles on roadways, landings on tailing ponds, electrocution from powerlines, and encounters with flare stacks (Loss 2016). In addition, incidental destruction of nests through spring and summer vegetation clearing has the potential to contribute to annual losses in recruitment of young that are estimated at upwards of 10,200 individuals in the Western Canadian Sedimentary Basin (Hobson et al. 2013). The spatially expansive footprint of these development features means many of the effects of these features on birds are poorly quantified and their relative effects cannot be accurately identified (Bayne & Dale 2011, Hobson et al. 2013, Loss 2016). Associated noise pollution, light, and human activity can influence foraging efficiency, vocal communication, and pairing success, potentially degrading habitat quality or spatially displacing individuals (Habib et al. 2007, Francis et al. 2011, Ortega 2012, Kleist et al. 2017). Indirect impacts on reproduction, space use, or movement can also contribute to local population declines, but effects may differ by both species and feature type (Bayne et al. 2016, Loss 2016).

Avian responses to changes in vegetation structure and composition are well-documented (Hobson & Bayne 2000, Schieck & Song 2006, Venier & Pearce 2007, Venier et al. 2014) and can inform our understanding of responses to habitat perforation by energy sector development.

In mature forest habitats, songbird communities at well site locations differ from communities in adjacent forest habitats, with increased abundance of open habitat species, such as Clay-coloured Sparrows (*Spizella pallida*), Alder Flycatchers (*Epidimonax alnorum*), and Chipping Sparrows (*Spizella passerina*), and decreased abundance of mature forest associated species, such as Bay-breasted Warbler (*Setophaga castanea*), Brown Creeper (*Certhia americana*), and Black-throated Green Warbler (*Setophaga virens*) (Thomas et al. 2014, Wilson & Bayne 2019). In contrast, shrub- or canopy-nesting species may show similar densities near conventional (4-10 m wide) seismic lines as found in undisturbed forest because rapid canopy ingress minimizes the change in vegetation structure of these smaller features at this height in the canopy (Machtans 2006). However, some species respond even to small vegetation changes. Behavioural avoidance of conventional seismic lines by Ovenbirds (*Seiurus aurocapilla*) can lead to reductions in abundance at seismic densities of 8.5 km/km^2 (Bayne et al. 2005b). The variability in species responses reported across studies highlights an ongoing need to understand mechanisms linking species ecology to anthropogenic impacts (Northrup & Wittemyer 2013).

Whether birds react to development features the same way in all forest types is poorly understood. In young, high density vegetation or lowland habitats, for example, development features remain distinct from adjacent habitat for extended periods of time (Machtans 2006, Van Rensen et al. 2015). Despite comprising close to 60% of the oil sands region, there is a scarcity of avian research in lowland habitats including bogs and fens (Morissette et al. 2013). Additional multi-scale habitat analyses are needed to identify the key habitat variables and spatial scales influencing different species' responses to habitat change created by energy sector development, especially in these understudied lowland habitats (Mahon et al. 2016).

While individual avian species may show different types (e.g. positive, negative, or neutral) and strength of responses, specialized species, that use a narrow set of resources, may be more sensitive to anthropogenic changes than generalist species, that use a broader range of resources. Globally, there is increasing evidence that specialized species tend to be located in less fragmented and less disturbed landscapes and are being replaced by generalist species in more fragmentated and more disturbed landscapes (Devictor et al. 2008, Clavel et al. 2011). The dependence of specialized species to a single or a few habitat types may make them more susceptible to loss of that habitat, and less adaptable to changing habitat conditions (Devictor et al. 2008). Specialized species, for example, may have lower foraging plasticity and may be outcompeted by generalist species when habitat is lost or degraded (Clavel et al. 2011). Ultimately, losses or declines of specialized species can lead to increased genetic or functional similarity within and across community assemblages (Devictor et al. 2008). Increased community similarity, or biotic homogenization, is concerning due to the potential effects on ecosystem function and productivity (Clavel et al. 2011). Assessing the response of both specialist and generalist species to different energy development features may, therefore, be both an indicator and predictor of important impacts to avian communities.

The issue of scale and habitat selection

It is generally accepted that habitat use involves selection of environmental characteristics at multiple scales, including the geographic area, territory, and within-territory scales (Johnson 1980, Wiens 1989, Meyer & Thuiller 2006). As a result, the effects of landscape structural change, such as the amount and configuration of habitat impacted by development, may be revealed at multiple scales (Leonard et al. 2008). Selection at one scale, for example, can constrain the availability of resources at another scale (Barg et al. 2006). Biological responses to habitat alteration may vary with the size of the landscape considered because different ecological processes may be influenced by landscape structure at different spatial scales (Smith et al. 2011) and different species will perceive their environment at different scales (Wiens 1989). Therefore, the task of identifying appropriate, "organism-centred" scales to examine environmental variables for robust inference of animal habitat use patterns remains a challenge in ecological studies (Wheatley & Johnson 2009). Inadequate specification of the 'focal lens' or 'observational scale' at which to evaluate a process may lead to incorrect interpretations of the patterns due to scale effects (Wiens 1989, Thompson & McGarigal 2002, Wheatley & Johnson 2009).

Examining species responses to habitat characteristics at multiple scales improves our understanding of the scales at which species respond to their environment (Timm et al. 2016). Therefore, to understand avian responses to anthropogenically derived habitat changes, it is crucial to consider the influence of both landscape- and local-scale processes. Greater understanding of the scales at which species respond to different *in situ* development features and identifying the processes driving species responses at each scale is important to implement effective conservation and management strategies.

Thesis outline

In this thesis, I examine the response of an avian peatland generalist, Dark-eyed Junco (*Junco hyemalis*), and specialist, Palm Warbler (*Setophaga palmarum*), songbird species to different development features associated with *in situ* oil sands resource extraction. My main objective is to improve our understanding of the relationship between species-specific responses to different types of development features and scale of response. First, I investigate habitat and development factors influencing population-level occurrence of Dark-eyed Juncos and Palm Warblers across an *in situ* lease area (Chapter II). Second, I examine the influence of *in situ* development features on territory-level habitat selection and within-territory behaviours of individual breeding pairs (Chapter III). In general, I aim to address the following questions within this thesis:

1. Identify landscape-scale factors influencing distribution of an avian generalist and specialist in habitats altered by *in situ* oil sands development.
2. Identify the relative effect of different *in situ* oil sands development and habitat features on landscape- and local-scale habitat selection.
3. Identify potential behavioural mechanisms affecting responses to *in situ* oil sands development features on individual territory placement and within-territory habitat selection.

Chapter 2: Relative influence of *in situ* development features on lease area occurrence of an avian peatland generalist and specialist

2.1 Introduction

Understanding species' responses to anthropogenically-derived habitat loss and fragmentation remains a central issue for biological conservation and management. As global populations continue to grow, so does the need for energy and the corresponding intensity of anthropogenic footprint on the landscape (Northrup & Wittemyer 2013). In the boreal forest of northern Alberta, demand for non-renewable energy products is contributing to rapid alteration and perforation of forest habitats (Jordaan et al. 2009, Pickell et al. 2014, Rosa et al. 2017). Currently, over 40 percent of Canadian energy production is supplied by crude oil and, in 2016, crude oil contributed 86.1 percent of Alberta's $51.1 billion in energy resource exports (Alberta Government 2017b). Historically, the majority of bitumen supplied by the Alberta oil sands area has been extracted through surface mining techniques (i.e. digging for bitumen reserves within approximately 75 m of the earth's surface), however, less than 3 percent of the extent of bitumen deposits within the oil sands region are surface-mineable (Alberta Government 2017a). Recent transition to novel *in situ*, or below-ground, extraction methods has facilitated higher-efficiency access to the remaining 97 percent of the 142,200 km^2 extent of the Alberta oil sands area containing reserves located deep below the ground (Schneider & Dyer 2006, Alberta Government 2017a). The expanding steam-assisted gravity drainage (SAGD) extraction method (i.e. using below-ground injection of high-temperature steam to enhance the flow of bitumen for removal) requires locally intensive infrastructure for the extraction and processing of bitumen, such as facilities, borrow pits, extraction well sites, pipelines, powerlines, and road networks, hereafter called ‘permanent’ features.

In addition, extensive exploratory geological surveys are required to accurately determine the depth and extent of underground reserves. Exploratory surveys involve clearing of forest vegetation to enable access of survey machinery. This habitat alteration leaves a footprint of undeveloped features of different sizes and shapes, including: polygonal exploratory well sites- approximately 50 m by 80 m vegetation clearings, linear winter roads or conventional seismic lines- 5 to 20 m wide linear clearings, and low-impact (3D) seismic lines- 2 to 3 m wide linear features spaced every 30 to 100 m in a dense grid pattern (Figure 1). This intricate network of fine-scale and straight-edged features creates a different sort of footprint to forestry practices and has no natural analogue (Pickell et al. 2015). Exploratory features are widely considered to be temporary and low-impact relative to other development features. Thus, these features are often left to regenerate naturally. There is evidence, however, that such features may persist on the landscape for extended periods of 30-100 years (MacFarlane 2003, Lee & Boutin 2006, Van Rensen et al. 2015), and can lead to wide scale fragmentation effects (Pattison et al. 2016). Due to their high density, seismic lines have a greater impact on landscape structure metrics, including the number of habitat patches, mean patch size, and amount of edge, than other linear features types such as roads, railways, powerlines, and pipelines (Pattison et al. 2016). Projected increases in the proportion of extraction using *in situ* methods could increase the density of seismic lines from approximately 1.5 km per km^2, for conventional extraction methods, to approximately 8 km per km^2 within the next 100 years (Schneider et al. 2003).

Permanent and exploratory features contribute to wide-scale habitat loss, alteration, and fragmentation that influences habitat condition for wildlife populations. Fragmentation, or the subdivision of continuous habitat into smaller patches, can affect processes such as home-range selection (Tigner et al. 2015), movement patterns (Tigner et al. 2014, Dickie et al. 2017, Riva et al. 2018a), reproductive success (Ludlow et al. 2015, Bernath-Plaisted & Koper 2016), predator avoidance behaviours (Mumma et al. 2017), and foraging opportunities (Scrafford et al. 2017). For avian communities, the influence of energy development features on abundance, density, and nesting success is both species- and feature-specific (Thomas et al. 2014, Ludlow et al. 2015, Bayne et al. 2016, Farwell et al. 2016). Therefore, understanding the relative impacts of different feature types on individual species is important to enhancing our knowledge of the impacts to the broader avian community.

The process of habitat selection is thought to be hierarchical, whereby selection of habitat characteristics at a larger, e.g. landscape, scale will influence the availability of habitat at a smaller, e.g. home-range, scale (Johnson 1980). Development features that affect the presence, i.e. occurrence, of a species, therefore, could cause important population-level changes on the distribution or abundance of a species. Permanent and vegetated development feature types may have different impacts on relative occurrence of a species due to both the characteristics of the feature itself, and the influence of that feature on the surrounding habitat. Changes in vegetation structure can alter the microclimatic (e.g. temperature, moisture), resource availability (e.g. insect abundance), or biological influences (e.g. nest predation rates) associated with edge effects (Ewers & Didham 2006, Fischer & Lindenmayer 2007, Prevedello & Vieira 2010). Habitat alteration may also contribute positive, negative or neutral effects on the condition of the surrounding habitat patches and the response to habitat interfaces (Ries & Sisk 2004). Positive responses to changes in habitat quality include ‘landscape complementation’, or access to novel or increased resources provided by habitat in the development feature (Dunning et al. 1992, Ries

& Sisk 2004). A species' ability to use resources in anthropogenic features, therefore, can influence the intensity of fragmentation effects (Ewers & Didham 2006).

The structural contrast of an anthropogenic feature may be a good predictor of its habitat quality for forest-associated songbirds (Prevedello & Vieira 2010). For forest ecosystems, edge effects are strongest when the structural contrast of the development feature is high relative to the unaltered habitat (Kennedy et al. 2010). Ovenbirds (*Seirus aurocapilla*), for example, showed an increased probability of including linear features within territories for lines with smaller widths (Bayne et al. 2005a) and greater vegetation cover (Lankau et al. 2013). Strength of an edge response, therefore, may be mediated by the degree of change in the structure of different development feature types. Larger, more permanent development features not only lead to greater area of resource change, but may also have greater contrast, enhancing differences in microhabitat conditions such as sun exposure, temperature, or wind (Delgado et al. 2007, Stern et al. 2018). Thus, stronger edge effects may lead to a greater impact on the quality of the surrounding habitat.

Specialist species, i.e. those requiring a narrow set of resource attributes, may be more sensitive to habitat disturbance than generalist species, i.e. species with a broad ecological niche that utilize a wider range of resources (Clavel et al. 2011, Carrara et al. 2015). For example, in mixed hardwood and oak (*Quercus* species) dominated forests, specialized forest-interior species were less abundant at well sites than reference locations and showed declining abundance with increasing well site density at the 25-hectare scale, whereas generalist early successional species were more abundant at well sites than reference sites (Thomas et al. 2014). Furthermore, specialist species may be more sensitive to the characteristics of the altered habitat. Movement of forest specialists, for example, may be impeded by contrasting development features, potentially restricting specialists to larger patches of intact forest (Gillies & St. Clair 2010, Smith et al. 2011, Betts et al. 2014).

Here, I investigate whether a conifer generalist and specialist respond differently to *in situ* oil sands disturbance features of different sizes and types in peatland habitats. In northern Alberta, Dark-eyed Juncos (*Junco hyemalis*) and Palm Warblers (*Setophaga palmarum*) are both abundant in lowland habitats (Mahon et al. 2016, ABMI (Alberta Biodiversity Monitoring Insitute) 2017). Dark-eyed Juncos are common to both disturbed and undisturbed coniferous habitats across the boreal forest region, and are considered to be conifer generalists (Schieck & Song 2006, Handel et al. 2009, Mahon et al. 2016). Palm Warblers are closely associated with lowland black spruce habitats, including bogs and fens, are identified as a specialist species in the boreal forest (Calmé et al. 2002, Mahon et al. 2016), and are thought to be sensitive to disturbances in these systems, requiring large tracts of intact peatland habitat (Calmé & Desrochers 2000, Poulin et al. 2006). Although both species are ground nesters common in treed bog habitats, different resource-use strategies provide an ideal comparison for contrasting avian responses to different anthropogenic features created by multi-feature SAGD disturbances.

I had two main objectives: (1) determine if *in situ* oil sands development features contribute to positive, negative, or neutral effects on occurrence, beyond the influence of amount of habitat alone; and (2) determine the relative effect of different types of development features on Dark-eyed Junco and Palm Warbler occurrence. I hypothesized that a conifer generalist junco would show greater tolerance to development features than the peatland specialist warbler due to the potential for complementation of resources in the anthropogenically-derived habitat, i.e. a greater ability for juncos to use novel resources provided by the development feature.

Specifically, I hypothesized that Dark-eyed Juncos and Palm Warblers may respond differently to polygonal or linear permanent features, exploratory (vegetated) well sites, wide linear, and 3D seismic line development features due to: (1) vegetation structural differences of the feature types- where permanent (non-vegetated) features and vegetated (containing early seral regenerating habitat) features may provide different habitat value; (2) threshold effects based on feature size- where smaller features, such as seismic lines or other linear features, may not be perceived differently from natural vegetation gaps whereas larger features may be more distinct; or (3) microhabitat conditions- where the unique differences in habitat conditions of each feature create favourable or unfavourable conditions.

2.2 Methods

Study Area

This study was situated in the Brion Energy MacKay River Commercial Project (MRCP) lease area, located approximately 30 km northwest of Fort McMurray, Alberta (Figure 2). The MRCP is a small, 17,000-hectare, lease area for Steam Assisted Gravity Drainage (SAGD) bitumen extraction that was in the early stages of development at the time of the study. Upon completion of development, anthropogenic features on this lease area will include approximately 3,520 hectares of 2-dimensional (2D) and 3-dimensional (3D) seismic lines, exploratory and permanent production well sites, winter roads, permanent gravel roads, pipelines, and other industrial facilities (Matrix Solutions Inc. 2012). During the study, all features within the lease area were less than 8 years old and structurally similar, as all were in early stages of regeneration, exhibiting little to no regrowth of vegetation beyond forb-herb stage.

Occurring within the Boreal Mixedwood ecological region (Beckingham & Archibald 1996), the habitat within MRCP primarily consists of lowlands, including open, shrubby, or treed bogs and fens. Vegetation communities in the nutrient poor, acidic conditions of bogs are comprised mainly of black spruce (*Picea mariana*) in the canopy and shrub layers. Dominant groundcover species include labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), and bog cranberry (*Vaccinium vitis-idaea*). Nutrient-rich fens are more diverse and are comprised of black spruce, tamarack (*Larix laricina*), alder (*Alnus*), birch (*Betula*), and willow (*Salix*) species in the main foliage layers. Low ground cover in fens may include sedges (*Carex*) and horsetail (*Equisetum*) species. Other less common habitat types in the study area include mesic deciduous or coniferous-dominated upland forests, with leading canopy composition species including trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsaminifera*), or white spruce (*Picea glauca*). Low-bush cranberry (*Viburnum edule*) and prickly rose (*Rosa acicularis*) are common mesic shrub species. Drier or low nutrient upland sites are dominated by jack pine (*Pinus banksiana*) or black spruce canopy species and may include sparse blueberry (*Vaccinium myrtilloides*), Canada buffalo-berry (*Shepherdia canadensis*), or Labrador tea in the understory.

Avian sampling

Standard avian point-count techniques (Ralph et al. 1995, Matsuoka et al. 2014, Turgeon et al. 2017) were used to sample Dark-eyed Junco and Palm Warbler occurrence within the lease area. Survey sites were selected using a two-step process: (1) sites were stratified across all habitat types within the survey area; and (2) sites within each habitat type were selected to achieve a range in both the amount and types of development features within a 250-m buffer of each location. Skilled observers visited a total of 284 sites during the breeding season between June 4 and July 1, 2014, however I focused our analysis on a subset of 157 locations, that: (1) contained a minimum of 20% lowland habitat within 100 m of the survey site; and (2) were within the extent of available high-resolution habitat data (Figure 2). At each location, observers recorded songbirds seen and heard within a 100-m, limited-radius sample area and over a 10-minute sampling duration. Surveys occurred during good weather (no rain, light wind) and during peak hours of avian activity between approximately 04:00 and 9:45. Sites were placed a minimum of 500 m apart (greater than the average detection radius for most songbird species) to ensure independence of individual detections between sites (Matsuoka et al. 2012), and were limited to distances within 2.5 km of the nearest gravel roadway to meet access constraints. Point-count surveys were conducted once during the breeding season, prioritizing the importance of a larger sample size (Ralph et al. 1993) to examine a greater range of development feature combinations.

Habitat attributes

Habitat variables for this study were derived from three sources: (1) an avian habitat class layer derived from human-classified aerial imagery (Mahon et al. 2016); (2) 2009 LiDAR data (bare ground and full feature light detection and ranging data); and (3) 2013 Pleiades 50-cm resolution multispectral satellite imagery. Broad habitat types were identified from the avian habitat class layer which distinguishes vegetation into 12 types based on stand-level vegetation associations, such as leading species composition, and includes up to 6 different structural stage classes for each habitat type. I derived finer-resolution vegetation structure characteristics, including vegetation height, vegetation class density, and topographical surface roughness (slope variability) using LiDAR data. Vegetation productivity has also been correlated with avian abundance and richness in a number of different forest-dominated systems (Hurlbert & Haskell 2003, Evans et al. 2006, St-Louis et al. 2014). I identified site productivity as the average value of the normalized difference vegetation index (NDVI) of lowland vegetation within 100-m of the survey site. NDVI indices, which are calculated using a ratio of near infrared (NIR) and visible (VIS) wavelength spectral reflectance from satellite imagery [NDVI=(NIR-VIS)/(NIR+VIS)], represent areas of high chlorophyll concentrations and are thought to correspond to differences in vegetation productivity or 'greenness' (Pettorelli et al. 2011).

My first step was to develop a habitat only (null) model for each species. The habitat model was developed using a limited number of *a priori* predictor variables representing three habitat characteristics: habitat amount, vegetation structure, and vegetation productivity. To identify the strongest variable for habitat amount, I examined combinations of lowland categories with different vegetation composition and structural stage attributes, characteristics important to forest-associated boreal birds (Machtans & Latour 2003, Schieck & Song 2006, Mahon et al. 2016). Categories included: (1) lowland (all stages of bog and fen combined); (2) shrubby bog (≤6 m tall vegetation); (3) shrubby fen; (4) treed bog (≥6 m tall vegetation); (5) treed fen; (6) shrubby lowland (bog and fen combined); and (7) treed lowland (bog and fen combined). After identifying the best predictor for habitat amount, I then determined if local vegetation structure and vegetation productivity attributes refined predictive capacity of models. Variables considered for vegetation structure included density and variability of lowland vegetation structure. Vegetation density was represented by percent area of preferred shrubby (1 to < 4 m tall) or regenerating (4 to < 10 m tall) vegetation within lowland habitat and variability in vegetation structure was represented by the standard deviation of vegetation heights within lowland vegetation. To avoid overspecification of models, only the single best predictor for each variable category (habitat amount, vegetation structure, vegetation productivity) was included in the final habitat model for each species, and vegetation structure or productivity variables were only included if they improved the habitat model above habitat amount alone.

Defining development features

A combination of automated and manual digitization techniques were used to delineate development features from both planning schematics and Pleaides 50-cm resolution satellite imagery (2013, 2015). Development features were grouped into five distinct categories for this analysis: (1) permanent polygonal features- borrow/gravel pits, developed well sites, and other industrial features; (2) permanent linear features- gravel roads (25-70 m wide); (3) well sites- undeveloped exploratory well sites (approximately 50 m by 80 m polygons, hereafter well sites); (4) wide linear features- traditional linear cut-line features, pipelines, and winter roads (5-20 m wide); and (5) seismic features- including only modern 2-3 m wide 3-dimensional (3D) linear seismic features (hereafter seismic). To identify whether different types of development features have different relative impacts on Dark-eyed Junco and Palm Warbler occurrence, I examined the percent area of different combinations of development feature types (Table 1).

Model selection and analysis

As evidence suggests avian species may respond to different factors at different scales (Leonard et al. 2008), and that multi-scale models may improve the predictive capacity of habitat selection models (Smith et al. 2011), I considered habitat and development variables at two spatial scales using circular buffers around the point-count station, a 500-m radius neighbourhood scale and a 100-m radius local scale. A 500-m neighbourhood was selected to: (1) be large enough to contain home ranges of multiple individuals, thus encompassing influential biological processes such as dispersal constraint and conspecific attraction (Desrochers et al. 2010); (2) fall within a range considered influential in the literature for songbirds (Desrochers et al. 2010); and (3) capture a representative gradient of composition across habitats and target development features types in the study area. I selected a 100-m local scale to: (1) match the zone of detection from the limited-radius sampling method, thus capturing local-scale differences in habitat around each station; and (2) represent local-scale processes such as nest site availability, microclimate, or food limitation (Desrochers et al. 2010, Farwell et al. 2016). For each habitat or disturbance variable, the scale was evaluated first, and the most predictive scale selected for inclusion in multi-scale models.

Once an appropriate scale was established for each variable, a two-step approach was used to compare model hypotheses. First, habitat models were developed for each species, then different combinations of development features were added to habitat models to compare relative influence of different features. Logistic regression models were used to model the probability of occurrence (1 = detected, 0 = not detected) for each species as a function of percent area of each development feature type, scaled to show the change in probability of occurrence per 10 percent change in explanatory feature. I assessed all models for variable collinearity using Variance Inflation Factors (all VIF< 3, Zuur et al. 2010). Development feature models were ranked by their ability to predict songbird occurrence relative to the null habitat quality model for each species using Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Models with the lowest AICc and greatest Akaike weights (w_i) were considered the most parsimonious and selected for each species. Strong positive or negative coefficients suggest correlations between development features and occurrence within the study area. Predictive accuracy of models was evaluated using the receiver operating characteristic area under the curve (ROC AUC). Analyses were completed in R (R Core Team 2018) and were facilitated using the packages lme4 (Bates et al. 2018), MuMIn (Barton 2018), and pROC (Robin et al. 2011).

2.3 Results

Occurrence and development

A total of 107 Dark-eyed Juncos and 96 Palm Warblers (singing males only) were detected within a 100-m sampling radius of point-count centres for 157 point-count stations included in the analysis. Dark-eyed Juncos occurred at 78 of these stations and Palm Warblers at 73. After exclusion of sites with less than 20 percent lowland within 100 m of the point-count station, the upper range for percent area lowland within 100 m of stations was 100 percent (mean 68.1 ±19.1) at the 100-m scale and 96.9 percent at the 500 m scale (mean 63.8 ±16.7; Table 1). Sampling stations contained 0-62.3 percent polygonal permanent features, 0-42.4 percent polygonal linear features, 0-24 percent exploratory well sites, 0-44.3 percent wide linear and 0-30.6 percent 3D seismic within 100 m, adding to an average of 25.8 percent area for all development feature types. A total of 28 point-count stations contained less than 5 percent development within 100 m.

Habitat null model

Inclusion of vegetation structure and productivity variables substantially improved habitat model fit for Palm Warblers, but not for Dark-eyed Juncos. For Juncos, the top habitat model included percent area of treed bog habitat within 500 m of point-count station but the model was not improved by inclusion of additional local-scale vegetation structure or productivity (Table 2; w_i: 0.04). Junco occurrence was 1.4 times more likely for every 10 percent increase in treed bog habitat (Figure 4, Table 3). For Palm Warblers, the top habitat model included percent area of shrubby lowland habitat (bog or fen) within 500 m of the point-count station and was improved by the inclusion of both lowland structure and vegetation productivity measures at the local scale (Table 4; w_i: <0.01). Palm Warbler occurrence was 1.2

times more likely for every 10 percent increase in the amount of shrubby lowland habitat. Occurrence was 0.37 times as likely for every 1 m increase in the standard deviation of tree height and 1.27 times more likely for every 0.001 increase in NDVI (‘greenness’; Figure 4, Table 5).

Feature-specific response to permanent development

The most supported development feature model for both Dark-eyed Junco and Palm Warbler occurrence was the permanent feature model. The top Dark-eyed Junco model (Table 2; w_i: 0.64) was supported with a ROC AUC of 0.617, indicating relatively weak predictive ability. For every 10 percent increase in the percent area of polygonal permanent features the odds of Dark-eyed Junco occurrence decreased by 0.6 times, whereas the odds of occurrence increased 1.7 times for every 10 percent increase in permanent linear features (Table 3, Figure 5). Percent area of linear permanent features within 100 m had the greatest relative impact on occurrence, followed by the percent area of permanent polygonal features within 500 m, and then percent area of treed bog within the 500-m neighbourhood scale (Figure 6). Only two other models showed more support than the habitat only null model, and both these models contained permanent features (linear only w_i: 0.14 and polygonal only wi: 0.08, Table 2). All models containing only vegetated features ranked well below the null habitat model based on AIC_c (Table 2, w_i: 0.03).

For Palm Warblers, the top occurrence model (Table 4, w_i: 0.63) was supported by a ROC AUC of 0.782, indicating a good model fit for prediction. Coefficients were standardized to a variance of 1 and mean of 0 to compare relative influence for variables with different measures. The most to least influential variables in the standardized Palm Warbler occurrence model were percent area of polygonal permanent features at a local scale, local tree height variability, local NDVI, neighbourhood percent area shrubby lowland, and neighbourhood percent area linear permanent features (Figure 7). Odds of occurrence decreased 0.4 times for every 10 percent increase in permanent polygonal features within a 100-m local scale and increased 3.9 times for every 10 percent increase in area of permanent linear features within a 500-m neighbourhood (Table 5, Figure 5). All models including development features ranked better than the habitat quality null model (Table 4).

2.4 Discussion

In situ oil sands development features are expected to become increasingly prevalent in northern Alberta boreal forests (Schneider & Dyer 2006). Understanding the relative sensitivity of different species to different types of development features is important for predicting and managing population-level responses to these expanding anthropogenic footprints. This study shows that both Dark-eyed Juncos and Palm Warblers are influenced by the presence of permanent development features, with both species showing a negative response to polygonal permanent features and a positive response to permanent linear features. In contrast, despite differences in specificity of habitat requirements, both these species are commonly present within areas perforated by smaller vegetated development features, supporting the notion that exploratory features are lower impact than more permanent features.

Responses to permanent features

Permanent features showed consistent impacts to occurrence for both Dark-eyed Juncos and Palm Warblers, despite differences in habitat preference between these two species. The addition of polygonal and linear permanent features improved model fit relative to the best habitat model for both species, supporting hypotheses that permanent features are not equivalent to natural habitats and have a greater influence on the overall suitability of a location relative to exploratory development features. Polygonal permanent features showed a strong negative influence on the probability of occurrence. In this study area, permanent polygonal features include developed SAGD well sites, borrow pits, and industrial facilities. Associated human activity, industrial noise, movement-impeding infrastructure, and high contrast to the surrounding habitat could contribute to why permanent polygonal features provide unsuitable areas for these songbirds.

Contrary to predictions, both species showed a positive response to permanent linear features and the relative strength of responses were similar to those of larger polygonal features, suggesting that feature area may not be a good predictor of relative impact. In this study area, all permanent linear features were unpaved gravel roads. In forested ecosystems, responses to unpaved roads on abundance or density of passerines is variable (Ortega & Capen 2002). Road networks have known effects on bird populations through various direct and indirect mechanisms. Direct negative impacts may include habitat loss, mortality from vehicle collisions, or poisoning from roadside pollution, whereas indirect effects may include influences of artificial light or noise on breeding success, physical barriers to movement, or edge effects (Kociolek et al. 2011). Positive influences on passerines may include provision of novel early successional habitat in the verge and potentially in the forest edge, therefore increasing landscape heterogeneity (Helldin & Seiler 2003), or increased food sources (Morelli et al. 2014).

Ortega and Capen (2002) also reported a positive road response for Dark-eyed Juncos, observing increased abundance of juncos within 150 m of unpaved roads relative to forest interiors. They attributed this response to low herbaceous and woody vegetation along roadsides due to observations of juncos foraging within low vegetation and directly on unpaved road surfaces. In this study area, juncos were also observed foraging both on gravel substrates and along roadside edges (Carpenter et al, Ch II), so gravel roads may influence availability or diversity of insect prey species for ground-foragers in this system. Although, as foliage gleaners, Palm Warblers do not commonly feed within herbaceous vegetation or along the ground, they might also be benefitting from impacts to insect populations along the interface of gravel roads and surrounding peatland vegetation. Increased light or moisture along roadside edges can increase the abundance or diversity of insect prey species within the surrounding vegetation, leading to shifts in the insect community that may impact predator-prey dynamics for avian species (Muñoz et al. 2015, Riva et al. 2018b). Conversely, aerial insect abundance may decline with increasing road traffic and the abundance of some species can be lower closer to roadside edges (Muñoz et al. 2015, Martin et al. 2018), so positive responses could potentially be limited to low-traffic gravel roads similar to those in this study area.

Interestingly, roads in peatland habitats can have variable impacts to surrounding vegetation depending on the type of peatland and road orientation. When roads intersect peatlands at an orientation perpendicular to the direction of the underlying hydrological flow they may act as water barriers, causing different effects on either side of the road (Willier 2017). The upstream side of the road can become waterlogged, leading to widescale vegetation mortality, whereas drier conditions on the downstream side of the road may enhance woody vegetation growth. The road networks in this study area are relatively novel and intersect the peatland habitat at various orientations, suggesting that edge effects on vegetation would likely be variable. Additional investigation into the mechanism behind these responses, the consistency of this response over time, and the consistency of positive responses for other passerine species, or other peatland survey areas, is warranted.

In general, this work supports findings that impacts from roads differ from cutlines (wide linear or 3D seismic features) and cannot be directly extrapolated (Linke et al. 2008). While cutlines create greater edge per unit area than other features (Linke et al. 2008, Bayne et al. 2016), they may also create ‘softer’ edges that are not perceived by avian species as structurally distinct to natural openings (Machtans 2006). Additionally, factors including resilience and threshold effects may contribute to the relatively weak influence of vegetated development features on Dark-eyed Junco and Palm Warbler occurrence.

Resilience or threshold effects

The boreal forest is a naturally heterogenous ecosystem which may help explain why small exploratory development features did not have a strong influence on occurrence of either species. The high frequency of natural disturbance events, including fire and insect outbreaks, has created a patchy mosaic of upland and lowland forest types in various stages of succession (Bergeron et al. 2014). As a result, species that evolved in the dynamic boreal forest ecosystem may be adapted to heterogenous vegetation structure, and thus fairly resilient to small-scale changes in vegetation structure created by disturbances (Schmiegelow et al. 1997, Drapeau et al. 2016). Vegetation structure in peatland habitats is closely tied to underlying patterns of nutrient and moisture regimes and naturally includes small vegetation gaps and variation in tree height, although perhaps at a finer scale than in neighbouring upland habitats. The low nutrient availability and high moisture regime may limit overall heterogeneity in species composition, and corresponding vegetation structure leading to naturally more variegated habitats (Harper et al. 2015). With a lower tree density and wider spacing, peatland habitats may be less impacted by small structural changes created by exploratory features.

Moreover, fragmentation effects, such as patch isolation, may be stronger in highly disturbed landscapes, such as urban or agricultural areas, where habitat availability is low and the matrix has greater risk during movement (Betts et al. 2010, Villard & Metzger 2014). In the boreal forest region, energy sector developments may act more like within-patch perforation of larger contiguous forest than factors inducing patch isolation effects. In hardwood and oak ecosystems, avian communities at sites with low well site densities comparable to this study area (4-20 well sites per km^2) were similar to reference sites, but these communities diverged at higher development densities (>20 well sites per km^2), suggesting a threshold effect. Ovenbird responses to conventional seismic lines were also similar, with no change detected between 0-8.6 km of seismic per km^2 and 19% declines for each km/km^2 above that threshold (Bayne et al. 2005b). Development feature densities for vegetated features in this study area may be likewise below thresholds for strong Dark-eyed Junco and Palm Warbler responses.

Generalist and specialist responses

Despite similar directions of response to permanent features by these two species, these findings add to existing evidence that specialized species, with narrow ecological niche breadths, may be more susceptible to habitat change than species that use a broader range of habitat characteristics. For Palm Warblers, occurrence in lowland habitats was increased with shorter vegetation heights, lower variability in vegetation height, and greater vegetation productivity, suggesting that they select areas with a greater aggregation of shrubby vegetation strata. This is consistent with observations of Palm Warblers using tall black spruce shrubs for both singing and foraging behaviours in this study area (Chapter III). Additionally, standardized coefficients suggest that vegetation productivity has the greatest positive effect on Palm Warbler occurrence in this study. Conservation and management of this species therefore requires careful consideration of the structural integrity and productivity of these habitats. If this habitat specificity holds true across their range, it may explain why this species is considered area-sensitive in eastern boreal forests (Poulin et al. 2006). In this study area, lowland habitats were widespread and fairly contiguous, with large mean patch sizes relative to other habitat types, so area sensitivity of Palm Warblers may not be apparent under these conditions. As energy features begin to recover, however, regenerating vegetation may also mitigate these impacts to some extent.

The relatively poor model fit for Dark-eyed Junco indicates that juncos are commonly absent from apparently suitable habitat or present in areas where models do not predict they would be. Although not unexpected, this flexibility in habitat use makes it difficult to identify the key factors influencing habitat suitability. Most species in the boreal exhibit generalist rather than specialist niches (Schieck & Song 2006, Mahon et al. 2016), and this work suggests that predicting responses to development features for generalists is more likely to be complex and challenging.

Management implications

These findings support other evidence in the literature that habitat amount has a stronger affect than fine-scale fragmentation (Fahrig 2003), while still showing important effects of different permanent development features on surrounding habitat. This study, however, does not make conclusions about the effects of small-scale development features on habitat quality, or evaluate potential behavioural implications for species that occur in these developed habitats. I recommend additional, more detailed studies to address these outstanding questions.

These findings also emphasize the importance of minimizing impacts from widespread permanent features. As energy development from *in situ* oil sands sources expands in northern

Alberta, so will densities of associated permanent infrastructure, including gravel or paved roads, SAGD well sites, and facilities. Moreover, these impacts will not be occurring in isolation, but in conjunction with other industries such as forestry and natural gas extraction. Impacts from different features in the boreal forest region can show additive or interactive effects (Mahon et al. 2019). It will become increasingly important to consider forward planning to minimize forest alteration and integrate land use across industries and lease holders.

2.5 Tables

Table 1. Summary of the mean percent area (± SD) for habitat and development feature types within 100 m and 500 m of point-count centres for n = 157 stations included in occurrence models. *Stations selected for analysis included a minimum of 20 percent lowland habitat within 100 m of point-count centre.

	Local-scale (100-m radius)		**Neighbourhood (500-m radius)**	
Variables	Mean percent area	Range	Mean percent area	Range
Habitat				
Lowland*	68.1 ±19.1	20.7-100*	63.8 ±16.7	19.7-96.9
Shrubby lowland	8.9 ±19.2	0-100	8.7 ±11.0	0-69.8
Treed bog	47.3 ±31.8	0-100	44.7 ±24.5	0-95.2
Other habitats	5.9 ±12.9	0-69.2	11.3 ±14.0	0-63.6
Development features				
Polygonal permanent	2.9 ±11.4	0-62.3	3.8 ±9.2	0-57.3
Linear permanent	2.7 ±8.3	0-42.4	2.7 ±3.7	0-12.6
Well sites	2.1 ±5.3	0-24.1	1.3 ±1.0	0-5.6
Wide linear	4.2 ±6.9	0-44.3	3.7 ±2.9	0-13.3
Seismic	13.9 ±10.2	0-30.6	13.5 ±9.2	0-25.4

Table 2. Akaike's information criterion corrected for small sample sizes (AIC_c), changes in AIC_c (ΔAIC_c) and relative weights (w_i) for predictive models of Dark-eyed Junco occurrence, where K is the number of model parameters and LL is the log-likelihood of each model.

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Model	*K*	LL	AIC$_c$	ΔAIC$_c$	w_i
Permanent					
Habitat + permanent polygonal$_{500}$ + permanent linear$_{100}$	4	-102.257	212.777	0.000	0.643
Linear permanent					
Habitat + permanent linear$_{500}$	3	-104.775	215.707	2.930	0.149
Polygonal permanent					
Habitat + permanent polygonal$_{500}$	3	-105.357	216.871	4.093	0.083
Habitat (null)					
Treed bog$_{500}$	2	-107.190	218.458	5.680	0.038
All features					
Habitat + permanent polygonal$_{500}$ + permanent linear$_{100}$ + well site$_{500}$ + wide linear$_{100}$ + seismic$_{500}$	7	-101.946	218.644	5.867	0.034
Wide linear					
Habitat + wide linear$_{100}$	3	-106.927	220.010	7.233	0.017
Seismic					
Habitat + seismic$_{500}$	3	-107.111	220.380	7.603	0.014
Well site					
Habitat + well site$_{500}$	3	-107.173	220.502	7.725	0.014
Large vegetated					
Habitat + well site$_{500}$ + wide linear$_{100}$	4	-106.924	222.112	9.335	0.006
Vegetated					
Habitat + well site$_{500}$ + wide linear$_{100}$ + seismic$_{500}$	5	-106.820	224.037	11.260	0.002

Table 3. Summary of parameter estimates (β), standard errors (SE), *P*-value (P), odds ratio, 95% confidence intervals, and standardized odds ratio (OR$_{STD}$) in the best supported Dark-eyed Junco occurrence model.

Variable	**β**	**SE**	**P**	**Odds Ratio**	**Confidence Interval**	**OR$_{STD}$**
(Intercept)	-0.285	0.226	-1.263	0.752	(0.480, 1.166)	1.166
Treed bog (500 m)	0.352	0.171	2.056	1.421	(1.035, 2.031)	2.031
Polygonal permanent (500 m)	-0.462	0.235	-1.961	0.630	(0.358, 0.948)	0.948
Linear permanent (100 m)	0.552	0.250	2.210	1.737	(1.116, 3.064)	3.064

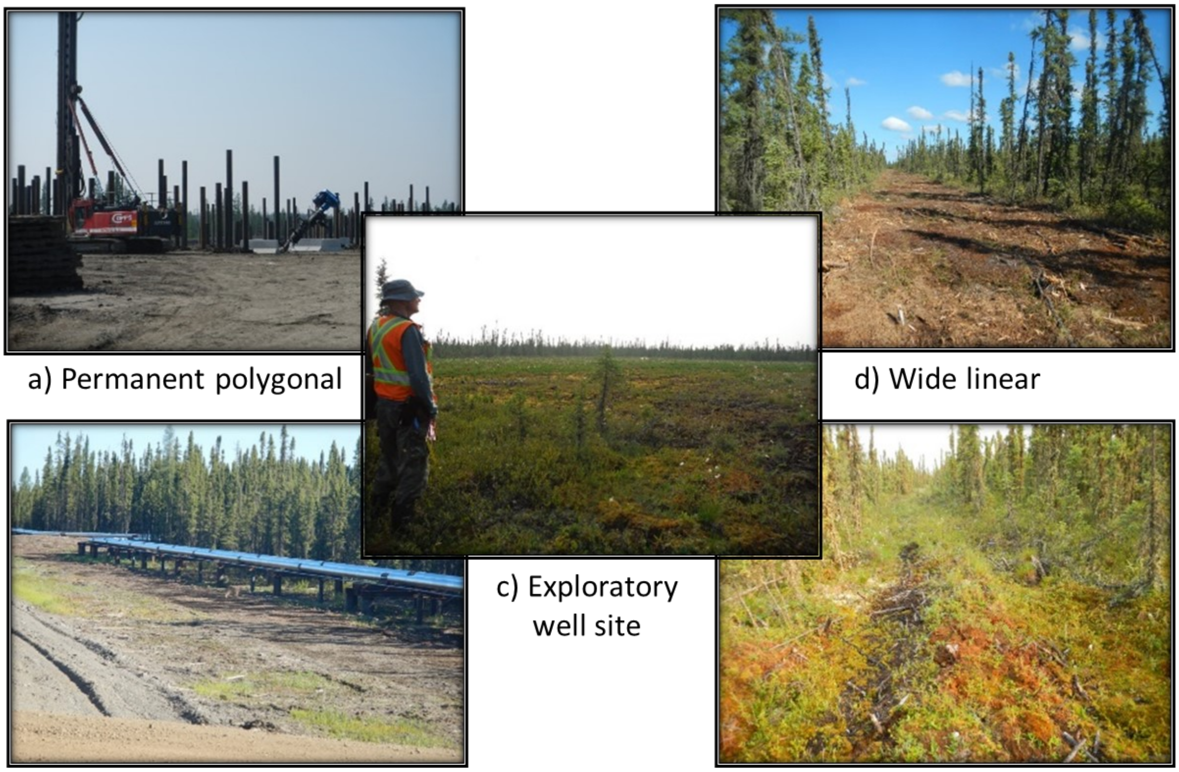
Table 4. Akaike's information criterion corrected for small sample sizes (AIC$_c$), changes in AIC$_c$ (ΔAIC$_c$) and relative weights (w_i) for predictive models of Palm Warbler occurrence, where *K* is the number of model parameters and LL is the log-likelihood of each model.

Model	K	**LL**	**AIC_c**	**ΔAIC_c**	**w_i**
Permanent Habitat + permanent polygonal$_{100}$ + permanent linear$_{500}$	6	-86.517	185.594	0.000	0.626
Linear permanent Habitat + permanent linear$_{500}$	5	-88.829	188.055	2.461	0.183
Polygonal permanent Habitat + permanent polygonal$_{100}$	5	-89.678	189.754	4.159	0.078
All features Habitat + permanent polygonal$_{100}$ + permanent linear$_{500}$ + well site$_{100}$ + wide linear$_{500}$ + seismic$_{500}$	9	-85.354	189.932	4.338	0.072
Seismic Habitat + seismic$_{500}$	5	-91.364	193.126	7.531	0.015
Well site Habitat + well site$_{100}$	5	-91.843	194.082	8.488	<0.001
Large vegetated Habitat + well site$_{100}$ + wide linear$_{500}$	5	-92.061	194.520	8.925	<0.001
Wide linear Habitat + wide linear$_{500}$	5	-92.061	194.520	8.925	<0.001
Vegetated Habitat + well site$_{100}$ + wide linear$_{500}$ + seismic$_{500}$	7	-90.775	196.302	10.708	<0.001
Habitat (null) Shrubby lowland$_{500}$ + vegetation variability$_{100}$ + vegetation productivity$_{100}$	2	-101.072	206.222	20.628	<0.001

Table 5. Summary of parameter estimates (β), standard errors (SE), *P*-values (P), odds ratio, 95% confidence intervals, and standardized odds ratio (OR_{STD}) in the best supported Palm Warbler occurrence model.

Variable	**β**	**SE**	**P**	**Odds Ratio**	**Confidence Interval**	**OR_{STD}**
(Intercept)	-14.853	6.118	0.015	0.00	(0.00, 0.033)	0.704
Shrubby lowland (500 m)	0.219	0.102	0.031	1.245	(1.025, 1.532)	1.708
Vegetation variability (100 m)	-0.993	0.272	<0.001	0.370	(0.211, 0.617)	0.420
Vegetation productivity (100 m)	0.244	0.092	0.008	1.277	(1.076, 1.545)	1.991
Polygonal permanent (100 m)	-0.813	0.648	0.209	0.443	(0.052, 0.954)	0.395
Linear permanent (500 m)	1.370	0.562	0.015	3.936	(1.346, 12.348)	1.658

2.6 Figures



a) Permanent polygonal

d) Wide linear

c) Exploratory well site

b) Permanent linear

e) Seismic

Figure 1. Examples of different development feature types within the study area, including: (a) permanent polygonal feature- 125 by 250 m SAGD well site under construction (b) permanent linear - approximately 25-70 m wide gravel roads, (c) exploratory well site- approximately 50 m by 80 m clearing, (d) wide linear- 5 to 20 m wide winter road or conventional seismic line, and (e) seismic- 2 to 3 m wide 3D seismic linear feature.

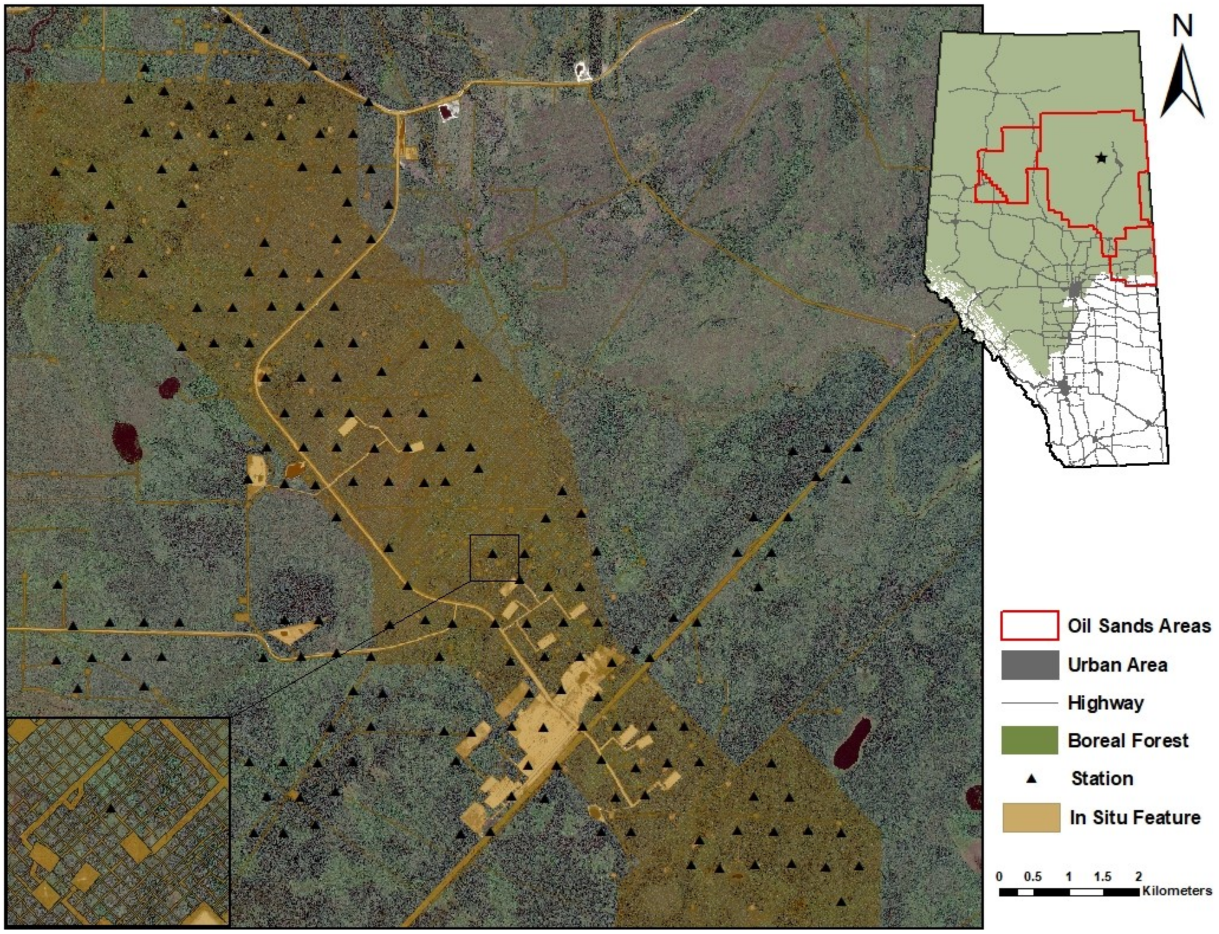


Figure 2. Locations of point-count survey sites within MacKay River Commercial Project *in situ* lease area, approximately 30 km northwest of Fort McMurray, Alberta. Development features are highlighted in brown to enhance contrast from satellite imagery.

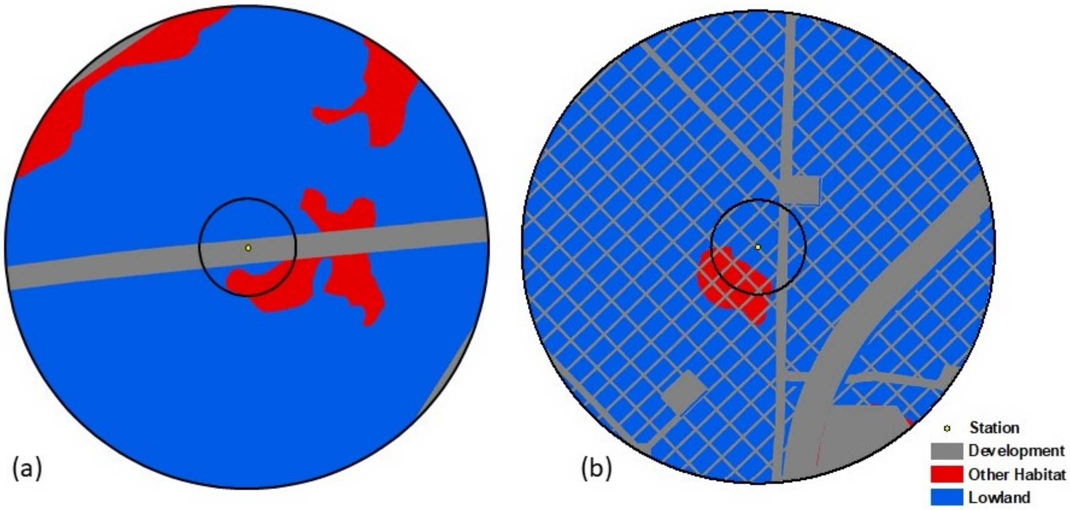


Figure 3. Examples of habitat configuration at the local-scale (100-m radius, inner circle) and neighbourhood-scale (500-m radius, outer circle) surrounding two point-count survey stations, (a) and (b) (yellow dot). These stations have similar percent area lowland (blue, approximately 50%) and percent area development (grey, approximately 30%) at the local scale, but have different development configurations and percent area developed at the neighbourhood scale, 7% and 35% for (a) and (b) respectively.

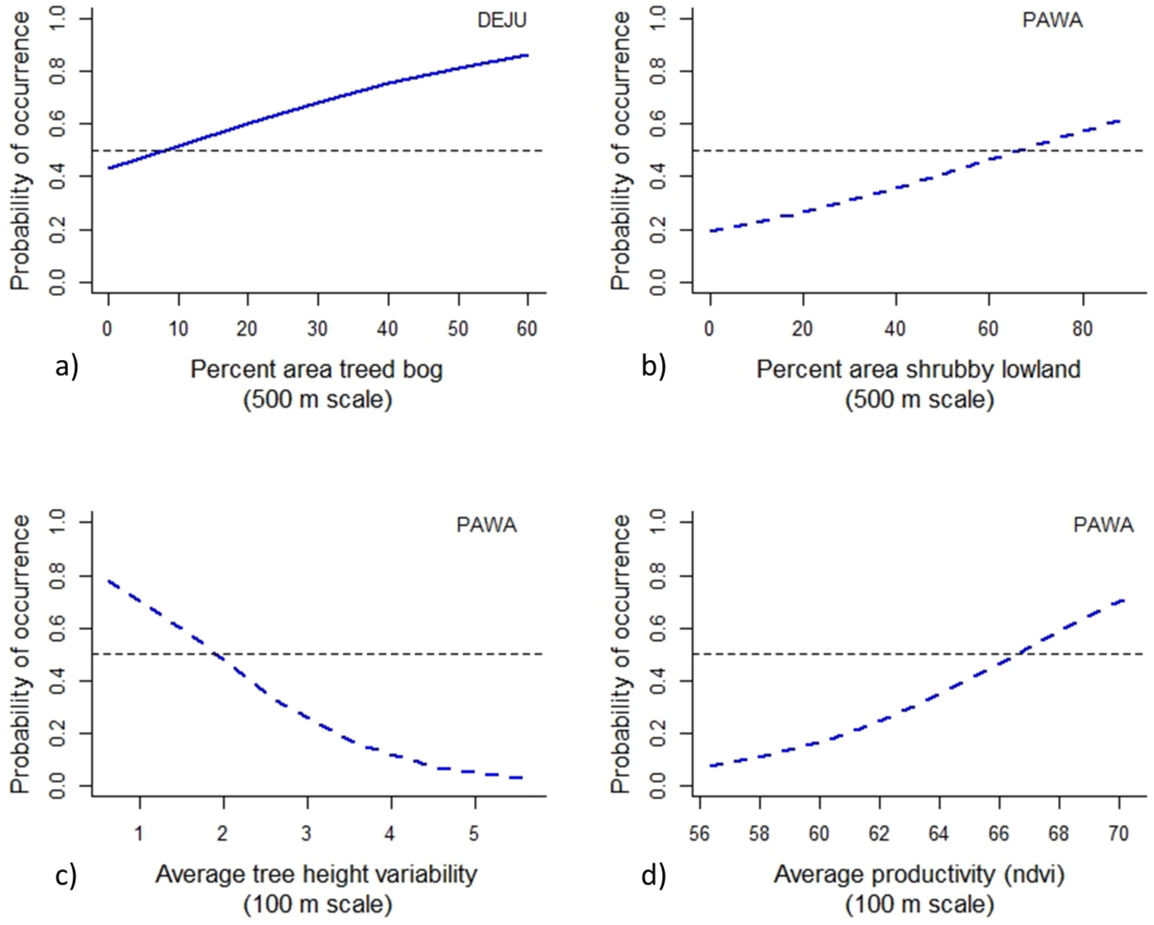


Figure 4. Probability of occurrence for Dark-eyed Juncos (solid line; a) and Palm Warblers (dotted line; b-d) across range of habitat features within 100 m of point-count survey sites under a ‘no development’ scenario (percent area permanent features held at 0), as predicted by the top-selected occurrence model. Non-focal habitat variables are set to represent the average habitat conditions across the sample area.

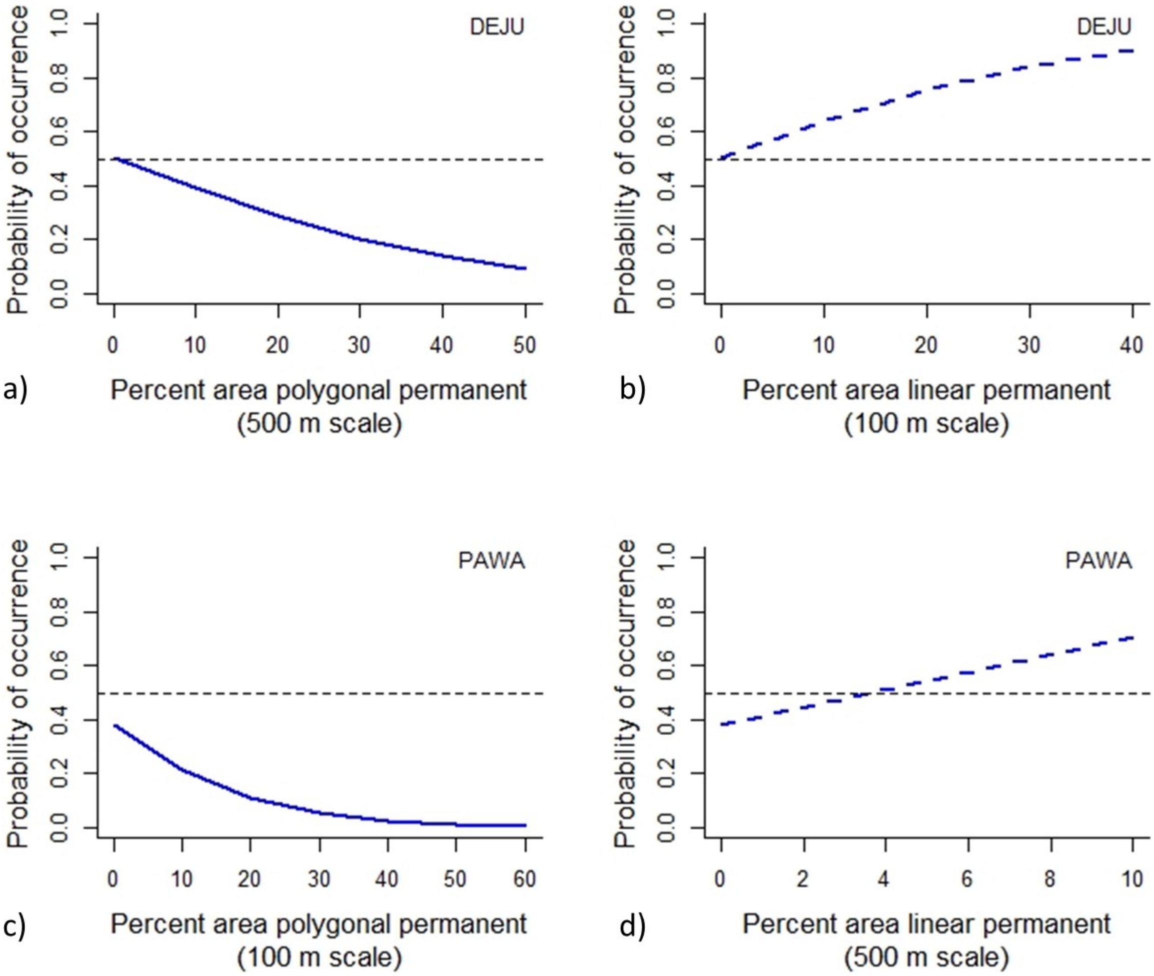


Figure 5. Probability of occurrence for Dark-eyed Juncos (top row) and Palm Warblers (bottom row) and across range of percent area of polygonal (a,c) or linear (b,d) permanent features and under average habitat quality conditions (e.g. for Palm Warbler, the average percent area shrubby lowland, variation in tree height, and productivity), as predicted by the top-selected occurrence model.

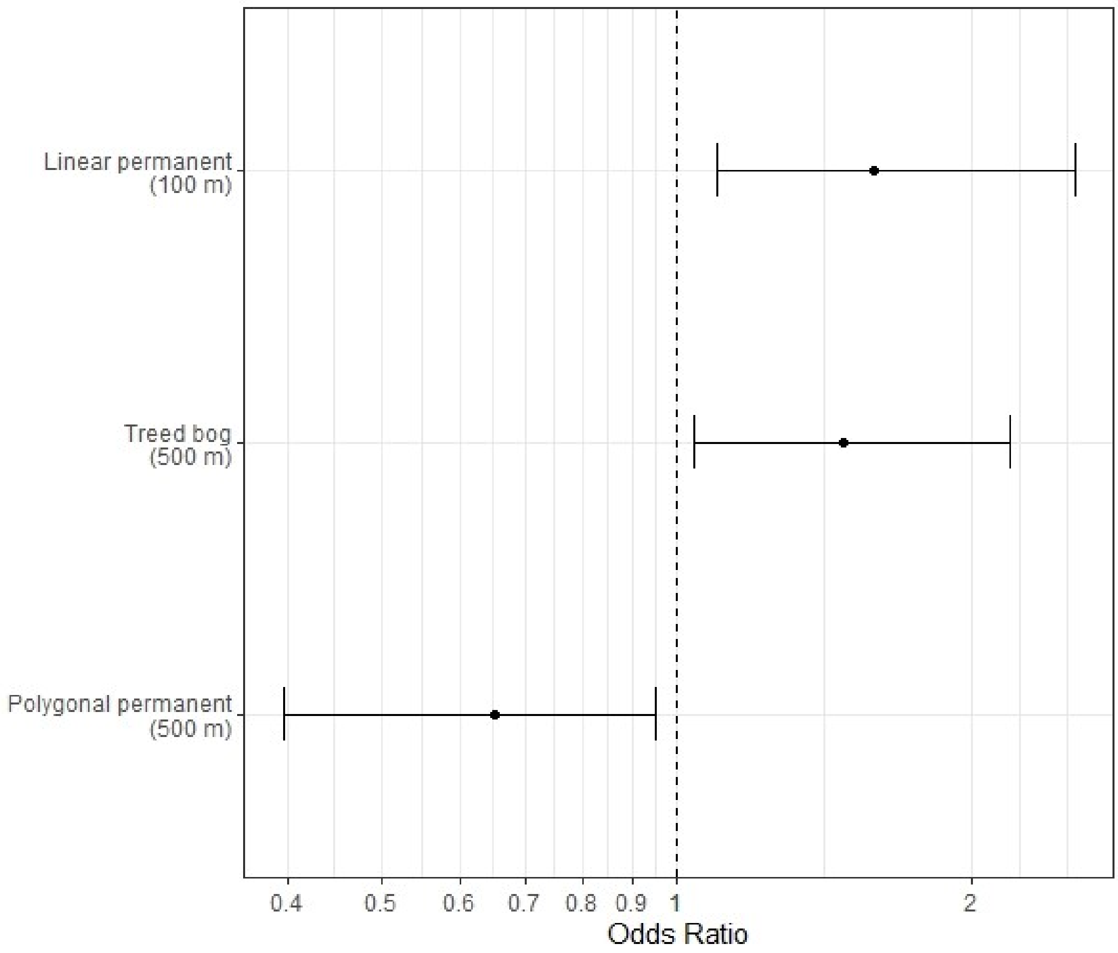


Figure 6. Direction and relative influence of habitat and disturbance variables from top-ranked Dark-eyed Junco occurrence models. Dots indicate standardized odds ratios with 95 percent confidence intervals (bars). Positive factors are displayed to the right of the dotted line, and negative factors to the left.

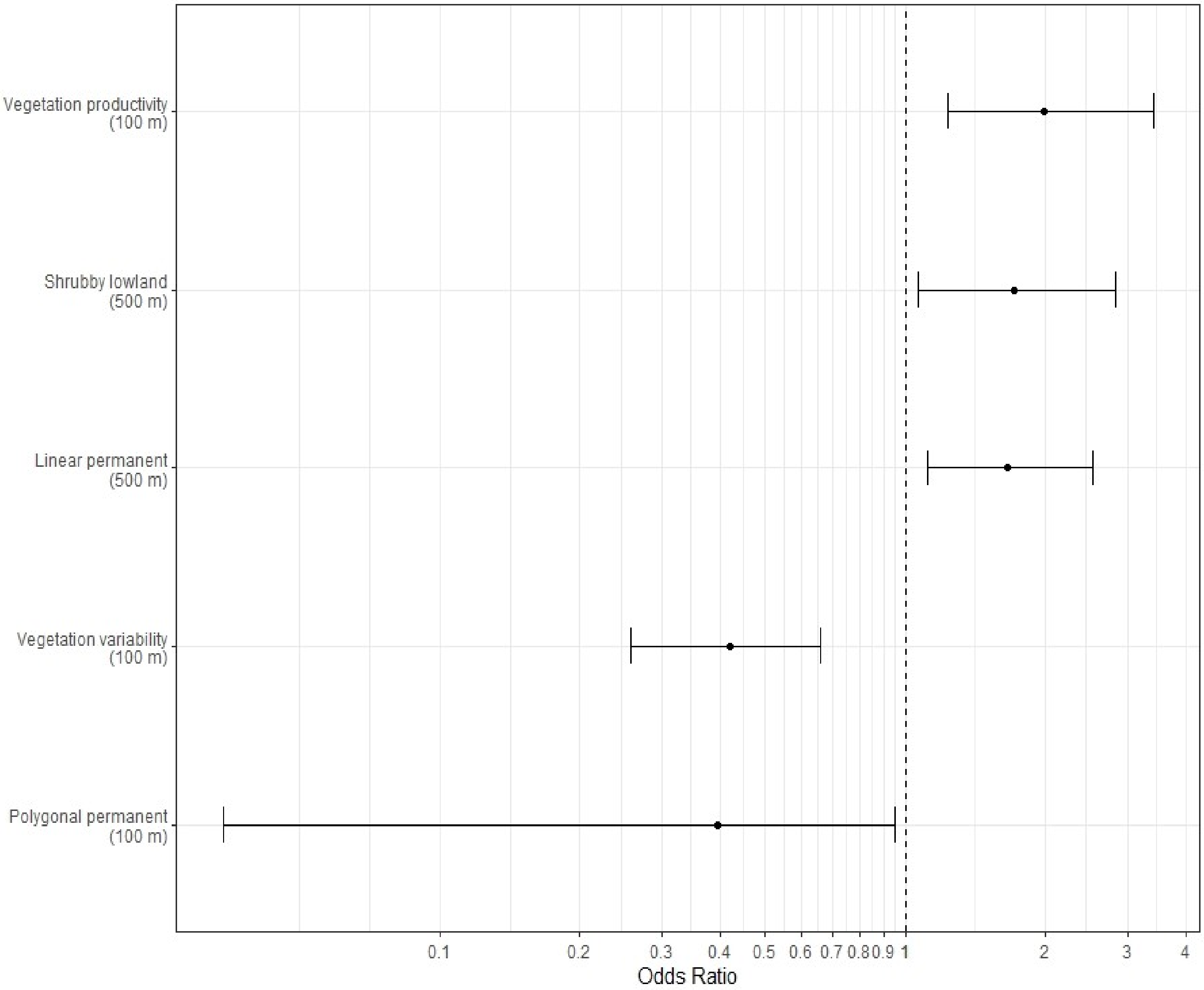


Figure 7. Direction and relative influence of habitat and disturbance variables from top ranked Palm Warbler occurrence models. Dots indicate standardized odds ratios (variance of 1 and mean of 0) with 95 percent confidence intervals (bars). Positive factors are displayed to the right of the dotted line, and negative factors to the left.

Chapter 3: Territorial and behavioural effects of *in situ* oil sands developments on habitat selection for two peatland songbirds

3.1 Introduction

Although large parts of the boreal forest region of northern Alberta are still considered relatively intact compared to urban and agriculturally dominated landscapes in the prairies, increasing global energy demand is driving a rapid expansion of the cumulative, multi-sector anthropogenic footprint within the region (Venier et al. 2014, Rosa et al. 2017, Mahon et al. 2019). Emerging *in situ* oil sands extraction techniques, including Steam-Assisted Gravity Drainage (SAGD), have enabled new access to extensive bitumen reserves that are too deep to be mined (Schneider & Dyer 2006, Rosa et al. 2017). SAGD extraction processes, whereby steam is injected deep into the ground to mobilize bitumen for removal, involve modifications to natural habitats, including clearing of vegetation to locate or access bitumen reserves, and development of infrastructure for bitumen removal and processing. Exploratory development features, where vegetation is cleared to enable access for equipment, but substrate is often left to naturally regenerate, include seismic lines, winter roads, and undeveloped (exploratory) well sites, while permanent features include gravel roads, above-ground pipelines, power lines, and industrial facilities (Figure 8). Although these development features create less localized disturbance to habitats than conventional open pit mining extraction methods, they are pervasive across the oil sands region and cumulatively lead to an extensive network of small-scale linear and polygonal development features on the landscape. Projections suggest that pursuit of *in situ* recovery for all accessible reserves in Alberta will accumulate to approximately 13.8 million hectares of disturbed habitat (Schneider & Dyer 2006).

Avian responses to development features vary by species, with some early successional species favouring anthropogenic vegetation gaps and some mature forest associated species responding adversely to loss in vegetation structure (Thomas et al. 2014, Bayne et al. 2016, Farwell et al. 2016). A resource distribution framework suggests that species responses to changes in vegetation structure may be positive, neutral, or negative depending on whether the novel habitat provides an increased, decreased or equal distribution of resources (Ries & Sisk 2004). During the breeding season, resources are required for activities including advertising for a mate, nest building, foraging, and feeding young. Understanding the habitat characteristics that support these breeding season behaviours for different species guilds can be used to predict the direction of response to development features by individual species. Generalist species, that can utilize more expansive resource types, may capitalize on access to alternate resources present in disturbed areas and edges, whereas specialist species, which have narrow habitat requirements may be unable to use novel resources, resulting in edge avoidance (Ries & Sisk 2004, Carrara et al. 2015). For example, Ovenbirds (*Seiurus aurocapillus*), a mature forest species, excluded seismic lines from their territories in aspen (*Populus tremuloides*) dominated deciduous forests due to decreased protective cover and arthropod abundance (Lankau et al. 2013). Additionally, territories for ground or shrub-nesting birds that overlapped seismic lines in the Northwest Territories, were approximately 30% larger than territories in undisturbed habitats, suggesting that individuals were compensating for reduced habitat quality associated with the vegetation clearing (Machtans 2006).

Vegetation structure can also influence other aspects of avian habitat use unrelated to foraging resources. Both naturally occurring and anthropogenically-derived sharp changes in vegetation structure may influence the spatial placement of defended breeding territories by providing landmarks, or distinct structural characteristics, that differ from resource attributes used within territories (St-Louis et al. 2004). Territory boundaries for species including the Black-Throated Blue Warbler (*Dendroica caerulescens*) and Ovenbird, for example, are associated with structural heterogeneity (St-Louis et al. 2004). Ovenbirds show similar responses to the structural heterogeneity created by conventional 8-m wide seismic line features, placing territory boundaries along the edges of lines so these features are excluded from within territories (Bayne et al. 2005b, Lankau et al. 2013). Placement of territories along heterogenous boundaries, such as vegetation gaps, may benefit territorial defense through increased song projection or visibility to neighbouring males (Perkins & Wood 2014). Spatial displacement away from development features, on the other hand, could lead to impacts greater than the development footprint itself, as observed in one study with Ovenbirds (Machtans 2006). Understanding the influence of *in situ* oil sands development features on territory placement and territorial defense behaviours for avian species will inform development planning and mitigation strategies.

Furthermore, the magnitude of avian responses to development features may be influenced by the surrounding forest structure. Areas with higher vegetation density may show different effects than areas where the forest is sparse due to differences in microclimate at the edge and on the disturbance (Lankau et al. 2013). Ovenbirds (*Seiurus aurocapillus*), for example, were more likely to forage on seismic lines with increased canopy cover, potentially due to both increased protective cover and prey availability in leaf litter (Lankau et al. 2013). The contrast in vegetation between development features and the surrounding forest may be greater in peatland habitats dominated by black spruce (*Picea mariana*), i.e. moisture saturated, lowland ecosystems, than upland hardwood ecosystems. Aspen saplings and various shrub species may quickly colonize linear feature gaps in hardwood dominated upland sites, creating dense shrubby habitat along lines. In contrast, seismic line features in peatland habitats may show little natural regeneration of black spruce up to approximately 35-50 years post disturbance (Lee & Boutin 2006, Van Rensen et al. 2015). Slow vegetation recovery suggests that impacts of development features may be long lasting for avian species that rely on peatland vegetative structure for foraging and nesting resources. These moisture-saturated peatlands comprise close to 65% of the boreal forest habitat within oil sands region (Rooney et al. 2012). Despite the prominence and apparent sensitivity of these ecosystems, very little work on wildlife, other than caribou, has occurred in peatlands.

Understanding how and why responses vary due to micro-scale habitat characteristics, intrinsic behavioural traits, and type of development features is needed to refine our predictive capacity and inform our mitigation strategies, especially for peatland ecosystems. My objectives were to: (1) identify the relative impact of different polygonal and linear features from *in situ* oil sands developments on generalist and specialist avian habitat selection at the territory- and within-territory level in peatland habitats; (2) determine if development feature responses are enhanced or mediated by the structure or quality of the surrounding habitat; and (3) evaluate relative support for two hypotheses identifying mechanisms driving species-specific responses, the 'landmark hypothesis' and the 'resource guild' hypothesis, by developing process-focused habitat use models for singing and foraging locations. The landmark hypothesis suggests that structural vegetation change may influence habitat selection unrelated to resources directly used, i.e. by creating distinct boundaries for defense of territories (St-Louis et al. 2004, Lankau et al. 2013). The resource guild hypothesis suggests that structural changes in vegetation may influence availability of food resources, differentially affecting species that forage in different vegetation strata (Machtans 2006, Kennedy et al. 2010, Lankau et al. 2013).

As a generalist species, Dark-eyed Juncos (*Junco hyemalis*), hereafter 'DEJU', are abundant in both natural and disturbed habitats throughout the boreal forest region (Leupin et al. 2004, Handel et al. 2009). Palm Warblers (*Setophaga palmarum*), hereafter 'PAWA', are considered boreal peatland specialists in northern Alberta, found almost exclusively in shrubby or treed peatland habitats and thought to be sensitive to disturbances in these systems (Calmé and Desrochers 2000; Mahon et al. 2016). Although both species are ground nesters common in shrubby bog habitats, DEJU are predominantly ground foragers, whereas PAWA primarily glean insects from within shrubby vegetation. These different foraging strategies provide an ideal comparison for investigating the processes underlying avian responses to multi-feature SAGD disturbances. At the territory level I predicted that: (1) permanent features would be unsuitable habitat for both species and excluded from within territory boundaries; (2) territories may be located closer to vegetated well sites and wide-linear features which may act as foraging habitats (resource guild hypothesis) or territory boundaries (landmark hypothesis); and (3) smaller 2-3 m wide linear features, hereafter 'seismic', may be included within territories because territory placement will be driven primarily by the suitability of habitat surrounding the features. At the within-territory level, I predicted that foraging behaviour would be the main driver of the influence of different development features on habitat selection for both DEJU and PAWA. For DEJU, I expected that broad habitat selection and ground foraging behaviour would enable them to capitalize on novel resources within development features. For PAWAs, I predicted foliage-gleaning behaviour specialized to shrubby peatland vegetation would lead to negative responses to development features due to decreased availability of foraging strata. For both species I predicted that the response to development features would be mediated by the quality of the surrounding habitat, whereby the strength of responses to development features would increase with greater structural contrast to the surrounding habitat and decrease in areas of higher productivity due to potential compensatory effects of the edge habitat.

3.2 Methods

Study area and survey site selection

Detailed local-scale habitat use was examined in 2014 and 2015 within 11, 25-hectare (500 m by 500 m) survey sites located within the MacKay River Commercial Project (MRCP) lease area. The MRCP is a 17,000 hectare *in situ* Steam-Assisted Gravity Drainage (SAGD) lease area located approximately 30 km northwest of Fort McMurray, Alberta. Situated within Boreal Mixedwood ecozone, an area characterized by fine-scale topographical and moisture gradients and a high frequency wildfire disturbance regime, the study area is comprised of an irregular patchwork of upland hardwood and lowland peatland ecotypes (Beckingham & Archibald 1996, Schmiegelow et al. 1997). Likewise, peatland habitats within the MRCP include a mix of open, shrubby, or treed bogs and fens. Vegetation communities in the nutrient poor, acidic conditions of bogs are comprised mainly of black spruce (*Picea mariana*) in the canopy and shrub layers. Dominant groundcover species include labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), and bog cranberry (*Vaccinium vitis-idaea*). Nutrient-rich fens are more diverse and are comprised of black spruce, tamarack (*Larix laricina*), alder (*Alnus*), birch (*Betula*), and willow (*Salix*) species in the main foliage layers. Low ground cover in fens may include sedges (*Carex*) and horsetail (*Equisetum*) species. Currently under development, the MRCP provided an ideal study site due to the novelty of features, within the last 0-8 years since development, and the relatively low risk of hazards for observers compared to sites in active production. All features surveyed in MRCP contained little to no vegetative regrowth beyond sparse ground cover, thus facilitating a stronger comparison of relative effects between different feature types.

Development feature and vegetation attributes within the MRCP lease area were identified using a combination of high-resolution satellite imagery (Pleaides 50-cm resolution imagery captured in 2013 and 2014), and detailed (2-m resolution) avian habitat mapping layers supplied by Environment and Climate Change Canada (Wyatt and Holloway 2016, unpublished). Potential study site locations were stratified along a gradient of low (0%) to high (38%) development, including development from multiple feature types, and constrained to shrubby bog habitat, which is known to be suitable to both Palm Warblers and Dark-eyed Juncos in northern Alberta (Mahon et al. 2016, ABMI 2019). I used a 500 m by 500 m survey site to: (1) capture a representative range of multiple feature types; (2) represent a range of total area of development footprint typical of SAGD lease areas within the region; and (3) balance sample sizes for study species with feasibility for observers to complete surveys on each visit. Survey sites contained five types of development features: (1) permanent polygonal SAGD production well sites approximately 125 m by 250 m; (2) 25-70 m wide permanent linear gravel roads; (3) undeveloped exploratory well sites approximately 50 m by 80 m (0.5 hectares); (4) 5-20 m wide linear features; and (5) 2-3 m wide seismic lines (Figure 8). Survey sites were spaced a minimum of 300 m apart, greater than the average home range diameter of small boreal passerines including sparrows and warblers, to maintain independence of individuals between survey locations (over 7 times an average diameter estimated at 1.3 ha/41 m, from Machtans 2006, Toms et al. 2006, Whitaker & Warkentin 2010). Habitat suitability and similarity between survey sites was confirmed on the ground prior to sampling and final survey site locations were selected to achieve a balanced representation of habitat both within and between sites (Table 8).

Avian field observations

Two different methods were used to identify habitat use locations for DEJU and PAWA within survey grids. Individuals or pairs occupying breeding territories within survey sites were initially located using standard spot mapping techniques (Bibby et al. 2000). Spot mapping surveys involved walking transects spaced at regular 100-m intervals across survey grids at a consistent pace of ~1km/hr to map locations, movement, and behaviour for all birds detected. Transect spacing balanced adequate detection of study species with survey efficiency by ensuring observers passed within 50 m of any location in the survey grid on each visit (Ralph et al. 1993, Bibby et al. 2000). Detections were plotted by hand on 1:2000 scale survey maps in the field and spatially georeferenced in ArcGIS (v 10.3.1). Evidence of breeding status (e.g. individuals carrying nest material or food), and territorial behaviour (e.g. countersinging) from spot mapping, was used to support delineation of territory boundaries identified by more detailed avian surveys methods and to ensure observers sampled all territories within the survey sites.

Habitat use, behaviour, and breeding status information were collected for each individual or breeding pair detected within the survey grids using burst sampling techniques adapted from Barg et al. (2005). Burst sampling involved following individuals for approximately 30-60 minute observation sessions to record their behaviour and GPS-mark each sequential use location with a handheld Garmin GPSMap 62ST unit. Skilled observers attempted to keep individual songbirds in sight for the duration of the session and recorded the activities and the time for each spatial change in location they observed (i.e. singing, foraging, perching, etc.; see Appendix 1 for a list of behaviours recorded). Each movement to a new substrate was considered a new location e.g. movement from tree to tree, whereas vertical changes in height within a single tree were not considered unique locations. To minimize potential observer influence on songbird behaviour, observers viewed songbirds from as far away as possible while maintaining visual detection with binoculars (approximately 10-20 m), and only marked use locations after birds had departed to a subsequent location. Occasionally observers would end these sessions early and return at a different time if they thought their presence was affecting bird behaviour, e.g. if alarm calling or other distressed behaviour was observed.

For both methods, surveys were repeated at regular intervals, approximately every 4-6 days, across the breeding season from mid-May to early July in 2014 and 2015. Surveys were conducted in good weather, with low upper limits for wind and rain, to maximize detectability (Ralph et al. 1995, Bibby et al. 2000). Spot mapping surveys occurred during hours of peak avian activity, beginning within 30 minutes of official sunrise and concluding within 5 hours (03:54-09:00). Burst sampling occurred directly following spot mapping surveys and concluded by approximately mid-day (04:00-14:15). To obtain representative sampling for each territorial pair across the season, 2-3 observers conducted surveys within each site on each visit. Observers attempted to follow each pair on every visit and randomized the order in which territorial pairs were located to achieve even temporal coverage across the follow period. Any pairs that could not be located during a visit were prioritized on the subsequent visit. In both years, visits to survey sites concluded when family groups became mobile (approximately July 2-4) because defended breeding territory boundaries began to dissolve when fledged young were able to move outside of territories as a roaming family unit. Wherever possible, field observers tried to include observations for both males and females, however we have a larger proportion of male observations due to increased vocal and visual detectability. Individuals in this study were unmarked and uniquely identified using a combination of song characteristics, overlapping sequences of consecutive follow locations, and behavioural evidence of territory boundaries, such as countersinging observations and aggressive chasing behaviour. Any locations that could not be confidently attributed to a known individual were excluded from both territory and within-territory analyses.

Territory and within-territory habitat selection

I examined responses to development features at both the territory-level (2nd order, Manly Design II) and within-territory level (3rd order, Manly design III, Johnson 1980, Manly et al. 2002) in a resource selection framework by comparing use locations to available locations with a generalized linear mixed-effect model (logistic regression with logit link, Boyce and McDonald 1999; Gillies et al. 2006). At the territory level (2nd order), I defined the territory size and location for the use sample as a 95% fixed-kernel density home range (*href* smoothing parameter). Kernel density estimators are a reliable method of home range analyses for ecological studies that generate a two-dimensional configuration of probability contours around locations of use (Worton 1987, 1995, Seaman & Powell 1996, de Solla et al. 1999). A bivariate probability density function gives the probability of relocating an animal at a point given the location of the coordinates (x,y). As non-parametric estimators, kernel densities are highly flexible to complex home range shapes, including multiple activity centres (Worton 1989, Kernohan et al. 2001). For highly mobile species, including songbirds, the ability for individuals to traverse the breadth of their territory in less than a minute renders spatial locations within short time intervals biologically independent (Barg et al. 2005), therefore all spatial locations observed for each territorial pair were included in analyses. Kernel density estimators are relatively tolerant of small sample sizes (Seaman et al. 1999) and temporally balanced sampling of individuals in a biologically relevant manner (i.e. consistently spaced throughout the observation window and across the breeding season) is more important than standardizing sample size across individuals or eliminating statistical autocorrelation between locations (de Solla et al. 1999, Otis et al. 1999, Barg et al. 2005). Therefore, to ensure territory boundaries were representative of use areas, I restricted territory-level analyses to territories with (1) a minimum sample size of 20 locations, spread across at least 3 different survey dates; and (2) those occurring predominantly within the survey site, as indicated by a territory centre located within the 500 m by 500 m site boundary.

I generated available territory locations by copying the shape of each observed territory boundary and shifting it to a randomly generated centroid location and randomly rotated orientation within the same 500 m study site. For each territory use location, I generated five available locations. Available centroids were spaced a minimum of 40 m apart (approximately equal to the average core area radius of the 40% home range isopleth) to prevent spatial autocorrelation between available locations and mimic the natural displacement of territories on the landscape relative to 'neighbour' territories.

At the within-territory level (3rd order), I compared use and available locations within the 95% probability home range contour for each territory with the same minimum sample size requirements (≥20 observed locations across ≥3 visits). Here, I also expanded the sample size to include additional territories along the edges of survey sites, whose territory centre was located just outside the 500-m survey grid boundary, if they met minimum sample size requirements. Available locations were placed randomly within territory boundaries at a ratio of 3:1 (available to use), but were constrained to a minimum separation distance of 11 m, as more regularly spaced sampling is expected to capture more variability with fewer locations (Northrup et al. 2013). A separation of 11 m was considered reasonable because it prevented sampling overlap between locations within the largest variable extraction buffer radius. Development features that were avoided by each species at the territory-level, i.e. excluded from within territory boundaries, were likewise removed from analyses at the within-territory scale. Territory boundaries were generated in R (R Core Team 2018) using package "adehabitatHR" (Calenge 2006) and placement of use and available locations for variable extraction was conducted in ArcGIS version 10.3.1.

Habitat and development variables

I identified fine-scale habitat and development characteristics from two, high-resolution spatial data sources: (1) Pleaides 50-cm resolution multi-spectral (red, green, blue, near infrared) satellite imagery, including separate imagery layers captured in 2013 and 2015; and (2) 1-m resolution full feature (first return) and bare ground (last return) Light Detection and Ranging (LiDAR) data captured in 2009. As development was ongoing between 2009 and the end of our study, I used year-specific development feature layers for 2014 and 2015 by adjusting features using Pleaides imagery and ground verification. I then adjusted full-feature LiDAR detections to 0 within the footprint of new development features to account for changes to vegetation height since 2009 and adjusted spectral values for any features present in 2014 that were missing from 2013 imagery to averages derived from surrounding features. I considered this reasonable in our study area as slow successional processes in peatland ecosystems lead to little structural change within short time periods (Lee & Boutin 2006, Van Rensen et al. 2015).

I then used corrected LiDAR and spectral data to measure attributes of vegetation structure, vegetation productivity, and vegetation composition, characteristics known to be valuable in predicting avian habitat use in peatland ecosystems (Table 8, Morissette et al. 2013). I characterized two aspects of vegetation structure, vegetation class and vegetation variability, using a tree height model (tree height = digital elevation model - digital terrain model) and a categorical vegetation class raster layer. I included five categories to describe vegetation class in the study area: (1) 'ground cover'- vegetation <0.5 m tall; (2) 'low shrub'- ≥0.5 to <1 m tall; (3) 'tall shrub'- ≥ 1 m to < 4 m tall; (4) 'regenerating tree'- ≥4 m to <10 m tall; and (5) 'tree'- ≥10 m tall vegetation. I measured vegetation variability, as the standard deviation in tree height. High standard deviation values indicate areas where there is a wide range in tree heights (high contrast), whereas low standard deviation values indicate areas where vegetation heights were similar (low contrast). I characterized vegetation productivity using the normalized difference vegetation index (NDVI) value. NDVI indices, which are calculated using a ratio of near infrared (NIR) and visible (VIS) wavelength spectral reflectance from satellite imagery [NDVI=(NIR-VIS)/(NIR+VIS)], represent areas of high chlorophyll concentrations and are thought to correspond to differences in vegetation productivity or 'greenness' (Tucker et al. 1985). I used probability of depression (pdep) as a proxy for peatland vegetation composition within these study sites, as depressional areas of high moisture can be associated with greater vegetation diversity, i.e. more 'fen-like' characteristics (Whitebox GAT geospatial tools software; Lindsay et al. 2004). All attribute layers were developed using standard terrain processing techniques (Wyatt and Holloway 2016, unpublished report).

Model building and selection

I developed territory and within-territory models for each species following a three-step process: (1) first, I identified the best scale and functional form for each predictor variable using univariate models; (2) second, I defined a habitat-only null model for each species; (3) third, I evaluated the best feature-specific disturbance measure to explain the type of use response for each species as either a local effect (area of features), distance effect (distance to features), or an interactive effect (interaction between features and vegetation structure or productivity). The same approach was used for both territory-level and within-territory models. As a final step at the within-territory scale, I also examined behaviour-specific (singing versus foraging) responses to different development feature types to provide insight to potential mechanisms underlying these selection patterns. To examine the relative influence of development feature types, I included all possible feature type combinations because: (1) I expected that different types of development features would have variable microhabitat conditions and edge effects, (2) I were interested in the relative influence of different features on habitat use, and (3) hypotheses are supported both by the features included in the top models and the direction of the responses to different features (Johnson & Omland 2004, Doherty et al. 2012). I considered a model to have strong support if it was $> \Delta$ 2 AIC lower than the next best model, i.e. if the model weight was $\geq$ 0.9 (Burnham & Anderson 2002). I considered a model to be competitive, i.e. showing similar support to a top-ranked model, if the weight of the best model was <0.9 and the model was within Δ 2 AIC of the top model. Competitive models were averaged using the zero method, where a zero is substituted into the each model for a parameter that is missing (Burnham & Anderson 2002, Grueber et al. 2011).

As I conducted repeat sampling of individuals, I specified a random effect for survey site to account for site-level correlation between individuals within a survey site, and individual-level selection heterogeneity (Gillies et al. 2006). I included a fixed effect for survey year and a nested effect for territories within survey sites to define population-level response models for these study sites ((1|site) + (1|site:territory), Bolker et al. 2019). Fixed effects were determined first and examined for multicollinearity using Variance Inflation Factors (VIF<3, Zuur et al. 2009). Random effects were specified after fixed effects to ensure I did not capture any fixed-effect variance within the random component of the model (Zuur et al. 2009). All models and figures were derived in Program R (R Development Core Team 2018) using packages "lme4" (Bates et al. 2016), "MuMIn" (Barton 2018), "car" (Fox et al. 2018), "ggplot2" (Wickham et al. 2018), and "jtools" (Long 2018).

Scale and functional form

Habitat selection is considered a multi-scale, resource-specific, and behaviour-specific process whereby organisms may select different resources at different scales and may require different resources for different ecological processes (Wilson et al. 2012, Laforge et al. 2015). To identify a biologically-based measurement for each variable, I used a multi-level, multi-scale approach with a "pseudo-optimized" selection of measurement scale or functional form for each habitat or development variable included in the models, i.e. an optimized selection of the best scale from a limited set of scales predicted to be biologically relevant to each species, rather than a large number of arbitrary increments (*sensu* McGarigal et al. 2016). I evaluated each scale or form in a univariate model and selected variables with the greatest Akaike weight of evidence for inclusion in a multi-scale model. I used this approach because it balances development of robust, multi-scale models with an *a priori* selection of scales I hypothesized to be biologically relevant to these study species (McGarigal et al. 2016).

For territory-level use, I used the 95% kernel density home range scale. To identify biologically relevant scales for within-territory use, I examined the movement patterns of DEJUs and PAWAs observed during continuous follow sequences. Shorter movement distances may correspond to within-patch use of high-quality habitat, whereas longer movement distances may correspond to travel between resource patches (Wilson et al. 2012). As I was interested in scales representing the characteristics of the local neighbourhood around use locations, I based scales on the Euclidean distance between two consecutive movement locations. For each species I considered the most frequent movement distance between two consecutive use locations (mode distance) for territorial behaviours (i.e. distance between two consecutive singing or countersinging locations) and for foraging behaviours (i.e. distance between two consecutive foraging locations). I also considered a scale using the 90% trimmed mean average foraging distance to exclude longer distances that may represent travel between suitable habitat patches. For DEJU, these scales were: (1) 5 m- mode for consecutive foraging movements observed; (2) 10 m- trimmed mean for foraging, and (3) 11 m- mode for consecutive singing locations. For PAWA distances included: (1) 6 m- mode foraging; (2) 7 m- mode singing; and (3) 10 m- mean foraging distance (See Appendix 2 for a summary of movement distances).

I also evaluated best functional form for measures of distance to development features. I hypothesized that response to development features would be greatest at the edge of a development feature and decline precipitously as distance from the feature increased, and therefore follow a pattern of decay. Similar to my approach for within-territory selection scales, I identified the best distance form by comparing linear, logarithmic, and exponential decay transformations. For exponential decays, I considered distance increments where the decay curve reached approximately 0 on the y-axis (90% decay) using biologically-based intervals. At the territory-level, I tested decay distances at 20 m increments, which represented a shift in placement of approximately 25% of the average territory diameter in this study area, and at the within-territory scale I considered decays values at 5 m increments (approximately equal to the most common movement distance for these species) up to 80 m, which represents the average territory-diameter, i.e. the farthest away an individual could get from a feature located within their territory without shifting the placement of their territory (Appendix 3).

Null habitat model and feature-specific response types

I conducted the model building process to align with my ecological expectations by including predictor variables in models in order of assumed biological importance (Table 6). For the null habitat model, I first included the best predictors for vegetation structure including (a) amount preferred vegetation class, and (b) vegetation structure variability. At the territory level I limited the number of vegetation class variables to two whereas at the within-territory scale I included a single variable for vegetation class, to prevent over-specification of models. I included vegetation structure variability in each model. Vegetation productivity and composition attributes were included only if they increased model fit relative to the vegetation structure model by greater than Δ 2 AIC.

For development feature responses, I tested three specific response types: a local effect, a distance effect, and an interactive effect (Table 6). I expected that if the influence of the development feature on the surrounding habitat was relatively low, the response to a development feature would be best predicted by the proportion of development (percent area) within a local area around the use location, whereas if development features have a strong edge effect, use may be best predicted by distance to the development feature. However, I predicted that the strength of avian responses to development features may decline as contrast to surrounding vegetation declines. Therefore, I expected that the response to development features may be exacerbated or mediated by the attributes of the surrounding habitat. For singing use, I expected that probability of use may be increased with increasing contrast to surrounding vegetation. As all the features in this study area were similar in age and exhibited little regeneration, contrast with the surrounding habitat is higher in areas with taller, higher density vegetation adjacent to the development features and lower in areas with shorter or sparser vegetation adjacent to the features. Therefore, to determine if probability of use was altered by contrast with the surrounding vegetation structure, I examined the interaction between development features and the standard deviation in tree height (variability), where increased standard deviation represents greater contrast. For foraging use, I expected use of development features may be greater when vegetation adjacent to the development feature was higher productivity (greenness). I selected the best response type for each development feature prior to inclusion in model selection. Interactive effects were only selected if they improved model fit by greater than Δ 2 AIC_c (territory level models) or Δ 2 AIC (within-territory level models).

3.3 Results

General

I surveyed a total of eleven, 25-hectare (500 m by 500 m) study sites in 2014 and 2015 (n = 9 and n = 10 respectively), with 8 sites visited in both years and 3 sites visited only a single year. Survey sites contained a range of development intensity from 0-38.2% percent area development (Table 7). Of these, 3 sites were considered control sites (0-1.5% development), 2 sites primarily contained 2-3 m wide exploratory seismic (11.7-13.1%), 4 sites included a range of all exploratory development feature types (e.g. seismic, winter roads, well sites, 15-18.5%), and 2 sites contained both exploratory and permanent features (e.g. exploratory as well as permanent SAGD well sites and/or gravel roads, 23.7-38.2%). All sites were dominated by shrubby bog habitat with a 42.4% (±10.6 SD) average proportion of shrub cover (0.5-4 m height) and 70.6% (±26.1 SD) average proportion of the site in low to mid topographical depression, i.e. was lowland with little topographical variation (Table 8). The vegetation in site ‘PE01’ was slightly taller and higher density and had the greatest deviation from average conditions, with 34.1% area tree coverage (≥ 10 m height trees) and 86.8% percent in the upper topographical position.

Within these study sites there were a total of 144 DEJU and 125 PAWA territories (n = 54; 90, and n = 57; 68 respectively in 2014 and 2015). Of these, 80 DEJU and 82 PAWA territories contained at least 20 use locations that (1) I was able to confidently attribute to a known individual or pair and were (2) spread across a minimum of 3 separate survey dates within the breeding season. For within-territory analyses I included all 80 DEJU and 82 PAWA territories, whereas for territory-level analyses I excluded territories with centres located outside 500 m by 500 m boundaries to increase certainty in our identification of available habitat characteristics, leaving 60 DEJU and 61 PAWA territories in 2nd order use models.

Local, local interaction, and distance effects

At the territory scale, models including local area effects were the most supported. The only exception was for the PAWA response to seismic features, where distance from territory centre was the most supported effect, however seismic features did not occur in any of the top competitive models for PAWA territory use. Habitat interactions for territory-level use did not improve the fit for any feature types by greater than Δ 2 AIC and were, therefore, not included in territory use models. At the within-territory scale, the most supported response type differed by species and feature type. Local percent area effects were most common for permanent polygonal, permanent linear, and well site features, whereas local habitat interaction effects were included for wide linear and seismic features in in 2/4 top models for DEJU and 3/4 top models for PAWA.

Territory-level selection (2nd order)

The average size of breeding territories was approximately 5.7 (±2.7 SD) hectares for DEJU and 5.0 (±3.0 SD) for PAWA (95% kde for territories with minimum sample size). For both species, habitat-only territory use was best predicted by vegetation structure class variables. Models were not improved with the addition of either productivity (average greenness) or overall moisture (proportion of each topographical depression class) for either species, although direction of response to vegetation structure classes differed for different depression classes. For example, DEJU territory use was negatively associated with ground cover vegetation <0.5 m tall in the low or moderate topographical position class (depressional areas), but positively associated with ground cover vegetation in the upper topographical position class. The most supported null habitat model for DEJU predicted the odds of DEJU territory use was 0.9 times lower for every 10% increase in depressional ground cover and 0.8 times lower for every 10% increase in upper topographical tree cover. The odds of PAWA territory use was 1.04 times more likely for every 10% increase in 1-4 m tall shrub in either low or moderate topographical depression areas.

At the territory scale, competitive use models for both species included permanent and well site features, but not wide linear or seismic features. DEJU territories included up to 48% of the area for all development features with an average of 14% (±12.6 SD). Total area of development features within territories ranged from 0-32% permanent and 0-37% vegetated features. There were 5 competitive territory use models within Δ 2 AIC_c of the top model, but only 2 of these models ranked better than the habitat only model, so I averaged parameter estimates for the top 4 models (Table 9). Model averaged odds of DEJU territory use was a decrease by 0.91 times for every 10% increase in permanent polygonal features, 0.98 times for permanent linear and only 0.99 times for well site features (Table 10, Figure 13).

PAWA territories included up to approximately 20% total area of development features with an average of 8% (±7.3 SD). Total area of development features within territories was a maximum of 0.1% permanent polygonal features in 1 territory, up to 2.7% permanent linear in 2 territories, up to 7.8% well sites in 11 territories, up to 5.6% wide linear in 27 territories, and up to 17.1% seismic in 31 territories. There were 2 competitive territory use models within Δ 2 AIC_c of the top model (Table 11). Model averaged odds of PAWA territory use was decreased 0.97 times for every 1% increase in permanent linear features and 0.91 times for every 1% increase in well site features (Table 12,Table 14). I was unable to assess the territory-level response to permanent polygonal features for PAWA, as no territories contained this feature type.

Dark-eyed Junco within-territory use (3rd order use or selection)

For DEJU singing use, there were 5 models within Δ 2 AIC of the top model (Table 13 w_i = 0.15-0.06) that were more supported than the habitat only model. Model averaged parameters included all feature types except seismic. Odds of singing use decreased by 0.99 times for every 10% percent increase of permanent polygonal features within 5 m, decreased by 0.71 times every 10% increase in permanent linear features and decreased 0.98 times for every 10% increase in well site features (Table 14, Figure 15). Odds of wide linear feature use was greater in high contrast habitat (above average variability) and showed a relatively neutral response to increasing proportion development, whereas odds of use in habitat with below-average structural contrast was lower but showed a weakly positive response to increasing proportion development.

For foraging use, there were 4 models within Δ 2 AIC of the top model (Table 17. w_i = 0.23-0.09) that were included in model averaging. DEJU had a weakly positive increase in odds of use of 1.06 times for every 10% increase in permanent polygonal features within 5 m (Table

18, Figure 15). DEJU also responded positively to proportion of permanent linear features within 11 m, however odds of use had a faster rate of increase for every 10% increase in features in habitats with above-average greenness conditions than in habitats with below-average greenness. For exploratory features, odds of well site foraging use was 0.96 for every 10% increase in features within 5 m, whereas odds of wide linear foraging use increased 1.19 times for every 10% increase in features within 11 m. Although DEJU odds of seismic use in average habitat greenness was relatively neutral to proportion of seismic features within 5 m, odds of use increased within increasing proportion seismic in above-average habitat greenness and decreased with increasing seismic within 5 m in below-average habitat greenness.

Palm Warbler within-territory use

For singing use, the global model, including all exploratory feature types, was highly supported (Table 11, $w_i = 0.97$). Odds of singing use decreased by 0.80 times for every 10% increase in well site development. Use of wide linear features was most supported by an interaction with habitat structure (Table 12, Figure 16). Odds of wide linear feature use was greatest when contrast with surrounding vegetation was above average variability and showed a positive response to proportion of wide linear features within 10 m, whereas when contrast with surrounding vegetation was below average variability, PAWAs were less likely to use wide linear features and showed a slightly negative response to increasing proportion of development. Similarly, for seismic features, PAWA showed increased probability of singing use of under high contrast conditions (i.e. above-average variability), however odds of use declined with increasing proportion of seismic within 6 m. At below average contrast, PAWAs responded neutrally to seismic features.

For foraging use, there were two competitive models within Δ 2 AIC of the top model (Table 15, $w_i = 0.32, 0.19, 0.16$). Model-averaged odds of well site feature use decreased by 0.88 times per 10% increase in proportion within 6 m (Table 16, Figure 16). Wide linear features showed the lowest relative influence on use with a neutral response. Contrary to predictions, in habitat with above-average greenness, PAWAs response to seismic features for foraging use was negative, whereas the response in habitat below average-greenness was positive. PAWA were only observed within a vegetated feature 14 times during the study, so standard error for these features in PAWA models is high, particularly for well site and wide linear features.

3.4 Discussion

The aim of this study was to examine the influence of *in situ* oil sands development features on territory- and within-territory habitat use of two peatland songbirds with different foraging strategies to: (1) identify the relative effect of different *in situ* polygonal and linear development features on generalist and specialist avian habitat selection at the territory- and within-territory level in peatland habitats; (2) determine if development feature responses are enhanced or mediated by the structure or quality of the surrounding habitat; and (3) evaluate relative support for two hypotheses identifying mechanisms driving species-specific responses, the 'landmark hypothesis' and the 'resource guild' hypothesis. In agreement with other studies, the relative influence of different development features varied by feature type, scale of selection, and avian species (Thomas et al. 2014, Bayne et al. 2016, Farwell et al. 2016).

Territory habitat use

At the territory level, larger or permanent features, including permanent polygonal, permanent linear, and well site features, had a greater influence than smaller, exploratory linear features for both species. DEJU and PAWA were both less likely to occupy territories as the amount of permanent features (extraction sites, gravel roads) and exploratory well sites increased, supporting predictions that these features provide unsuitable breeding habitat for these species. This is not surprising as avian species occurrence is highly correlated to vegetation structure (Cumming et al. 2014) and both these species occur in treed or shrubby habitat types (Schieck & Song 2006). For both species, territory-level avoidance of these features could lead to population-level declines as development intensity increases (Bayne et al. 2005a, Thomas et al. 2014, Thompson et al. 2015).

Interestingly, although avoidance of permanent polygonal features at the territory level is consistent with declines in occurrence across the same *in situ* lease area at a broader scale (Carpenter, ChI), avoidance of permanent linear features at the territory level is contrary to increased occurrence at across the lease area in the same study. It is unclear whether these discrepancies represent different selection mechanisms at the broader landscape scale relative to the breeding territory (Leonard et al. 2008) or if they are driven by methodological differences between standard point-count surveys used in the occurrence study and higher resolution territory mapping techniques used in this study. For example, avian species have increased detectability along roadsides (Yip et al. 2017), suggesting that a positive roadside response at the broader scale could be a detection bias caused by sounds travelling further near roads making distance estimation more difficult. Territory mapping techniques may have increased power to accurately detect treatment effects for permanent linear features (Newell et al. 2013, Thompson et al. 2015).

DEJU showed greater tolerance to development features than PAWA. DEJU placed territories right up to the edge of permanent features and vegetated well sites and included these features within the periphery of defended breeding territories to a larger extent than PAWA.

Whereas DEJU territories included up to 21% polygonal, 16% linear permanent, and 23% exploratory well features, PAWA territories included up to a maximum of 3% permanent linear features and 11% exploratory well features. Additionally, whereas permanent features were exclusively within the perimeter of defended breeding territories for PAWA, i.e. within the outermost 90-95% breeding territory contours, and therefore were only included within the area of greatest uncertainty for kernel density home range estimators, for DEJU permanent features occurred to some extent throughout territories (40-95% contours). One DEJU pair even made their nest within an exploratory well site, although this nest was not successful. These findings support the hypothesis that specialist species, that occur within a narrow range of habitat conditions, may be more sensitive to development features than generalists (Devictor et al. 2008, Mahon et al. 2016).

Consistent support for local area effects over distance (edge) effects at the territory-level supports other inferences that the direct loss of local vegetation structure is greater than the relative influence of fragmentation or edge effects, i.e. degradation effects extending beyond the development feature itself that lead to spatial avoidance (Fahrig 1997, Trzcinski et al. 1999, Carrara et al. 2015). These results differ from a similar study in grassland ecosystems, where some songbirds were shown to decrease in abundance within 150 m of gravel roads and within 267 m of conventional natural gas wells (Thompson et al. 2015). These authors concluded that avoidance of roads was likely directly influenced by heavy traffic associated with roads. A distinction between the design of these studies, is that Thompson et al. 2015 restricted their study to active well sites, whereas the well sites in this study area were not actively producing at the time. This means that factors associated with production, such as noise and human activity, were either absent from study sites (e.g. in sites with only exploratory features) or inconstant during periods of drilling or construction. Whether these responses remain similar under production scenarios warrants further study.

Furthermore, although territory-level tolerance to permanent *in situ* feature proximity suggests the total footprint for each feature is primarily contained within the extent of the area altered (i.e. with minimal edge effects), the total population-level effects from having individuals that place territories in close proximity to *in situ* features, remains unclear. Proximity to roadsides, for example, could lead to negative impacts, such as increased mortality from motor vehicle collisions or exposure to dust or toxins along road edges, or positive impacts, such increased foraging opportunities for insect prey (Kociolek et al. 2011, Morelli et al. 2014). DEJU were observed foraging along the edges of permanent wells and gravel roads, suggesting that these features do provide some resources to a ground-foraging generalist, although quantification of the relative availability of resources, was beyond the scope of this study. Although there is little evidence to support declines in nest productivity due to some linear feature types (pipelines, seismic lines, and service roads) in upland boreal ecosystems (Ball et al. 2008), surrounding habitat loss from energy development is associated with declines in nest survival in sagebrush ecosystems (Hethcoat & Chalfoun 2015). It is important to further examine the influence of *in situ* feature proximity on fitness and reproductive success in this system.

For linear exploratory development, i.e. winter roads and seismic lines, both species incorporated features within their home ranges similarly to their availability on the landscape, supporting other studies that indicate boreal songbirds may be capable of altering their space use in response to moderate amounts of anthropogenically-derived structural change (Leupin et al. 2004, Machtans 2006, Leonard et al. 2008, Whitaker et al. 2008, Ashenhurst & Hannon 2008).

As highly mobile species, with the ability to traverse 100-200 metres across their breeding territories in less than a minute (Barg et al. 2005, Carpenter personal observation), boreal songbirds may be relatively adapted to inclusion of small, 2-8 m wide, development features within breeding territories, as they appear to have little influence on a songbirds ability to traverse their territories. Although linear features have different spatial configurations and increased edge, these features may be perceived similarly to the natural openings within the heterogenous vegetation structure of the boreal forest region (Schmiegelow & Mönkkönen 2002). Territory-level tolerance to decreased vegetation structure, however, is not analogous to no effect, as development features may influence within-territory habitat quality. Songbirds may compensate for changes in habitat quality, for example, by adjusting the size of their territory or the relative use of space within their territory (Bayne et al. 2005a).

Within-territory behavioural use

Development features within territories were important predictors of singing and foraging habitat use for both species. The only exception was that DEJU singing behaviour was not influenced by narrow seismic line features, as these features were not included in top singing use models. Consistent with territory-scale responses, local area effects had greater relative support for within-territory use than distance effects for both species. This is supported by other work that indicates the effects of well sites and roads on vegetation characteristics is relatively local, i.e. extends less than 20 m from features (Ortega & Capen 2002, Bayne et al. 2005b, Thomas et al. 2014). For singing use, DEJU responded negatively to permanent polygonal, permanent linear, and well site features. Avoidance of these features for song use was not influenced by the contrast of features to the surrounding vegetation. Similarly, PAWA singing use was negatively effected by well sites, regardless of the structure of the vegetation nearby. Possibly the larger size of these feature types supersedes any potential influence of the surrounding habitat, i.e. differences in microhabitat conditions within features are greater than potential compensatory effects of surrounding habitat characteristics. Although decreased singing activity in areas with greater amounts of well sites is contrary to predictions under the landmark hypothesis, it is also possible that decreased territorial defense effort is required in proximity to well site features. For example, neighbouring males may be less likely to cross large vegetation gaps greater than 40 m (Rail et al. 1997, although DEJU gap crossing was uninfluenced by feature width in this study), so males may be able to concentrate defense efforts along territorial boundaries that intruders are more likely to cross.

For some feature types, however, I saw that within-territory responses were influenced by local habitat characteristics. DEJU and PAWA were both more likely to sing near wide linear features when they were more distinct from the surrounding vegetation, whereas the response was relatively neutral under conditions of low contrast to surrounding vegetation. PAWA had a similarly positive singing response in conditions where seismic lines were more contrasting to the surrounding vegetation, although this response declines rapidly within increasing amount of seismic, possibly due to the narrow width of seismic features because PAWA only sing along the edges of seismic features and not from within the features themselves. The singing response to wide linear features is compatible with hypotheses that wide linear features may provide distinct boundaries for territorial defense efforts (St-Louis et al. 2004), however it suggests that in peatland habitats the value of singing near these features is primarily only enhanced under conditions of above average vegetation height or density.

As expected, the influence of development features on DEJU and PAWA foraging behaviours were quite different. DEJU responded positively to most feature types, and were even observed foraging on gravel substrates along the edges of permanent roads and developed SAGD well pads, whereas PAWAs exclusion of permanent features at the territory scale was associated with no observations of foraging on permanent features. On the other hand, DEJU and PAWA within-territory foraging activities were both negatively influenced by exploratory well site features, decreasing 0.96 times per 10 percent increase, and 0.80 times per 1 percent increase respectively.

Interestingly, although DEJU within-territory foraging models indicate a decreased probability of use for well site features, DEJU were frequently observed foraging within some exploratory well sites, so the well site response may be more complex than I was able to describe with the breeding territory models. Occasionally the proximity of multiple unmarked individuals prohibited the ability to confidently attribute all well site use locations to a known individual, so these unknown observations were excluded from territory and within-territory models. Additionally, long flights observed to and from well sites suggest some DEJU may be using well sites communally, in areas beyond the edge of their defended breeding territories (CL Mahon, personal observation). Furthermore, foraging use of well site features was variable across study sites, suggesting foraging may be dependent on feature characteristics, such as substrate moisture or occurrence of regenerating plant species. I recommend further investigation of DEJU use of exploratory well site features.

Wide linear and seismic exploratory features also influenced DEJU and PAWA foraging behaviour. While DEJU foraging responded positively to wide linear features, PAWA foraging response was neutral. Foraging use of wide linear features was not influenced by the productivity of the surrounding vegetation for either species. For DEJU this suggests that wide linear features may either provide access to novel or supplementary resources or increase foraging efficiency (Ries & Sisk 2004). PAWA foraging, which occurs on vegetation surrounding wide linear features, is uninfluenced by potential edge effects associated with this feature type, similar to patterns observed for Ovenbird response to 6-8 m wide linear features in upland boreal habitat (Bayne et al. 2005a).

Seismic lines were included in the top foraging models for both species, suggesting that even small 2-3 m wide features may influence resource availability or foraging efficiency for songbirds. Despite differences in preferred foraging strata, both species are predominantly insectivorous during the breeding season and even fine-scale linear development features may influence abundance or diversity of insect prey sources. For example, aerial insect abundance along peatland edges at 5-7 m wide clearing strips was greater than along edges of large clearings (Deans et al. 2005). Furthermore, foraging responses to seismic lines was influenced by the productivity of the habitat at each location of use. Both DEJU and PAWA showed positive responses to the amount of seismic lines under low productivity conditions and negative responses under high productivity conditions. These habitat-mediated responses to development features could influence the cumulative, population level effects to species at the landscape-scale, causing greater total impacts if development largely occurs under conditions where features have negative impacts on avian space use compared to conditions where features may have positive impacts. This finding suggests that defining habitat requirements based on the average amount of development may be misleading because it overlooks variability in avian responses to habitat heterogeneity (Moreau et al. 2012).

Support for hypotheses

Lack of support for distance effects, i.e. singing closely to development features more often and placing territories closer to features such as well sites, suggests that the landmark hypothesis is not strongly supported in this system. This may be because the relatively low vegetation density relative to upland habitats naturally enables greater sound projection (Yip et al. 2017). In work on Ovenbirds, landmarks effects were only observed under conditions of high individual density (Lankau et al. 2013), suggesting that even in habitats with greater structural complexity landmark responses may be relatively weak compared to foraging resource pressures. This is not surprising, as song perches are likely not limiting in forested habitats and the natural structural heterogeneity may already provide appropriate conditions for broadcast opportunities. In this study, DEJUs, a ground foraging species, showed positive foraging responses to most feature types, and were observed within developments approximately 107 times, whereas PAWAs showed negative, or relatively weak responses to feature types and were only observed within features 3 times within the study. This suggests that foraging resources, or avian foraging guilds, are a stronger predictor of development effects. In open grassland habitats or closed canopy forests, where song perches can be limited, however, landmark effects may be stronger.

Furthermore, DEJU singing and foraging responses to some features were opposite, suggesting that focusing research efforts on singing detections, may provide an incomplete understanding of the influence of development features on space use, especially for species that have different requirements for singing and foraging behaviours. This is an especially important consideration for songbird species, as their highly conspicuous singing behaviour leads to the common use of song detections to explain avian responses to habitat change (Hobson & Schieck 1999, Matsuoka et al. 2001, Sólymos et al. 2013). Recent advancement in technology for wildlife monitoring has led to the rapid expansion of the use of Acoustic Recording Units (ARUs) for avian monitoring due to the benefits as a cost-effective means to collect large amounts of data (Shonfield & Bayne 2017). Although ARUs have many benefits including reduced time spent in the field and the ability to non-invasively conduct repeat sampling, avian monitoring techniques relying solely on acoustic detection of songs may not comprehensively represent avian responses to habitat change. Individual males in this study area were frequently observed to have one or more 'favourite' singing perches that the returned to regularly (Carpenter personal observation). Although these locations were often in tall, contrasting vegetation located in close proximity to vocal neighbouring males, the vegetation characteristics, i.e. height, was variable depending on the overall habitat within the study site and it is unlikely that availability of song perches is limiting. As demonstrated in other studies, intensity of habitat use may not be indicative of the importance of that habitat for wildlife (Beyer et al. 2010; Wilson 2012). Here I demonstrate, that while some avian species will regularly sing and forage in similar microhabitats, e.g. PAWA, other species may show different microhabitat preferences for each behaviour, e.g. DEJU commonly forage on the ground, whereas they commonly sing in tall vegetation. Therefore, characterizing habitat use solely on data derived from song detections or on pooled behavioural data may bias: (1) predictions of avian responses to habitat change; and (2) our understanding of the behavioural mechanisms affecting responses. I recommend using fine-scale behavioural work to complement other monitoring techniques and to test mechanistic hypotheses.

Caveats

It is important to note that development in this study area was in the early stages of exploration and construction, providing relatively novel features with little vegetation regeneration. In peatland ecosystems these development features may remain only partially recovered, potentially showing only graminoid or sparse shrub establishment, for up to 50 years post-disturbance (Lee & Boutin 2006, Van Rensen et al. 2015). Given the slower successional processes in peatlands, it is imperative to examine these responses over time. While these changes could benefit species that use sparsely vegetated areas, lengthy recovery timelines may increase the potential for threshold or cumulative effects as development feature intensity increases. Altered conditions within the development features, including increased exposure to sunlight, wind, and hydrological effects, could lead to increasingly degraded habitat for avian species if these changes are unfavourable to vegetation or insect communities along feature edges (Van Wilgenburg et al. 2001, Laurance et al. 2009). Alternatively, successional processes could lead to long-term increases in structural heterogeneity of local vegetation that may benefit early successional species at moderate intensities (Mayor et al. 2012).

Furthermore, this study was conducted in relatively contiguous stands of shrubby bog habitats that were located within a larger peatland complex, habitat already known to support high abundances of these study species (Nolan Jr. et al. 2020, Wilson Jr. 2020, ABMI 2019), and therefore, presumably, to be high quality habitat. As a result, avian responses within these sites likely represent ideal conditions where species have a greater ability to compensate for habitat change relative to more patchy habitats. Yet spatial pattern of development features may only be influential under conditions where the amount of suitable habitat in the landscape is low (Betts et al. 2006, Cunningham & Johnson 2016). It is important, therefore, to consider the possibility of non-linear fragmentation effects. Previous work on Ovenbirds suggests there may be a threshold effect, i.e. a sharp decline in the tolerance to linear features, at densities above 8.5 km/km^2 (Bayne et al. 2005b) and that large shifts in songbird communities occur at densities of 10-60 wells per square kilometre (Thomas et al. 2014). As the density of development features within this study area is relatively low, with 0-10 well sites per square kilometre, I recommend continued efforts to decrease the size of development features and the amount of habitat conversion to minimize potential adverse effects at higher development intensities.

Conclusions

Accurate estimates of the impacts of development features to wildlife populations are essential for sustainable resource use and effective conservation planning. Here I document the influence of different development feature types on habitat selection for two peatland songbirds. Both species shifted territory placement to avoid permanent (e.g. polygonal or linear) or larger exploratory features (e.g. well sites) at the territory scale, but relative use of development features was greater for a ground-foraging generalist than a foliage gleaning peatland specialist.

For smaller exploratory features (e.g. winter roads and seismic lines), I found species-specific responses that differed for singing and foraging behaviours for some feature types, suggesting that foraging strategy may offer insight to predicting songbird responses to development in the boreal forest region. Furthermore, I show evidence that relative use of development features may be mediated or exacerbated by the vegetation structure or productivity of the habitat surrounding the feature. Greater understanding of the conditions where development features have the greatest influence on habitat use, could provide recommendations for where mitigation or reclamation efforts should be focused.

These results highlight the importance of considering both behaviour and local habitat conditions when evaluating avian responses to habitat change. This study provides an example of how supplemental behavioural monitoring can enhance our understanding of coarse-scale responses derived from standard point-count sampling methods. I recommend additional study of behaviour-focused habitat use to connect the mechanisms driving species-specific responses to different development feature types and suggest caution against the bias towards the use of singing detections in avian habitat selection and management studies.

3.5 Tables

Table 6. Predicted model structure for 3 sets of development feature response hypotheses- (a) response type, (b) relative impact, and (c) behavioural mechanism.

Hypothesis set	Model	Model structure		Description
a) Response type	Null	Habitat		Avian habitat use is closely tied to vegetation structure and composition attributes, with development features having a neutral effect
	Local area	Habitat + feature area		Increasing area of total development will have a localized positive or negative effect, depending whether development features add to or detract from area of suitable habitat
	Local interaction	Habitat *feature area		Development features will have a localized impact that is dependent on the characteristics of the surrounding habitat
	Distance	Habitat + distance to feature		Disturbance features may create an anthropogenic edge effect, influencing habitat use beyond the area directly within them.
b) Relative impact	Feature type	Permanent features		Permanent features are expected to be unsuitable habitat and elicit a decreased probability of use relative to other development features
	Feature size	Permanent polygonal > permanent linear > well site > wide linear > seismic		Larger permanent and exploratory features will have a greater relative impact than smaller features due to increased contrast in the microhabitat conditions within each feature.
	Microhabitat conditions	Various		Strength of avian response to development features will vary by feature type due to differences in suitability of novel habitat conditions generated by new features
c) Mechanism		Singing	Foraging	
	Landmark	positive	neutral	Vegetation gaps created by development features will provide areas of decreased territorial defence effort.

	Resource guild	neutral	positive or negative	Vegetation gaps created by development features will create resources for species that use early seral habitats for foraging.
	Both	positive	positive or negative	Development features will influence both territorial defence and foraging resources.

Table 7. Area in hectares of each development feature type and total proportion (percent area) of development within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Study sites were surveyed in both years except sites marked with an asterisk, which were only surveyed in either 2014 or 2015 (SE01, SE04, SW10). Values in brackets indicate the area or proportion in 2015 if the amount of development differed across study years.

Study Site	Permanent polygonal	Permanent linear	Well Site	Wide Linear	Seismic	Percent Total Development
CO03	0	0	0.1	0.3	0	1.5
CO04	0	0	0	0	0	0
CO05	0	0	0	0	0	0
SE01*	0	0	0	0	2.9	11.7
SE04*	0	0	0.2	0.2	2.9	13.1
SW02	0	0	0.5 (0.7)	0.4 (0.8)	2.9 (2.7)	15 (16.6)
SW03	0	0	0.3	0.5	3.0	15.2
SW04	0	0	0.5	0.3	3.1	15.8
SW10*	0	0	0.6	0.6	3.4	18.5
PE01	4.2 (4.3)	1.2 (1.5)	1.5	0.2	2.1	36.7 (38.2)
PE03	0	2.1	1.1	0.3	2.5	23.7

Table 8. Proportion (percent area) of vegetation for each height class and topographical depression class within each survey grid by types within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Study sites were surveyed in both years except sites marked with an asterisk, which were only surveyed in either 2014 or 2015 (SE01, SE04, SW10). Values in brackets indicate the area or proportion in 2015 if the amount of development differed across study years.

Grid	Ground Cover (<0.5 m)	Low Shrub (0.5 - <1 m)	Tall shrub (1 - <4 m)	Regenerating trees (4 - <10 m)	Tree (≥10 m)	Depression	Moderate	Upper

CO03	24.1	10.3	44.9	15.5	0	29.7	31.3	38.9
CO04	15.9	8.8	39.7	26.2	1.9	13.9	35.9	50.2
CO05	37.2	11.8	37.1	16.9	0.2	39.5	50.3	10.3
SE01*	11.4	7.6	26.8	31.6	4.5	15.2	26.5	58.3
SE04*	35.6	6.7	33	19.6	0	55.3	31.7	13
SW02	27.8 (27.3)	7.6 (7.4)	33.6 (33)	17.1 (16.8)	0.3 (0.3)	29.7	45.9	24.4
SW03	24.1	9	40.7	9.2	0	21.7	62.4	15.9
SW04	32.3	11.2	35	4.5	0	18.9	73.1	8
SW10*	26.2	7.7	39.2	7.1	0	23.2	66.6	10.2
PE01	3 (2.9)	2.7 (2.6)	13.6 (13.2)	34.1	2.7	6	7.2	86.8
PE03	27.3	8.1	31.4	9	0	16.8	75.3	7.9

Table 9. Top 10 candidate models for Dark-eyed Junco territory-level (2nd order) probability of use for n = 80 breeding territories using a 95% probability kernel density estimate. Territories were located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) and evaluated for support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. Models in **bold** were included in model averaging.

Model	***K***	**LL**	**AIC_c**	**ΔAIC_c**	**w_i**
Habitat + Permanent polygonal	**4**	**-157.838**	**323.789**	**0.000**	**0.139**
Habitat + Permanent polygonal + Permanent linear	**5**	**-157.027**	**324.223**	**0.434**	**0.112**
Habitat + Permanent polygonal + Well site	**5**	**-157.615**	**325.400**	**1.611**	**0.062**
Habitat only (null)	**3**	**-159.753**	**325.573**	**1.784**	**0.057**
Habitat + Permanent linear + Wide linear	5	-157.773	325.715	1.926	0.053
Habitat + Permanent polygonal + Permanent linear + Well site	6	-156.764	325.766	1.977	0.052
Habitat + Permanent polygonal+ Seismic	5	-157.812	325.794	2.005	0.051
Habitat + Permanent linear	4	-158.978	326.068	2.279	0.045
Habitat + Permanent polygonal + Permanent linear + Seismic	6	-156.945	326.128	2.339	0.043
Habitat + Permanent polygonal + Permanent linear + Wide linear	6	-157.004	326.246	2.456	0.041

Table 10. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and odds ratios (OR) for competitive Dark-eyed Junco logistic regression models of territory-level (2nd order) probability of use for a 95% kernel density breeding territory estimate.

Variables	**β**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR**
Intercept	-0.949	0.301	0.002	-1.542	-0.357	0.387
Depression ground cover	-0.145	0.070	0.040	-0.283	-0.007	0.865
Upland treed	-0.424	0.259	0.102	-0.934	0.085	0.654
Permanent polygonal	-0.090	0.096	0.351	-0.295	0.082	0.914
Permanent linear	-0.017	0.038	0.664	-0.158	0.048	0.983
Well site	-0.005	0.022	0.825	-0.120	0.062	0.995

Table 11. Top 10 candidate models for Palm Warbler territory-level (2nd order) probability of use for n = 82 breeding territories using a 95% probability kernel density estimate. Territories were located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion corrected for small sample sizes (ΔAIC$_c$) and evaluated for support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. Models in **bold** were included in model averaging.

Model	***K***	**LL**	**AIC$_c$**	**ΔAIC$_c$**	**w_i**
Habitat + Well site	**3**	**-162.274**	**330.615**	**0.000**	**0.231**
Habitat + Permanent linear + Well site	**4**	**-161.908**	**331.928**	**1.313**	**0.120**
Habitat only (null)	**2**	**-164.089**	**332.211**	**1.596**	**0.104**
Habitat + Well site + Distance to seismic	4	-162.254	332.620	2.005	0.085
Habitat + Well site + Wide linear	4	-162.268	332.647	2.032	0.084
Habitat + Permanent linear + Well site + Wide linear + Distance to seismic	3	-163.377	332.820	2.205	0.077
Habitat + Permanent linear + Well site + Distance to seismic	5	-161.870	333.907	3.292	0.044
Habitat + Permanent linear + Well site + Wide linear	5	-161.899	333.965	3.351	0.043
Habitat + Wide linear	3	-163.991	334.049	3.434	0.041
Habitat + Distance to seismic	3	-164.033	334.132	3.518	0.040

Table 12. Model averaged parameter parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and odds ratios (OR) for competitive Palm Warbler logistic regression models of territory-level (2nd order) probability of use for a 95% kernel density breeding territory estimate.

Variables	**β**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR**
Intercept	-2.103	0.623	0.001	-3.329	-0.877	0.122
Tall shrub (low-moderate depression)	0.019	0.019	0.341	-0.020	0.057	1.019
Well site	-0.098	0.091	0.285	-0.293	0.039	0.907
Permanent linear	-0.029	0.096	0.766	-0.427	0.210	0.972

Table 13. Top 10 candidate models for Dark-eyed Junco within-territory (3rd order) probability of use for observed **singing** locations within a 95% probability kernel density home range for n = 82 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for relative support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. All candidate models included a random effect for site and territory nested within sites.

Model	***K***	**LL**	**AIC**	**ΔAIC**	w_i
Habitat + Permanent linear	**7**	**-3778.111**	**7570.221**	**0.000**	**0.153**
Habitat + Permanent linear + Wide linear*Variability	**9**	**-3776.155**	**7570.310**	**0.089**	**0.146**
Habitat + Permanent linear + Well site	**8**	**-3777.701**	**7571.402**	**1.181**	**0.085**
Habitat + Permanent linear + Well site + Wide linear*Variability	**10**	**-3775.793**	**7571.585**	**1.364**	**0.077**
Habitat + Permanent polygonal + Permanent linear	**8**	**-3777.977**	**7571.953**	**1.732**	**0.064**
Habitat + Permanent polygonal + Permanent linear + Wide linear*Variability	**10**	**-3776.040**	**7572.080**	**1.859**	**0.060**
Habitat only (null)	6	-3780.328	7572.656	2.434	0.045
Habitat + Wide linear*Variability	8	-3778.357	7572.714	2.493	0.044
Habitat + Permanent polygonal + Permanent linear + Well site	9	-3777.546	7573.092	2.871	0.036
Habitat + Permanent polygonal + Permanent linear + Well site+ Wide linear*Variability	11	-3775.659	7573.318	3.097	0.032

Table 14. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and standardized odds ratios (OR$_{STD}$) for fixed effects in the competitive Dark-eyed Junco logistic regression model of within-territory (3rd order) probability of use for **singing** observation locations within a 95% kernel density home range estimate. All models within Δ2AIC of top mode were included l in model averaging. Subscript values indicate the scale for each variable that was used in the model selection. All candidate models included a random effect for site and nested effect for territory within site (not shown).

Variables	**β_{STD}**	**SE**	**$Pr(>\vert z\vert)$**	**2.50%**	**97.50%**	**OR_{STD}**
Intercept	-2.196	0.139	0.000	-2.469	-1.923	0.111
Regeneration$_{5}$	-0.135	0.047	0.004	-0.228	-0.042	0.874
Variability$_{5}$	0.868	0.047	0.000	0.776	0.960	2.382
Depression$_{10}$	0.004	0.039	0.913	-0.071	0.080	1.004
Permanent linear$_{5}$	-0.241	0.159	0.129	-0.552	0.070	0.786
Wide linear$_{11}$	0.019	0.028	0.511	-0.020	0.097	1.019
Wide linear$_{11}$*Variability$_{5}$	-0.023	0.031	0.463	-0.104	0.010	0.977
Well site$_{5}$	-0.017	0.047	0.718	-0.204	0.081	0.983
Permanent polygonal$_{5}$	-0.008	0.039	0.838	-0.192	0.116	0.992

Table 15. All candidate models for Palm Warbler within-territory (3rd order) probability of use for observed **singing** locations within a 95% probability kernel density home range for n=82 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for relative support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. All candidate models accounted for territories nested within study sites.

Model	***K***	**LL**	**AIC**	**ΔAIC**	**w_i**
Global	**11**	**-7965.044**	**15952.089**	**0.000**	**0.972**
Habitat + Well site + Seismic*Variability	9	-7970.625	15959.249	7.160	0.027
Habitat + Wide Linear*Variability + Seismic*Variability	10	-7973.437	15966.874	14.786	0.001
Habitat + Seismic*Variability	8	-7978.776	15973.553	21.464	<0.001
Habitat + Well site + Wide Linear*Variability	9	-7990.796	15999.591	47.502	<0.001
Habitat + Well site	7	-7996.330	16006.660	54.571	<0.001

Habitat + Wide Linear*Variability	8	-7999.188	16014.377	62.288	<0.001
Habitat only (null)	6	-8004.488	16020.976	68.887	<0.001

Table 16. Parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and standardized odds ratios (OR$_{STD}$) for the most supported (w_i = 0.97) Palm Warbler logistic regression model of within-territory (3rd order) probability of use for **singing** observation locations within a 95% kernel density home range estimate. Subscript values indicate the scale for each variable that was used in the model selection. The model accounted for territories nested within study sites (not shown).

Variables	**β_{STD}**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR$_{STD}$**
Intercept	-1.510	0.114	0.000	-1.734	-1.286	0.221
Regeneration$_6$	0.100	0.028	0.000	0.045	0.156	1.105
Variability$_6$	0.568	0.037	0.000	0.496	0.641	1.765
Depression$_6$	-0.052	0.021	0.014	-0.094	-0.010	0.949
Well site$_6$	-0.229	0.087	0.009	-0.400	-0.058	0.795
Wide linear$_{10}$	-0.037	0.024	0.118	-0.083	0.009	0.964
Seismic$_6$	-0.129	0.024	0.000	-0.175	-0.083	0.879
Wide linear$_{10}$*Variability$_6$	0.082	0.033	0.013	0.017	0.147	1.086
Seismic$_6$*Variability$_6$	-0.140	0.023	0.000	-0.185	-0.095	0.869

Table 17. Top candidate models for Dark-eyed Junco within-territory (3rd order) probability of use for observed **foraging** locations within a 95% probability kernel density home range for n = 82 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for relative support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. Table excludes any models with w_i < 0.01, except the null model. All candidate models included a random effect for site.

Model	***K***	**LL**	**AIC**	**ΔAIC**	**w_i**
Habitat + Permanent polygonal + Permanent Linear*Greenness + Wide Linear + Seismic*Greenness	**13**	**-2486.662**	**4999.323**	**0.000**	**0.230**

Habitat + Permanent Linear*Greenness + Wide Linear + Seismic*Greenness	**12**	**-2488.086**	**5000.171**	**0.848**	**0.150**
Habitat + Permanent Linear*Greenness + Wide Linear	**10**	**-2490.256**	**5000.512**	**1.189**	**0.127**
Habitat + Permanent polygonal + Permanent Linear*Greenness + Wide Linear	**11**	**-2489.465**	**5000.931**	**1.607**	**0.103**
Global	**14**	**-2486.560**	**5001.121**	**1.797**	**0.094**
Habitat + Permanent polygonal + Wide Linear + Seismic*Greenness	11	-2489.861	5001.722	2.399	0.069
Habitat + Permanent Linear*Greenness + Well site + Wide Linear + Seismic*Greenness	13	-2487.979	5001.959	2.635	0.062
Habitat + Permanent polygonal + Permanent Linear*Greenness + Wide Linear + Seismic*Greenness	11	-2490.065	5002.130	2.806	0.057
Habitat + Permanent polygonal + Permanent Linear*Greenness + Well site + Wide Linear	12	-2489.464	5002.928	3.605	0.038
Habitat + Permanent polygonal + Well site + Wide Linear + Seismic*Greenness	12	-2489.513	5003.027	3.704	0.036
Habitat + Wide Linear + Seismic*Greenness	10	-2492.583	5005.165	5.842	0.012
Habitat only (null)	7	-2510.395	5034.791	35.467	<0.001

Table 18. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and standardized odds ratios (OR_{STD}) for fixed effects in competitive Dark-eyed Junco logistic regression models of within-territory (3rd order) probability of use for **foraging** observation locations within a 95% kernel density home range estimate. All models within Δ2AIC of the most supported model were included in model averaging. Subscript values indicate the scale for each variable that was used in the model selection. The model accounted for a site effect (not shown).

Variables	β_{STD}	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	OR_{STD}
Intercept	-2.730	0.104	0.000	-2.934	-2.526	0.065
Tall shrub$_5$	-0.163	0.053	0.002	-0.267	-0.059	0.850
Variability$_5$	0.273	0.049	0.000	0.177	0.370	1.314
Greenness$_5$	-0.124	0.064	0.051	-0.249	0.000	0.883
Depression$_{11}$	0.048	0.052	0.354	-0.053	0.149	1.049
Permanent polygonal$_5$	0.055	0.062	0.380	-0.020	0.201	1.056
Permanent linear$_{11}$	0.147	0.070	0.036	0.010	0.284	1.158

Wide linear$_{11}$	0.170	0.032	0.000	0.108	0.232	1.185
Seismic$_5$	-0.007	0.039	0.858	-0.102	0.081	0.993
Permanent linear$_{11}$*Greenness$_5$	0.049	0.021	0.017	0.009	0.090	1.051
Seismic$_5$*Greenness$_5$	-0.098	0.087	0.256	-0.273	-0.020	0.906
Well site$_5$	0.004	0.024	0.878	-0.092	0.148	1.004

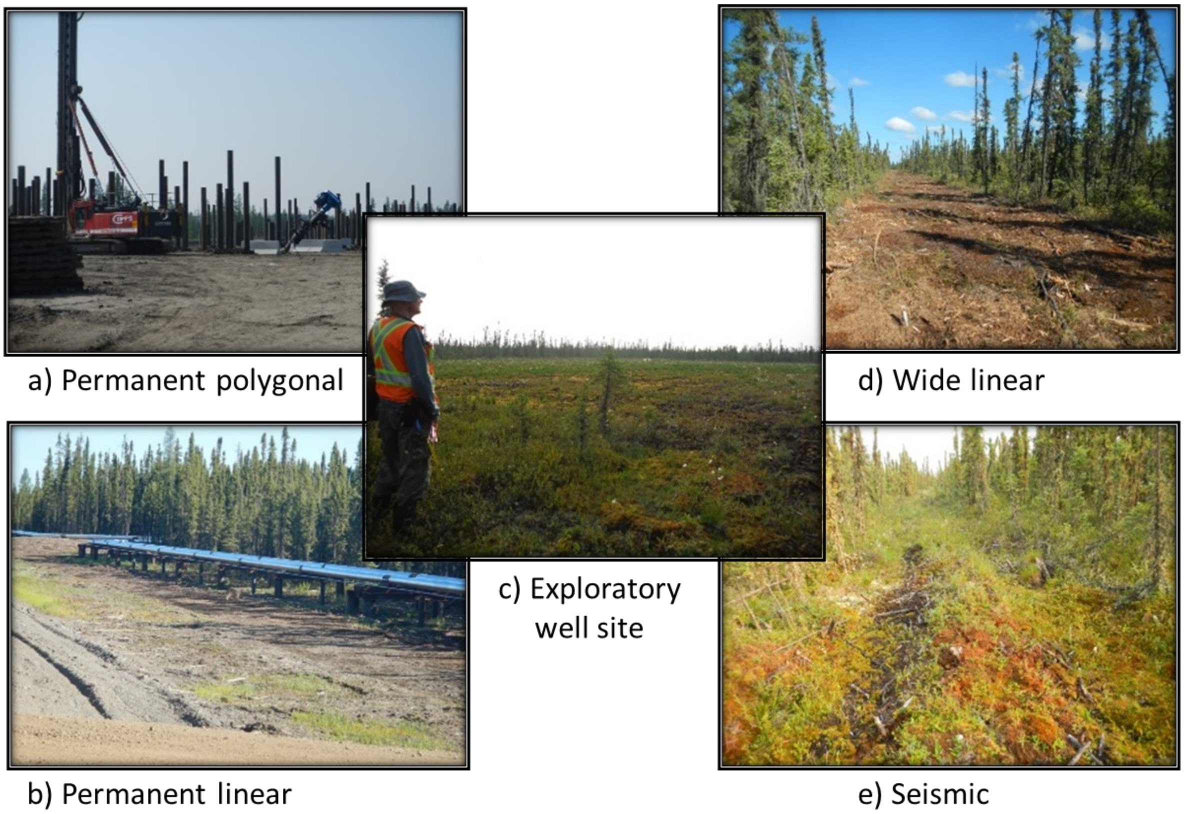
Table 19. All candidate models for Palm Warbler within-territory (3rd order) probability of use for observed **foraging** locations within a 95% probability kernel density home range for n=82 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for relative support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. All candidate models accounted for a nested effect of territory within site (not shown).

Model	***K***	**LL**	**AIC**	**ΔAIC**	w_i
Habitat + Well site + Seismic*Greenness	**11**	**-2954.673**	**5931.347**	**0.000**	**0.322**
Habitat + Seismic*Greenness	**10**	**-2956.162**	**5932.324**	**0.977**	**0.198**
Global	**12**	**-2954.337**	**5932.675**	**1.328**	**0.166**
Habitat + Well site	9	-2957.756	5933.511	2.164	0.109
Habitat + Wide linear + Seismic*Greenness	11	-2955.765	5933.529	2.182	0.108
Habitat + Well site + Wide linear	10	-2957.577	5935.153	3.806	0.048
Habitat only (null)	8	-2959.932	5935.863	4.516	0.034
Habitat + Wide linear	9	-2959.704	5937.409	6.062	0.016

Table 20. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, and standardized odds ratios (OR$_{STD}$) for fixed effects in the top Palm Warbler logistic regression model of within-territory (3rd order) probability of use for foraging observation locations within a 95% kernel density home range estimate. All models within Δ2AIC of the most supported model were included in model averaging. Subscript values indicate the scale for each variable that was used in the model selection. The model accounted for a nested effect of territory within study site (not shown).

Variables	**β_{STD}**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR_{STD}**
Intercept	-3.240	0.267	0.000	-3.763	-2.717	0.039
Regeneration$_6$	0.176	0.045	0.000	0.088	0.264	1.192
Variability$_6$	0.111	0.028	0.000	0.056	0.167	1.118
Greenness$_{10}$	0.121	0.053	0.022	0.018	0.224	1.128
Depression$_6$	0.059	0.041	0.154	-0.022	0.139	1.060
Well site$_6$	-0.125	0.142	0.379	-0.449	0.098	0.883
Seismic$_6$	0.015	0.047	0.742	-0.076	0.107	1.016
Seismic$_6$*Greenness$_{10}$	-0.099	0.045	0.027	-0.186	-0.012	0.906
Wide linear$_6$	0.008	0.023	0.736	-0.041	0.105	1.008

3.6 Figures



a) Permanent polygonal

d) Wide linear

c) Exploratory well site

b) Permanent linear

e) Seismic

Figure 8. Examples of development features types associated with bitumen energy extraction in the MacKay River Commercial Project *in situ* Steam-Assisted Gravity Drainage lease area

located approximately 30 km northwest of Fort McMurray, Alberta. (a) Permanent polygonal (b) Permanent linear (c) Exploratory well site (d) Wide linear (e) Seismic.

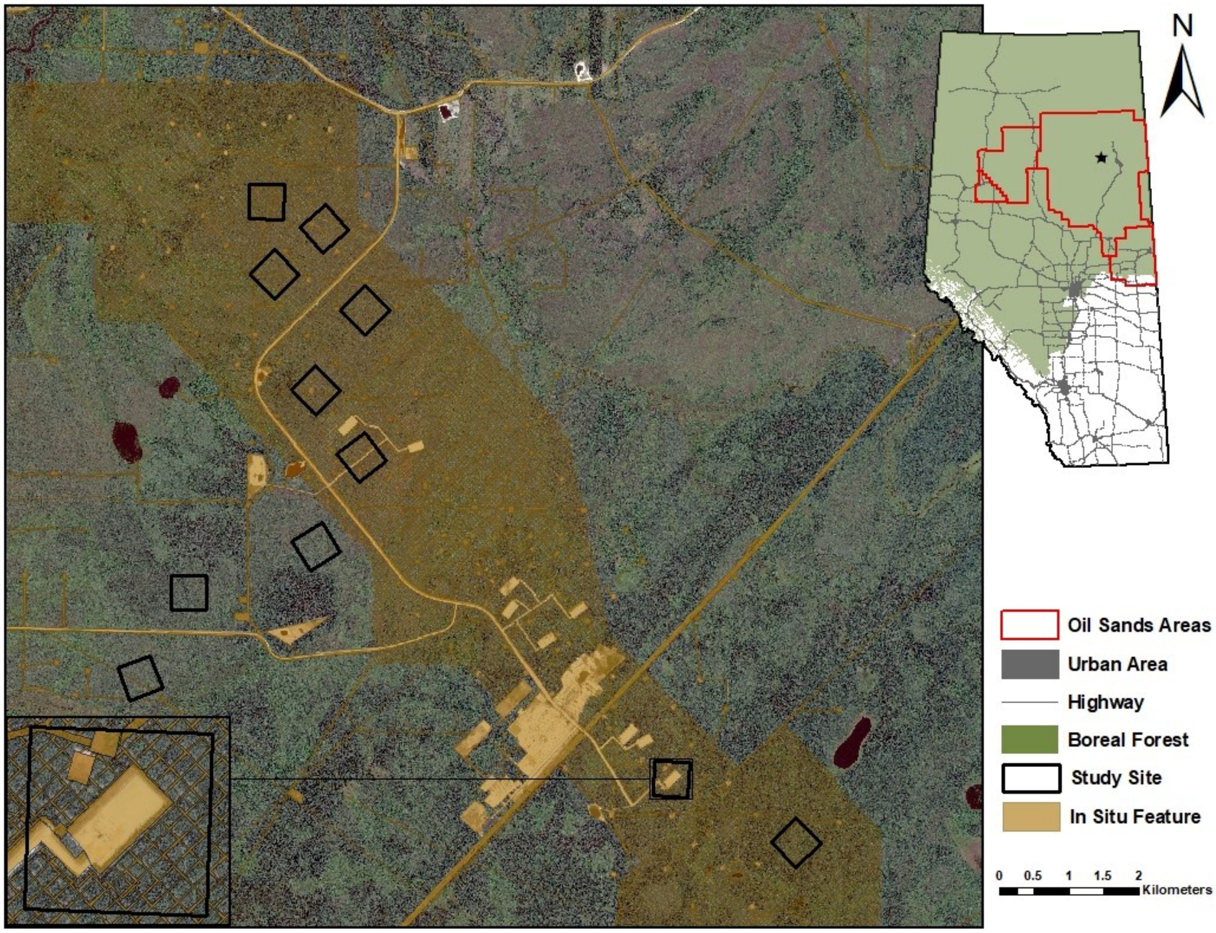


Figure 9. Placement of study sites within MacKay River Commercial Project lease area located approximately 30 km northwest of Fort McMurray, Alberta. Study sites (500 m by 500 m survey grids) were placed across a gradient of disturbance intensity.

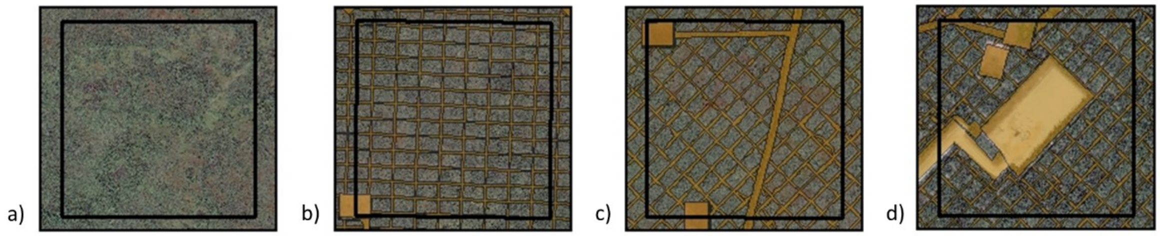


Figure 10. Examples of four, 25-hectare (500 m by 500 m) survey grids placed across a gradient of disturbance intensity. Development features are highlighted with a green fill to aid visual interpretation and survey grid boundaries are represented by solid black lines. (a) Control sites (n = 3)- ranged from 0-1.5% development features, (b) Seismic sites (n = 2)- primarily contained 3D seismic development from 11.7-13.1%, (c) Seismic-well sites (n = 5)- contained 3D seismic, wide linear development (i.e. winter roads), and exploratory wells with a total of 15-18.5% development, (d) Seismic-well-permanent sites (n = 2)- contained all types of development features including permanent SAGD well sites and/or gravel roads from 23.7-38.2% development.

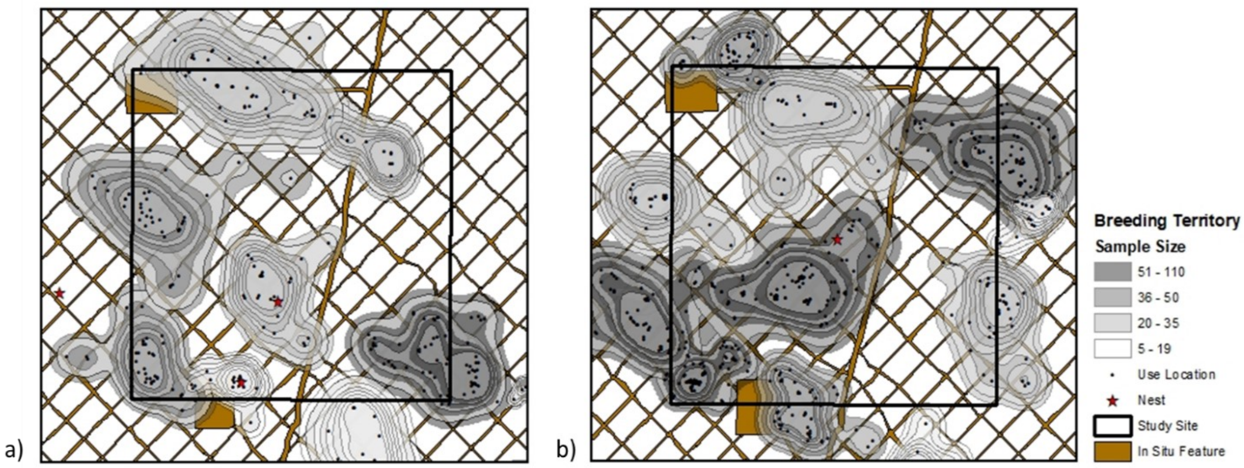


Figure 11. Territory (2nd order) and within-territory (3rd order) habitat use for (a) Dark-eyed Junco (*Junco hyemalis*) and (b) Palm Warbler (*Setophaga palmarum*) within a 25-hectare survey site with moderate (18.5%) development intensity. Black dots represent locations of use from burst sampling surveys where observers followed individuals during 30-60-minute observation sessions and recorded all observed locations of use. These locations represent within-territory

habitat use. Grey contours represent probability contours derived from kernel density analyses of all use locations for each territory (30, 40, 50, 60, 70, 80, and 95% probability of use). Territories with darker contours have greater relative sample sizes.

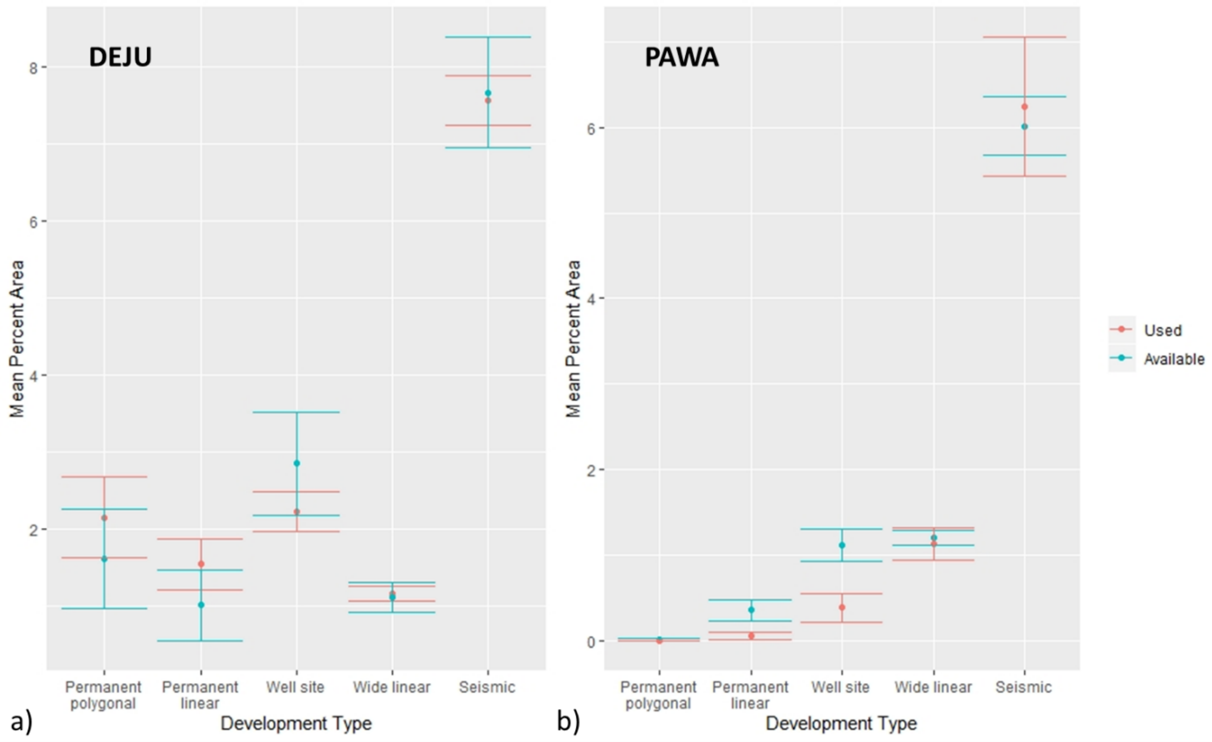


Figure 12. Average used and available proportion (percent area) of each development feature type within territory boundaries of 95% kernel density estimate of breeding territories for (a) Dark-eyed Junco (DEJU) and (b) Palm Warbler (PAWA). Error bars represent standard error values and development feature types include: permanent polygonal, permanent linear, exploratory well sites, wide linear features, and seismic lines.

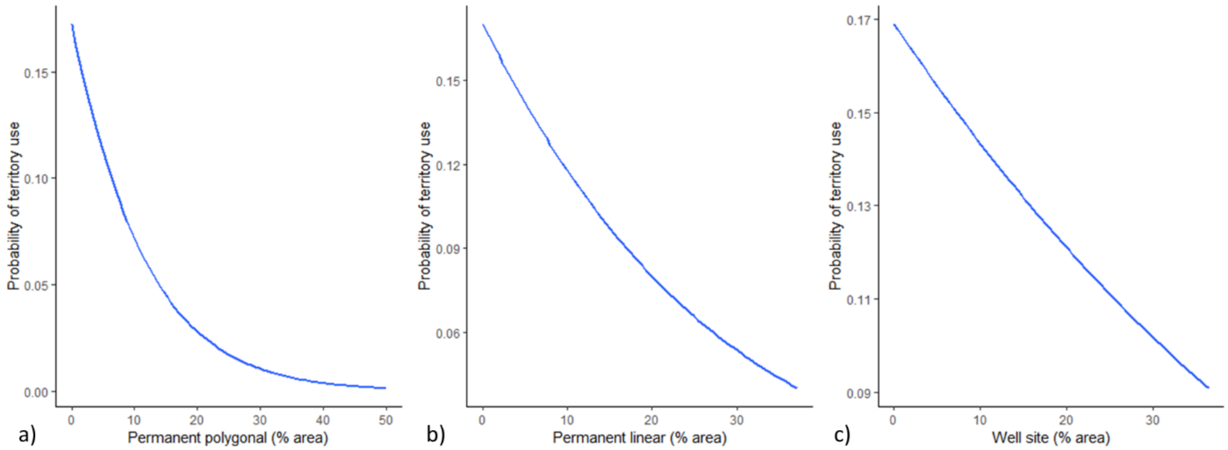


Figure 13. Model-averaged predicted response for Dark-eyed Junco territory-level probability of use of different development features included within competitive models for 95% probability kernel density breeding territory estimates for n = 80 territories, including (a) permanent polygonal features, (b) permanent linear features, and (c) well site features.

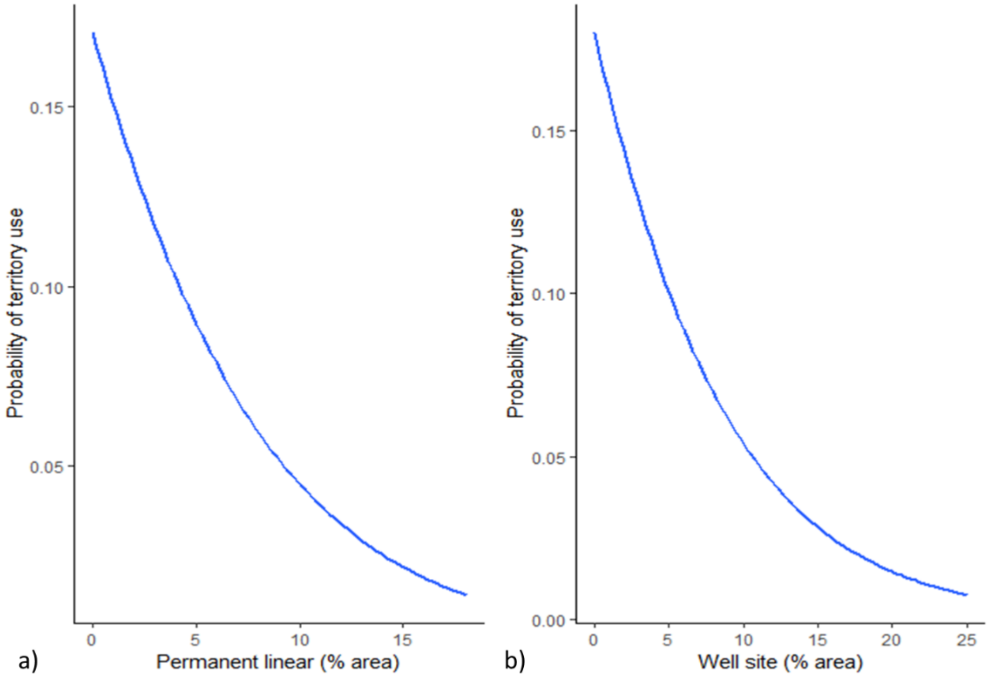


Figure 14. Model-averaged predicted response for Palm Warbler territory level probability of use of different development features included within competitive models for 95% probability kernel

density breeding territory estimates for n = 82 territories, including (a) permanent linear, and (b) well sites.

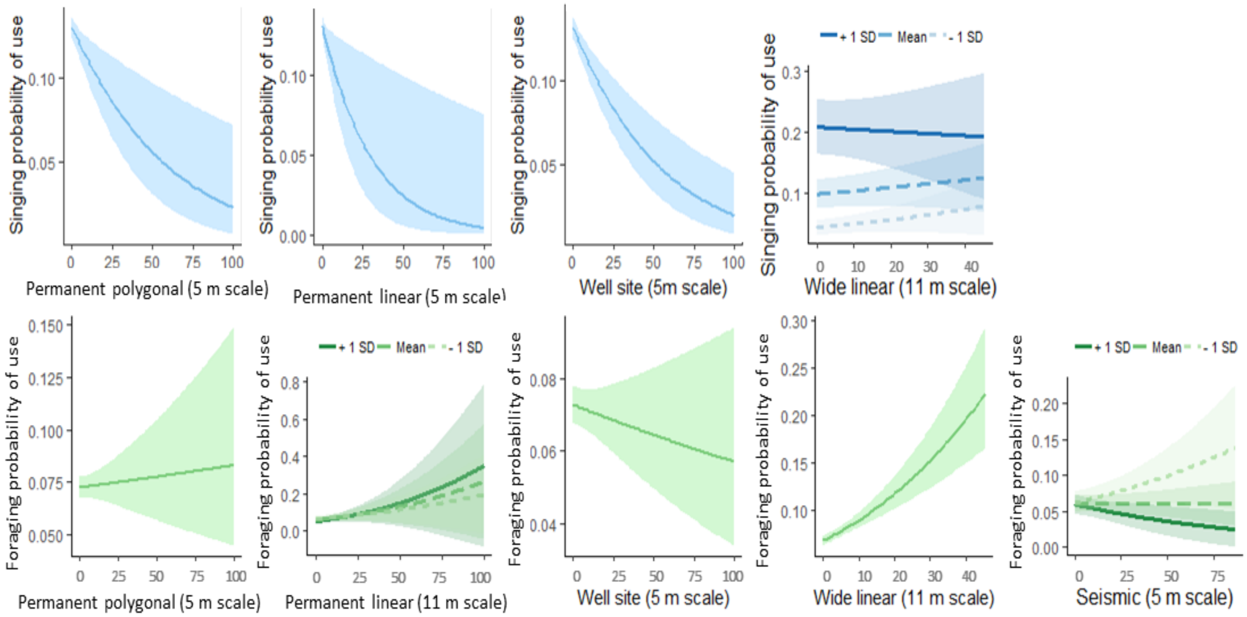


Figure 15. Predicted response for Dark-eyed Junco within-territory probability of use of different development features included in within top model for 95% probability kernel density home range estimates for n = 80 territories. Probability of use was modelled separately for singing observation locations (blue) and foraging observation locations (green). For interactions between development features and habitat characteristics, a solid line indicates the response at one standard deviation above the mean, dark dotted line indicates the mean, and light dotted line indicates response at values one standard deviation below the mean. Random effects include a nested effect for territory identifier within each site, but confidence intervals reflect only the variance of the fixed effects.

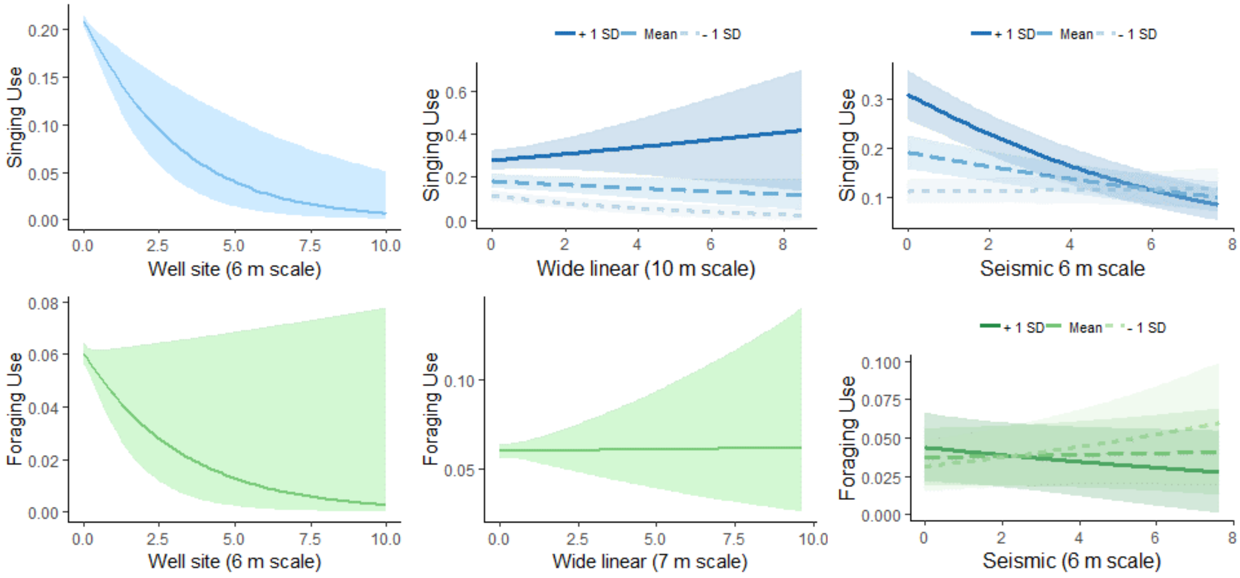


Figure 16. Predicted response for Palm Warbler within-territory probability of use of different development features included within top model for 95% probability kernel density home range estimates for n = 82 territories. Probability of use was modelled separately for singing observation locations (blue) and foraging observation locations (green). For interactions between development features and habitat characteristics, a solid line indicates the response at one standard deviation below the mean, dark dotted line indicates the mean, and light dotted line indicates response at values one standard deviation above the mean. Random effects include a nested effect for territory identifier within each site, but confidence intervals reflect only the variance of the fixed effects.

Chapter 4: General conclusion

Predicting and managing the impact of expanding human developments on biodiversity and ecosystem health remains an important social, economic, and ecological challenge (Northrup & Wittemyer 2013, Rosa et al. 2017). In the boreal forest region, there is need for increased understanding of the impacts of expanding small-scale *in situ* oil sands development features on avian habitat use, particularly in peatland ecosystems (Morissette et al. 2013). Identifying the relationships between different types of development features and species-specific response patterns across multiple spatial scales can provide insight into the variable ecological processes and response pathways to consider in sustainable resource development planning. This study focused on evaluating the relative effect of different *in situ* oil sands development features on landscape occurrence, territory selection, and within-territory habitat selection for two songbird species with different habitat specificities and preferred foraging strata. My main objectives were to: (1) identify landscape-scale factors influencing distribution of an avian generalist and specialist in habitats altered by in situ development; (2) identify the relative impact of different *in situ* and habitat features on landscape- and local-scale habitat selection; and (3) identify potential behavioural mechanisms driving responses to in situ development features on individual territory placement and within-territory habitat selection. I focused on a conifer generalist, Dark-eyed Junco (*Junco hyemalis*), and peatland specialist, Palm Warbler (*Setophaga palmarum*), to gain a broader understanding of the extent that different foraging strata might relate to predictability of responses.

For both species, the amount of permanent polygonal and permanent linear development features influenced occurrence, whereas exploratory features did not, suggesting that permanent development features have a greater impact on peatland habitat suitability. Minimizing the direct loss of habitat from permanent features through activities, such as strategic development planning and coordinated multi-sector access management planning, will be valuable for managing human impacts to avian species overall. Although smaller exploratory features, including well sites, did not influence occurrence within the lease area, both species avoided including these features within breeding territories, indicating that point-count occurrence data does not fully capture exploratory development feature responses for these species.

Point-count surveys are widely used for monitoring avian populations (Ralph et al. 1995, Matsuoka et al. 2014), so it is important to be aware of these limitations. Point-counts may show density-related biases (Howell et al. 2004), fail to capture responses identified by finer-resolution territory mapping or transect techniques used within the same study site (Newell et al. 2013, Thompson et al. 2015), and display different observed responses depending on the size of the point-count radius (Bayne et al. 2016). I found that point-count surveys were able to detect responses to larger, more permanent features on species occurrence, but missed meaningful territory and within-territory responses to smaller exploratory development features for both species. Small-scale features, such as wide linear and 3D seismic, may require methods with finer resolution to properly quantify their impacts to avian populations. I recommend that broad regional studies be paired with more detailed local-scale and behavioural work to improve our understanding of the mechanisms driving species-specific responses to different feature types.

Despite limited evidence for numerical responses to wide linear or seismic features in this study, even small, 1-2 m wide seismic features influenced how individuals used habitat within breeding territories, including selection of singing or foraging locations, highlighting the importance of fine-scale behavioural work for a comprehensive understanding of the effects of habitat alteration on avian populations. Responses to development features may ultimately lead to habitat degradation and population-level impacts when habitat availability is low or species density is high (Bayne et al. 2005a, Lankau et al. 2013).

Consistent support for local habitat composition, rather than distance, for territory and within-territory habitat selection suggests that DEJU and PAWA both use habitat in close proximity to development features. These results support observations that boreal forest species may be resilient to moderate amounts of habitat disturbance (Schmiegelow & Mönkkönen 2002). Although development features create different spatial patterns than natural disturbance regimes (e.g. fire, Pickell et al. 2015), in some cases, small exploratory features also contribute to vegetation heterogeneity, which can be beneficial to some species, potentially even enhancing local species diversity (but see Stirnemann et al. 2015).

However, this study targeted relatively contiguous areas of shrubby bog habitat, with at least 20% (0.63 ha) within 100 m of point-count sites and consistent for territory mapping sites. If responses to disturbances are strongest under conditions of low amounts of preferred habitat availability, e.g. more highly fragmented or smaller landscapes (Smith et al. 2011, Villard & Metzger 2014), this study may show modest impacts relative to the potential range within the region. Furthermore, even within focal territory mapping sites that contained high availability of preferred vegetation types, I found that the strength of the response to development features can be influenced by the environmental characteristics in the vicinity of the feature, i.e. along the habitat-feature interface. I recommend additional work to evaluate the consistency of responses across a gradient of landscape-level availability of shrubby bog habitat. Increasing our understanding of how these relationships differ under diverse habitat conditions, can guide future sustainable development planning and support prioritization of restoration efforts.

Understanding how species responses vary across scales can inform our understanding of the underlying ecological processes that resource activities may influence, enhance our predictive capacity, and improve our landscape management decisions. I recommend continued efforts to conduct multi-scale studies that include behavioural observations to improve our understanding of the mechanisms driving species-specific responses to different development feature types.

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Appendices

Appendix 1. Behavioural observations

Table 21. Definitions and count for different songbird behaviours recorded during Dark-eyed Junco (*Junco hyemalis,* 'DEJU') and Palm Warbler (*Setophaga palmarum,* 'PAWA') observation sessions in 2014 and 2015. Of 9308 total observation locations collected, 7362 observation locations were included in within-territory analyses (80 DEJU and 82 PAWA territories). Note: behaviours do not sum to total observation locations because 1 or more behaviours may occur at a single spatial location, e.g. a bird may sing, perch silently, then give an alarm call at a single location.

Behaviour	**Definition**	**DEJU**	**PAWA**
Singing	Singing	1304	3141
Counter-singing	Singing closely back and forth with a neighbouring territorial male	148	454
Calling	Non-distressed call (e.g. contact call between male and female pair or flight calls)	601	321
Alarm call/distress call	Agitated call, indicating the presence of a perceived threat (e.g. predator or observer, often made in proximity to a nest or fledgling)	199	196
Perching	Perching silently	511	234
Preening	Preening	51	52
Feeding/foraging	Actively searching for food and/or feeding (e.g. gleaning, pecking, etc.)	652	685
Chase	Aggressive chase (usually between two territorial males)	34	45
Carrying food	Food visible in bill	88	165
Pair bonding display	Male or female solicitation display	4	
Copulation	Copulation	5	2

Carrying nest material/nest building	Nest building materials visible in bill (e.g. grass, feathers, twigs, etc.) or actively working on a nest	10	10
Begging	Fledgeling observed begging for food	15	0
Distraction display	Made by male or female when a perceived predator is in close proximity to young (e.g. broken wing display)	1	5
Fledgling/Family group	Observation of a family group or fledgling within the breeding territory after young have fledged the nest	42	16
Nest site	Location of a known DEJU or PAWA nest that was built during that study year (including both successful and failed nests)	25	16
Total Locations		**3067**	**4295**

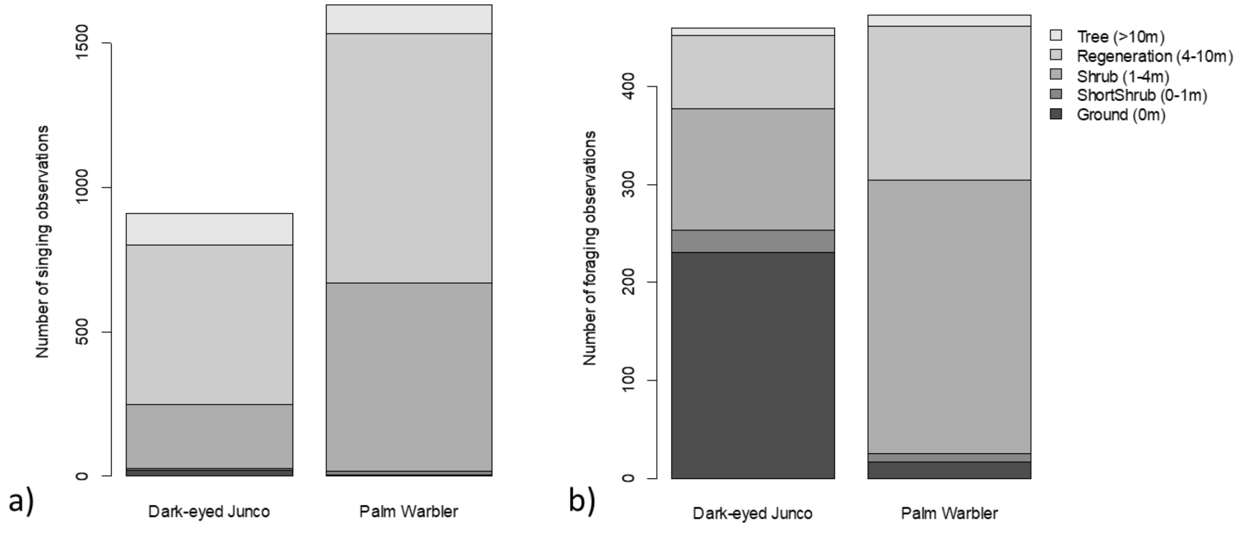

Figure 17. Raw number of singing (a) and foraging (b) observations for Dark-eyed Juncos (*Junco hyemalis*) and Palm Warblers (*Setophaga palmarum*) in different vegetation class categories, as collected by observers in the field. Vegetation classes include: tree (>10 m), regenerating tree (4-10 m), shrub (1-4 m), short shrub (0-1 m), and ground (0 m).

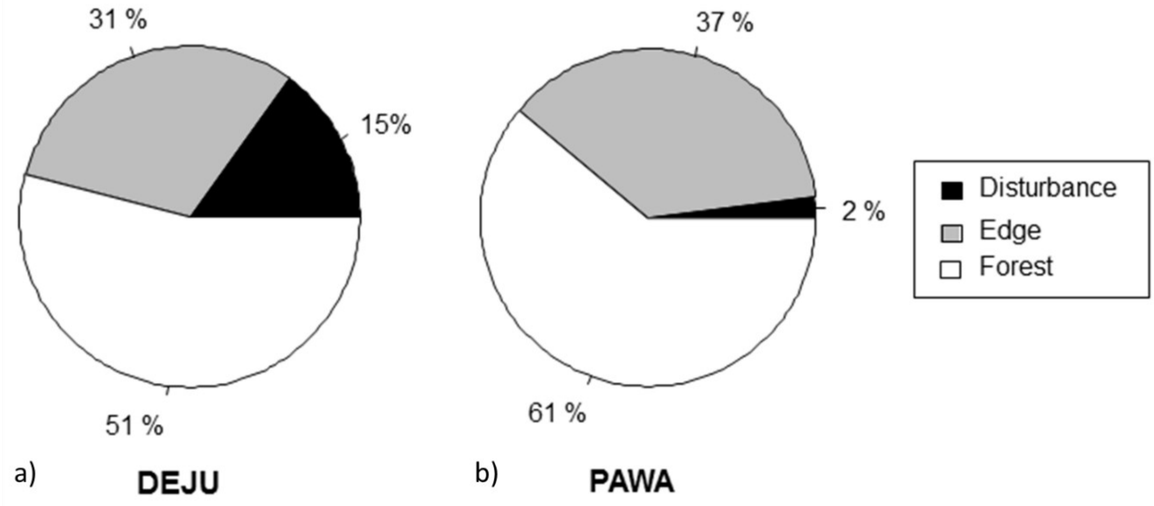

Figure 18. Raw proportion of total observations of (a) Dark-eyed Juncos (*Junco hyemalis*, 'DEJU') and (b) Palm Warblers (*Setophaga palmarum*, 'PAWA') in different disturbance classes, including: disturbance (observed on a development feature), edge (observed within 5 metres of a development feature), and forest (observed >5 m from a development feature).

Appendix 2. Selecting within-territory sample scale

To identify the local habitat and development characteristics, I examined variables within a circular radius around a location of use or availability. I determined a biologically relevant scale for the radius by evaluating the Euclidean movement distance between two consecutive use locations of use for each behaviour type, i.e. the distance from one foraging location to the next foraging location (or one singing location to the next singing location), when an individual was observed continuously. There was a higher frequency of movement lengths at distances less than 50 m for singing observation and less than 25 m for foraging observations, followed by a steep decline in frequency at greater distances, although there were many observations of Dark-eyed Junco singing movements between 50-100 m (Figure 19). The average distance between two consecutive singing observations for DEJU was 50 m, for PAWA was 36.6, whereas the average for foraging movements was 13 m for DEJU and 19 m for PAWA (Figure 19). For each species I considered 3 scales: (1) the mode distance between any consecutive movements, (2) the mode distance between singing or foraging movements, and (3) a 90 % trimmed mean between 2 consecutive foraging locations (Table 22). I expected that these distances were most representative of a local patch selection scale, whereas longer distances were more representative of travel between resource patches.

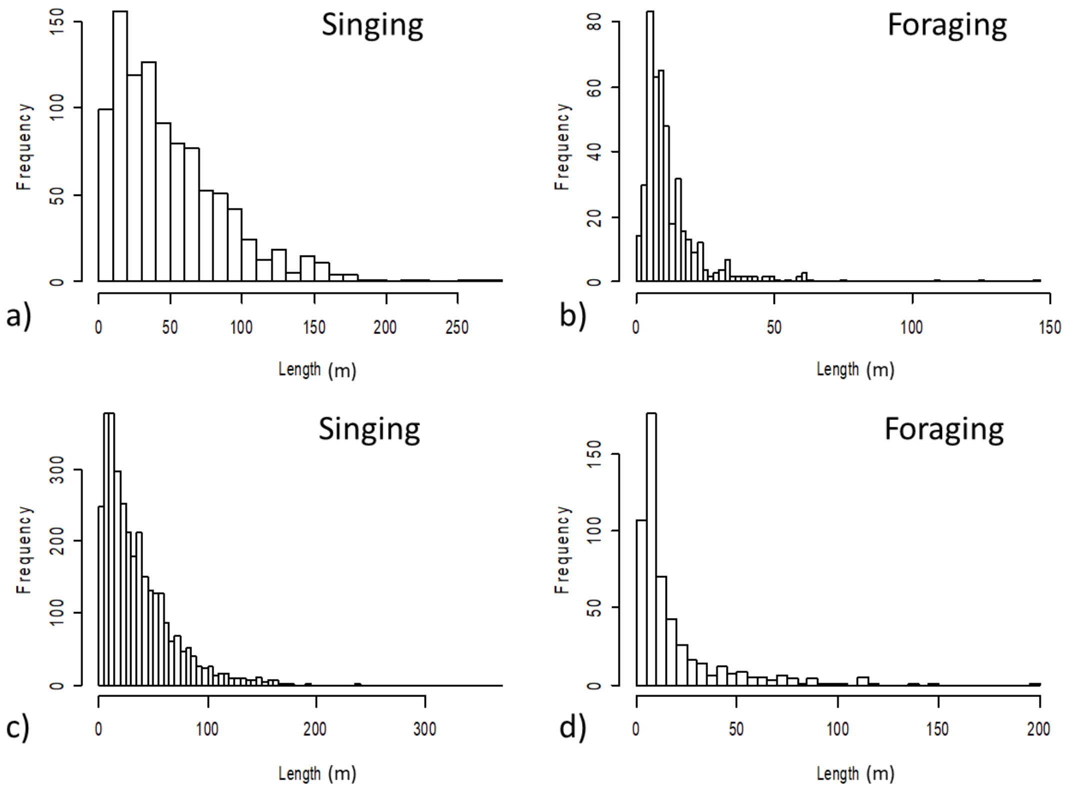

Figure 19. Frequency of movement distances between two consecutive Dark-eyed Junco (top row) and Palm Warbler (bottom row) singing (a, c) and foraging (b, d) use locations.

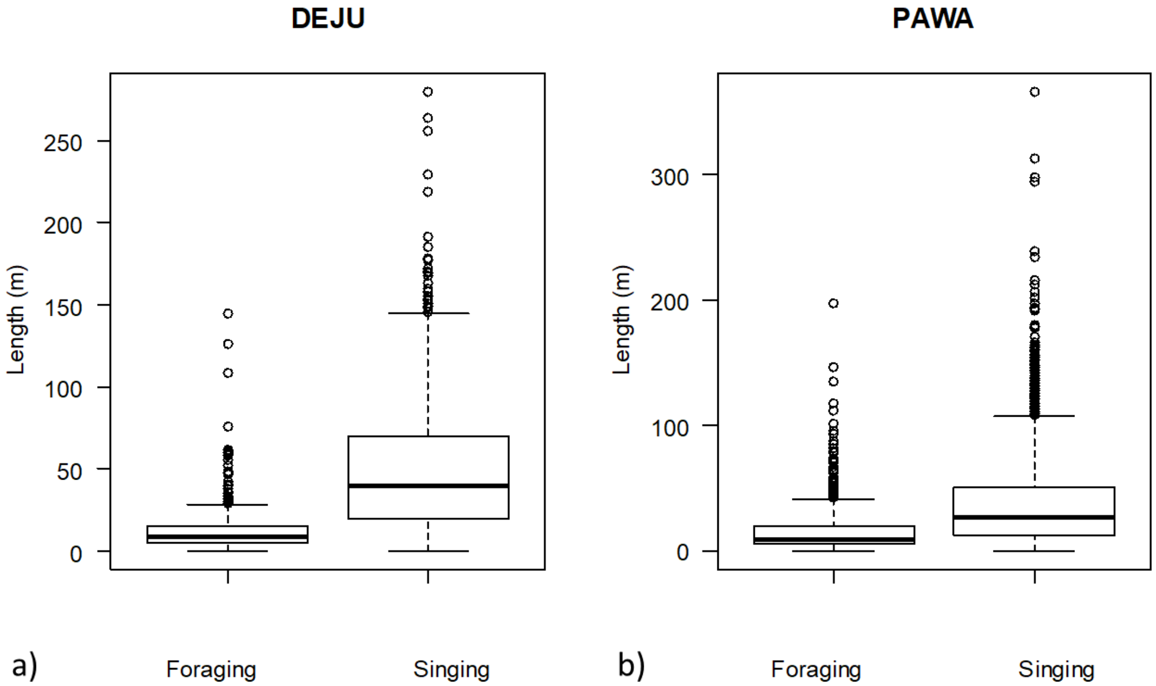

Figure 20. Comparison of average movement distance in metres between two consecutive foraging and singing use locations for Dark-eyed Juncos (a) and Palm Warblers (b).

Table 22. Means, median, and mode movement distances between observed use locations for DEJU and PAWA use locations. Values (in metres) represent distances between two consecutive observations for any behaviour, singing behaviours, and foraging behaviours. Values in **bold** indicate distances considered for selection scales. As the trimmed mean for foraging locations was similar for both species, I rounded both to the 10 m scale for this measure. Selection scales considered for Dark-eyed Junco were 5, 10, and 11 m radius around use location, whereas selection scales for Palm Warbler were 6, 7, and 10 m.

Measure	**Dark-eyed Junco**			**Palm Warbler**		
	All	**Singing**	**Foraging**	**All**	**Singing**	**Foraging**
Mean	32.7	50	13	33	36.6	19
Median	18.4	40	8.9	22.6	26.6	9.4
Mode	5	**11**	**5**	7	**7**	**6**
90% Trimmed mean	26	46.5	**10**	27.4	31.1	**9.4**

Appendix 3. Selecting best functional form for distance variables

I compared univariate measures of territory placement and within-territory habitat use for different distances to development features. I expected responses to development features (positive or negative) to be greatest near the development feature and rapidly decline with increasing distance from the features. I predicted that the development feature types with the greatest influence on probability of habitat use would have the longest distance to a decay of zero influence on probability of use, which is effectively reached at a value of approximately 90% of the decay function. At the territory-level I examined twenty metre decay intervals to represent a shift in territory placement of approximately a quarter the average territory radius from the territory centre (spatial centroid of the 95% kernel density isopleth), where the territory would be overlapping the feature, up to a maximum distance of 160 metres, approximately two times the average territory diameter. At the within-territory scale I examined five metre decay intervals, approximately equal to the most common movement distance for each species (five metres for Dark-eyed Junco and six metres for Palm Warbler), up to a maximum decay distance of 80 metres, approximately equal to the territory diameter, or the maximum distance at which an individual could be away from a feature that falls within its territory boundaries.

Table 23. Selection of best functional form for distance of Dark-eyed Junco territory placement relative to permanent polygonal development features. Univariate models including linear, logarithmic, and exponential decay transformations were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c). I examined decay transformations for 20-160 m distances (in 20 m increments) for territory centres. The functional form with the smallest AIC_c score and greatest Akaike weight of evidence (w_i) was selected for inclusion in territory habitat use models, excluding the smallest decay distance, which I considered equal to a local

area effect. β is the parameter estimate, K is the number of model parameters and LL is the log-likelihood of the model for each functional form.

Distance transformation	Intercept	β	K	LL	AIC_c	ΔAIC_c	w_i
40 m decay	-1.603	-0.280	2	-162.166	328.366	0.000	0.103
20 m decay	-1.604	-0.284	2	-162.169	328.371	0.005	0.102
60 m decay	-1.604	-0.191	2	-162.184	328.401	0.035	0.101
80 m decay	-1.606	-0.109	2	-162.195	328.425	0.058	0.100
Linear distance (Null)	-1.610	0.014	2	-162.197	328.428	0.061	0.099
Log distance	-1.649	0.014	2	-162.200	328.434	0.068	0.099
100 m decay	-1.608	-0.050	2	-162.201	328.435	0.068	0.099
160 m decay	-1.611	0.034	2	-162.201	328.436	0.069	0.099
140 m decay	-1.610	0.017	2	-162.202	328.437	0.071	0.099
120 m decay	-1.609	-0.010	2	-162.202	328.438	0.071	0.099

Table 24. Selection of best functional form for distance of Palm Warbler territory placement relative to permanent polygonal development features. Univariate models including linear, logarithmic, and exponential decay transformations were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c). I examined decay transformations for 20-160 m distances (in 20 m increments) for territory centres. The functional form with the smallest AIC_c score and greatest Akaike weight of evidence (w_i) was selected for inclusion in territory habitat use models, excluding the smallest decay distance, which I considered equal to a local area effect. β is the parameter estimate, K is the number of model parameters and LL is the log-likelihood of the model for each functional form.

Distance Transformation	Intercept	β	K	LL	AIC_c	ΔAIC_c	w_i
180 m decay	-1.623	18.752	2	-164.413	332.858	0.000	0.078
200 m decay	-1.624	13.990	2	-164.414	332.861	0.003	0.078
160 m decay	-1.621	27.184	2	-164.414	332.862	0.004	0.078
220 m decay	-1.626	10.720	2	-164.418	332.870	0.012	0.077
140 m decay	-1.620	43.169	2	-164.421	332.875	0.017	0.077
240 m decay	-1.627	8.621	2	-164.424	332.882	0.024	0.077
120 m decay	-1.618	78.637	2	-164.434	332.900	0.042	0.076
100 m decay	-1.617	177.289	2	-164.456	332.944	0.086	0.075
80 m decay	-1.615	575.177	2	-164.492	333.018	0.160	0.072

60 m decay	-1.613	4009.358	2	-164.555	333.144	0.286	0.067
Linear distance (Null)	-1.608	-0.066	2	-164.614	333.262	0.404	0.064
Log distance	-0.704	-0.300	2	-164.615	333.263	0.405	0.064
40 m decay	-1.610	1.69E+05	2	-164.654	333.341	0.483	0.061
20 m decay	-1.605	-1.24E+10	2	-164.718	333.469	0.611	0.057

Table 25. Selection of best functional form for distance of Dark-eyed Junco within-territory probability of use relative to wide linear development features. Univariate models including linear and exponential decay transformations were ranked using Akaike's Information Criterion (AIC). I examined decay transformations for 5-80 m distances (in 5 m increments) for use locations. The functional form with the smallest AIC score and greatest Akaike weight of evidence (w_i) was selected for inclusion in territory habitat use models, excluding the smallest decay distance, which I considered equal to a local area effect. β is the parameter estimate, *K* is the number of model parameters and LL is the log-likelihood of the model for each functional form.

Distance Transformation	**Intercept**	**β**	***K***	**LL**	**AIC**	**ΔAIC**	w_i
15 m decay	-1.114	0.409	2	-6894.188	13792.376	0.000	0.203
20 m decay	-1.116	0.378	2	-6894.374	13792.748	0.372	0.169
10 m decay	-1.111	0.429	2	-6894.417	13792.834	0.459	0.161
25 m decay	-1.117	0.345	2	-6894.746	13793.492	1.116	0.116
5 m decay	-1.108	0.434	2	-6895.082	13794.163	1.788	0.083
30 m decay	-1.117	0.314	2	-6895.163	13794.326	1.951	0.077
35 m decay	-1.118	0.286	2	-6895.569	13795.138	2.762	0.051
40 m decay	-1.118	0.261	2	-6895.938	13795.876	3.500	0.035
45 m decay	-1.118	0.239	2	-6896.264	13796.528	4.153	0.025
50 m decay	-1.118	0.220	2	-6896.553	13797.106	4.730	0.019
55 m decay	-1.118	0.204	2	-6896.801	13797.602	5.227	0.015
60 m decay	-1.118	0.189	2	-6897.022	13798.044	5.668	0.012
65 m decay	-1.118	0.176	2	-6897.210	13798.419	6.044	0.010
70 m decay	-1.118	0.164	2	-6897.375	13798.751	6.375	0.008
75 m decay	-1.118	0.154	2	-6897.522	13799.044	6.669	0.007
80 m decay	-1.118	0.145	2	-6897.649	13799.297	6.922	0.006
Linear distance (Null)	-1.094	0.000	2	-6898.981	13801.962	9.586	0.002

Table 26. Selection of best functional form for distance of Palm Warbler within-territory probability of use relative to wide linear development features. Univariate models including linear and exponential decay transformations were ranked using Akaike's Information Criterion (AIC). I examined decay transformations for 5-80 m distances (in 5 m increments) for use locations. The functional form with the smallest AIC score and greatest Akaike weight of evidence (w_i) was selected for inclusion in territory habitat use models, excluding the smallest decay distance, which I considered equal to a local area effect. β is the parameter estimate, *K* is the number of model parameters and LL is the log-likelihood of the model for each functional form.

Distance Transformation	**Intercept**	**β**	***K***	**LL**	**AIC**	**ΔAIC**	w_i
40 m decay	-1.085	-0.210	2	-9658.612	19321.224	0.000	0.094
35 m decay	-1.086	-0.218	2	-9658.626	19321.252	0.028	0.093
45 m decay	-1.085	-0.200	2	-9658.655	19321.309	0.085	0.090
30 m decay	-1.087	-0.223	2	-9658.715	19321.431	0.207	0.085
50 m decay	-1.084	-0.190	2	-9658.738	19321.476	0.253	0.083
55 m decay	-1.084	-0.180	2	-9658.847	19321.694	0.470	0.075
25 m decay	-1.089	-0.225	2	-9658.895	19321.790	0.566	0.071
60 m decay	-1.084	-0.170	2	-9658.974	19321.949	0.725	0.066
65 m decay	-1.083	-0.160	2	-9659.107	19322.213	0.990	0.058
20 m decay	-1.090	-0.221	2	-9659.170	19322.341	1.117	0.054
70 m decay	-1.083	-0.150	2	-9659.243	19322.486	1.262	0.050
75 m decay	-1.083	-0.141	2	-9659.379	19322.759	1.535	0.044
80 m decay	-1.084	-0.132	2	-9659.510	19323.019	1.796	0.038
15 m decay	-1.092	-0.211	2	-9659.516	19323.032	1.808	0.038
10 m decay	-1.094	-0.199	2	-9659.854	19323.707	2.484	0.027
5 m decay	-1.095	-0.197	2	-9660.059	19324.117	2.893	0.022
Linear distance (Null)	-1.090	0.000	2	-9660.784	19325.568	4.345	0.011

Appendix 4. Models including all use locations

Table 27. Top candidate models for Dark-eyed Junco within-territory (3rd order) probability of use for all observations within a 95% probability kernel density home range for n = 80 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and

2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for support relative to other models in the candidate set using Akaike weight of evidence (w_i). K is the number of parameters, and LL is the log-likelihood for each model. Table excludes any candidate models with w_i less than 0.01, except the null model. All candidate models included a random effect for site.

Model	K	**LL**	**AIC**	**ΔAIC**	w_i
Habitat + Permanent polygonal + Permanent linear + Well site + Wide linear*Variability	**11**	**-6664.098**	**13350.195**	**0.000**	**0.192**
Habitat + Permanent linear + Wide linear*Variability	**9**	**-6666.186**	**13350.373**	**0.178**	**0.175**
Habitat + Permanent polygonal + Permanent linear + Wide linear*Variability	**10**	**-6665.347**	**13350.695**	**0.500**	**0.149**
Habitat + Permanent linear + Well site + Wide linear*Variability	**10**	**-6665.696**	**13351.392**	**1.197**	**0.105**
Global	**13**	**-6662.910**	**13351.819**	**1.624**	**0.085**
Habitat Permanent linear + Wide linear*Variability + Seismic*Variability	11	-6665.311	13352.621	2.426	0.057
Habitat + Permanent polygonal + Permanent linear + Wide linear*Variability + Seismic*Variability	12	-6664.346	13352.693	2.497	0.055
Habitat + Wide linear*Variability	8	-6668.380	13352.760	2.564	0.053
Habitat + Permanent linear + Well site + Wide linear*Variability + Seismic*Variability	12	-6664.814	13353.627	3.432	0.034
Habitat + Permanent polygonal + Wide linear*Variability	9	-6668.178	13354.356	4.160	0.024
Habitat +Well site + Wide linear*Variability	9	-6668.244	13354.488	4.293	0.022
Habitat + Wide linear*Variability + Seismic*Variability	10	-6667.525	13355.051	4.856	0.017
Habitat + Permanent polygonal + Well site + Wide linear*Variability	10	-6667.935	13355.870	5.675	0.011
Habitat only (null)	6	-6678.969	13369.937	19.742	<0.001

Table 28. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>\|z\|)), 95% confidence intervals, standardized odds ratios ($\mathrm{OR}_{\mathrm{STD}}$), and odds ratios (OR) for fixed effects in competitive Dark-eyed Junco logistic regression models of within-territory probability of use of

all behaviours within a 95% kernel density home range estimate. All models within Δ2AIC of top model were included in model averaging. Subscript values indicate the scale for each variable that was used in the model selection. A random effect for site was included in this model (not shown).

Variables	**β_{STD}**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR_{STD}**	**OR**
Intercept	-1.164	0.066	0.000	-1.293	-1.036	0.312	0.495
$Regeneration_5$	-0.120	0.034	0.000	-0.186	-0.054	0.887	0.929
$Variability_5$	0.595	0.034	0.000	0.528	0.662	1.814	2.294
$Depression_{10}$	0.023	0.027	0.402	-0.031	0.076	1.023	1.027
$Greenness_{11}$	-0.158	0.045	0.000	-0.246	-0.071	0.854	0.970
Permanent $polygonal_5$	-0.039	0.045	0.392	-0.146	0.018	0.962	0.922
Permanent $linear_5$	-0.088	0.041	0.031	-0.168	-0.008	0.916	0.877
Well $site_5$	-0.028	0.038	0.464	-0.126	0.023	0.973	0.957
Wide $linear_{11}$	0.056	0.021	0.008	0.015	0.098	1.058	1.318
$Variability_5$*Wide $linear_{11}$	-0.053	0.020	0.009	-0.093	-0.013	0.948	0.893
$Seismic_{10}$	-0.003	0.012	0.815	-0.073	0.028	0.997	1.043
$Seismic_{10}$*$Variability_5$	-0.003	0.012	0.781	-0.074	0.017	0.997	0.964

Table 29. All candidate models for Palm Warbler within-territory (3rd order) probability of use for all observed locations within a 95% probability kernel density home range for n = 82 territories located within 11, 25-hectare study sites in MacKay River Commercial Project in 2014 and 2015. Models were ranked using in Akaike's Information Criterion (ΔAIC) and evaluated for support relative to other models in the candidate set using Akaike weight of evidence (w_i). *K* is the number of parameters, and LL is the log-likelihood for each model. All candidate models included study site as a random effect.

Model	***K***	**LL**	**AIC**	**ΔAIC**	**w_i**
Habitat + Well Site + Seismic	**6**	**-9308.735**	**18629.471**	**0.000**	**0.708**
Habitat + Global	**7**	**-9308.624**	**18631.248**	**1.777**	**0.291**
Habitat + Seismic	5	-9319.316	18648.631	19.160	<0.001

Habitat + Well site	5	-9320.203	18650.406	20.935	<0.001
Habitat + Wide Linear + Seismic	6	-9319.221	18650.443	20.972	<0.001
Habitat + Well Site + Wide Linear	6	-9320.201	18652.402	22.931	<0.001
Habitat + Habitat only (null)	4	-9330.025	18668.049	38.578	<0.001
Habitat + Wide Linear	5	-9330.024	18670.048	40.577	<0.001

Table 30. Model averaged parameter estimates (β), standard errors (SE), *P*-value (Pr(>|z|)), 95% confidence intervals, standardized odds ratios (OR$_{STD}$), and odds ratios (OR) for fixed effects in competitive Palm Warbler logistic regression models of within-territory probability of use of all behaviours within a 95% kernel density home range estimate. All models within Δ2AIC of top model were included in model averaging. Subscript values indicate the scale for each variable that was used in the model selection. A random effect for site was included in this model (not shown).

Variables	**β_{STD}**	**SE**	**Pr(>|z|)**	**2.50%**	**97.50%**	**OR$_{STD}$**	**OR**
Intercept	-1.252	0.114	0.000	-1.476	-1.027	0.286	0.075
Regeneration$_6$	0.000	0.027	0.990	-0.052	0.052	1.000	1.001
Variability$_6$	0.583	0.032	0.000	0.521	0.645	1.791	2.389
Well site$_6$	-0.218	0.073	0.003	-0.361	-0.076	0.804	0.736
Seismic$_6$	-0.100	0.021	0.000	-0.141	-0.059	0.905	0.925
Wide linear$_6$	-0.003	0.011	0.813	-0.047	0.029	0.997	0.988