Climate change implications for distribution, phenology and conservation of Olive-sided Flycatchers (*Contopus cooperi*) and Western Wood-Pewees (*C. sordidulus*) in northwestern North America.

by

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ABSTRACT

Northwestern North America is predicted to experience some of the world's greatest human-caused climate change. Understanding the impacts of associated changes will be imperative to the conservation and management of northern-breeding birds. In particular, long distance migrants and aerial insectivores, such as the Olive-sided Flycatcher (*Contopus cooperi*, OSFL) and the Western Wood-Pewee (*C. sordidulus*, WEWP), may be impacted disproportionately, in interaction of climate change with additional ex situ population stressors, such as habitat loss and changes to insect populations. Climate-mediated effects on distribution and abundance of these species, both of which have experienced dramatic population declines over the past half century, might be mediated independently of habitat loss by identification of areas of potential climate macrorefugia.

To describe contributions of habitat elements on distribution and abundance of these species I generated boosted regression tree models, using data from point counts conducted between 1992 and 2014 at 1049 unique locations in the boreal and hemiboreal zones of northwestern North America. Bootstrap runs of models randomly selected abundances and absences from each location, stratified by number of observations, then built stagewise models from a suite of climate, landcover, topographical and disturbance covariates. I included offsets for unequal detectability of birds by observers in model development. Covariates describing vegetation and landcover were most important in describing abundance, followed by those for climate and topography. Influences of many covariates were non-linear and specific to species, but overall they described habitat that was forested, mid-elevation, topographically complex, and moderate in temperature, precipitation and length of summer season. Relative habitat associations revealed that open forest types, tundra, wet areas, riparian habitat, and old burns were positively associated with predicted abundances of both species.

To predict the influence of climate change on distribution, I generated a second set of models with seven climatic covariates from a baseline time period of 1981 – 2010, and two future time periods: 2041-2070 and 2071-2100, under comparatively high (RCP8.5) and mid-low (RCP4.5) greenhouse gas emission trajectories. I included a small number of baseline landcover and topographical spatial covariates in these models to constrain prediction outside of the plausible range. Mean outputs projected to grids revealed high predicted relative abundances in the northwestern terrestrial regions of the study area, especially in riparian areas and mid-high elevation forest.

Applying a spatiotemporal gradient approach, I found areas of low climatic suitability (negative bioclimatic velocity) in central and northwestern BC, and this velocity became more pronounced with time. Areas of positive bioclimatic velocity occurred in small, isolated regions in far western Alaska and southern/interior BC, although at a micro-refugium level details were specific to species. Predicted population size was initially high, and either remained the same, or declined between the baseline and future scenarios for OSFL, but increased for WEWP. Similarly, areas of predicted abundance (higher than the median abundance from the baseline period) declined between the baseline and future scenarios for OSFL (as indicated by more areas of loss than gain), but increased for WEWP, underscoring the importance of planning proactively for future species-specific needs. Most predicted gains in distribution were in the far northeastern and northwestern portions of the study area, calling into question the utility of these potential refugia given size and accessibility. Most predicted losses in abundance were inland regions in the northern part of the study area (central Alaska and Yukon).

Climate change may alter phenology of community members, affecting timing of availability and abundance of essential insect prey for breeding birds. Data to support this general prediction remain scant, especially for North American birds. Phenological investigation into the abundance and diversity of insect prey, as well as breeding events and success of breeding birds in southern Yukon, revealed patterns of potentially declining insect abundance with year between 2013 and 2017, advancing laying dates with year, but not advancing arrival dates, highly variable and possibly declining nesting success with year. An index of daily abundance of insect prey was compared with phenology of these two flycatchers, but evidence of phenological asynchrony using was limited, in part because insect abundance did not reveal obvious or predictable annual peaks. Nonetheless, my results suggest that climate change will influence distribution, abundance, and breeding biology of these flycatcher species.

PREFACE

This thesis is an original work by Tara Stehelin. The research project, of which this thesis is a part, received approval from the University of Alberta Animal Care Committee Study ID # AUP00001199 and 15 May, 2014, renewal each year for 2015, 2016, and 2017 for research involving animals.

Some of the research conducted for this thesis forms part of an international research collaboration, the Boreal Avian Modelling [BAM] project. The Steering Committee or lead researchers for this group include Fiona K. A. Schmiegelow and Erin M. Bayne (University of Alberta), Samantha J. Song (Environment and Climate Change Canada) and Steven G. Cumming at Université Laval and many other contributing scientists (please see https://borealbirds.ualberta.ca/ for a current and complete list). Data used in regional modeling was obtained from this collaborative group and some of the early data processing was conducted by other members of the research team. Diana Stralberg formatted landcover layers used in analyses and Peter Sólymos calculated species-specific offsets for each bird observation. All other data processing, analyses and summaries were conducted by myself.

Chapters 2, 3 and 4 are being prepared for journal submission with the following proposed coauthor lists and titles:

Stehelin, T. E., F. K. A. Schmiegleow, E. M. Bayne, S. G. Cumming, D. Stralberg, P. Sólymos, N. K. S. Barker, and S. J. Song. *In prep*. Relative distribution and abundance of the Olive-sided Flycatcher (*Contopus cooperi*) and Western Wood-Pewee (*C. Sordidulus*) in northwestern North America using climate, landcover, disturbance, and topographical variables.

Stehelin, T. E. and F. K. A. Schmiegleow. *In prep*. Comparing present and future distribution and abundance for conservation and management of Olive-sided Flycatcher (*Contopus cooperi*) and Western Wood-Pewee (*C. sordidulus*) in western North America; areas of gain and loss and potential for dispersal under two climate change scenarios.

Stehelin, T. E. and F. K. A. Schmiegleow. *In prep.* Investigation into phenology of two aerial insectivorous birds and their potential insect prey (abundance, emergence times and diversity) in southern Yukon.

Also in collaboration with the BAM project, I contributed to the following thesis-related submissions during my PhD program:

COSEWIC. 2018. COSEWIC assessment and status report on the Olive-sided Flycatcher Contopus cooperiin Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 52 pp.(http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1).

Stehelin, T. E., E. M. Bayne, P. Sólymos and P. C. Fontaine. 2020. Status of the Western Wood-Pewee (*Contopus sordidulus*) in Alberta. Government of Alberta, Alberta Environment and Parks. Alberta Wildlife Status Report # , Edmonton, AB, *In press.*

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I gratefully acknowledge the many participants and volunteers involved in collecting Breeding Bird Survey data and BAM project data. I also thank local enthusiasts and biologists who generously provided observations, data and ideas on where to access bird territories (e.g., P. Sinclair, C. Eckert), and permission to access private property. I also thank the Wildlife Conservation Society for observations and hints on where to find bird territories. I thank both Dave Mossop and Marty Mossop for information on locations of breeding birds, equipment help, and data contributions. I also thank the able and dedicated field and lab assistants that I had the pleasure of working with (J. Vigliotti, K. Tatsumi, B. March, and C. Bradley). I thank Kwanlin Dün First Nation and Ta'an Kwäch'än Council for permission and encouragement to conduct research on their settlement lands.

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CHAPTER I: INTRODUCTION

Forty percent of the world's bird species are declining, another 44% are stable, and only 7% are increasing (BirdLife International 2018). In North America, declines of about 30% have been reported between 1970 and 2015 in all guilds of birds (BirdLife International 2018). Continued loss and fragmentation of tropical forest used in the non-breeding season is an often-cited cause of declines for forest-dependent migrants that breed in North America (Robbins et al. 1989, Rappole and McDonald 1994). However, some declines are too sharp or specific to breeding site to be explained exclusively by overwintering habitat degradation (Askins 1995, Böehning-Gaese et al. 1995, Pimm and Askins 1995). For some species, these sharp declines may be influenced by changes to land use in the vast North American boreal region. Such changes include those resulting from large-scale agriculture, forestry, energy-sector exploration and development, and urbanization (Hobson et al. 2002, Schmiegelow and Monkkonen 2002, Schieck et al. 2014), especially those causing ecosystem alteration and fragmentation (Askins and Philbrick 1987, Askins 1995). Many of the pressures resulting in declines may be exacerbated in poorly understood ways by climate change (Brandt et al. 2013). The North American boreal forest is shaped by natural disturbance, with wildfire, flooding, and insect outbreaks creating geographically diverse and dynamic landscapes (Schmiegelow et al. 1997, Hobson and Schieck 1999, Brandt et al. 2013). Influences of climate change on boreal bird populations have been relatively unexplored given that approximately half of all birds found in North America utilize the boreal forest to breed, including over 300 species and over three billion individuals (Wells et al. 2018).

Better prediction of potential changes to ranges and communities under climate change can be supported by recently-popularized species distribution modelling (SDM) techniques (Elith and Leathwick 2009, Franklin 2013, Engler et al. 2017). These techniques associate georeferenced data about species (often presence alone or presence and absence) across broad geographical areas, with multiple environmental attributes, to generate spatial predictions of occurrence or habitat suitability in both sampled and unsampled locations or times with respect to temporal scenarios like climate change predictions (Peterson 2001, Ortega-Huerta and Peterson 2004, Guisan and Thuiller 2005, Austin 2007, Cumming et al. 2010, Elith et al. 2011, Franklin 2013, Guillera-Arroita et al. 2015). I apply these techniques in Chapters II and III. Such modelling exercises guide decision-making for conservation of threatened species, diversity, or habitats and contribute to designing reserves (Lindenmayer et al. 2008), especially in the absence of trend information from long-term datasets in many locations (Stralberg et al. 2018a).

Localized declines may be attributable to community change, such as alteration to phenology or timing of life cycle stages occurring in response to climate change, and these changes may occur differentially between members of communities (Walther et al. 2002, Parmesan and Yohe 2003, Visser et al. 2004, Both et al. 2006a, Saino et al. 2011). As a potential example, in Chapter IV I investigate phenological asynchrony between insect prey and two species of aerial insectivorous birds breeding in northern Canada.

The global climate is changing at an unprecedented rate, although not equally across geographical regions; regions of higher altitude and latitude have experienced the greatest temperature changes (Pulido and Berthold 2004, IPCC 2014) and have the greatest future predicted changes by far (IPCC 2014). Canada warmed by 1.7°C between 1948 and 2016, twice the global average of 0.8°C, and northern Canada warmed by 2.3°C over the same period, or three times the global average (Zhang et al. 2019). Precipitation changes have also been documented, with some areas experiencing increases of 40% or more, but others such as southcentral Canada experiencing decreases. Furthermore, precipitation increases are not predicted to compensate for increased evapotranspiration associated with temperature changes in many regions (Price et al. 2013). These changes to climate may alter biomes, causing forest to be replaced by shrubland or grassland in the southern boreal and tundra and alpine to essentially disappear in the north (Gilg et al. 2012, Rehfeldt et al. 2012, Walker et al. 2012).

Impacts of climate change on organisms vary, but can include physiological stress (Somero 2010), such as that expressed in tree mortality (Allen et al. 2010), altered predation patterns (Cox et al. 2013), increased or altered competition with non-native species, alterations to parasitism, phenological adjustments, including asynchrony between interacting species (Walther et al. 2002, Parmesan and Yohe 2003, Both et al. 2004, Móller et al. 2008), decreased food abundance resulting from declines in prey species (Epps et al. 2004), range contraction (e.g., Chen et al. 2011, Matthews et al. 2011), elevational shifts (Sekercioglu et al. 2008, Tingley et al. 2012, Saracco et al. 2019), and altered community structure (Araújo and Rahbek 2006, Khaliq et al. 2017, Bowler et al. 2018). For example, Ivory Gull (*Pagophila eburnea*) populations have declined by over 70%, from loss of required pack and drift ice in the Canadian Arctic (Spencer et al. 2016). Climate change impacts have been associated with 136 local population extinctions (Cahill et al. 2013) and at least 20 species extinctions (IUCN 2018). Nonetheless, interpretation of causal links between extirpation and climate change are often tenuous because of interactions with impacts from habitat loss (Stralberg et al. 2015b), or increased competition from invasive species (Bellard et al. 2012).

Changing community dynamics from range-shifts and phenological influences on food supply may be the most detrimental of the aforementioned potential impacts of climate change on organisms, although few studies have explored proximate causes for declines (Cahill et al.

2013). Evidence of earlier migration and spring reproductive events exists for many birds, amphibians, fungi, insects, and plants (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Crick 2004). Meta-analysis of 16 – 1000 years of data of over 1500 species in multiple kingdoms found that ranges have shifted on average 6.1 km northward per decade and that spring phenology is advancing 2.3 days per decade (Parmesan and Yohe 2003). Many species have colonized new regions, and ranges of some arctic species have contracted considerably (Parmesan and Yohe 2003, Hitch and Leberg 2007, Gilg et al. 2012).

Among birds, earlier arrival on breeding grounds in response to global warming has been documented for many species, although not universally (Miller-Rushing et al. 2008). These phenological and geographical changes may result in new communities with unknown properties (Gilg et al. 2012). Range shifts may allow species to maintain physiological performance within their range of thermal tolerance, but altered competition, predation and parasitism, and time lags in vegetation change, present additional challenges, and overall range size may be constrained by geographical barriers.

Adaptation to climate change via microevolution (i.e. changes in allele frequency) generally require longer periods of time than those available to avoid extirpation effectuated by the fast-pasted anthropogenic climate change of the last 100 years. The importance of climate on evolutionary change cannot be underestimated; throughout earth's history, climate changes and associated habitat changes are probably the two largest factors driving natural selection (Pulido and Berthold 2004). Warming events of both smaller magnitude and much slower progression of warming than modern global warming predictions, are associated with four out of five of the biggest extinction events throughout geological time (Mayhew et al. 2008, Blois et al. 2013).

Long-distance migrants may be especially vulnerable to climate change because they do not alter the timing of migration in response to temperature to the same degree as short-distance migrants (Both and Visser 2001, Lehikoinen et al. 2004, Miller-Rushing et al. 2008, Saino et al. 2011, Laaksonen and Lehikoinen 2013). They rely more heavily on endogenous rhythms than external cues to time migration (Butler 2003, Miller-Rushing et al. 2008). For example, short-distance migrants arrived 13 days earlier on average, whereas long-distance migrants arrived 4 days earlier in the USA between 1951 and 1993 (Butler 2003). In Finland, migration distance explained negative population trends in 94 land-bird species with species breeding in agricultural, urban, wetlands, and coniferous forests faring the worst (Laaksonen and Lehikoinen 2013). The degree of behavioral plasticity available to respond to climate change varies across species (Møller et al. 2008). Species that did not adjust migration timing to climate change revealed population declines in Europe between 1990 and 2000 (Móller et al. 2008). Lower phenotypic plasticity may occur in long-distance migratory species because greater mobility lessens a need for physiological tolerance of temperature extremes.

A lower propensity for phenological shift could be disadvantageous for long-distance migrants, because shifts are more likely to be asynchronous among interacting species in a community (Perrins 1991, Buse et al. 1999, Reed et al. 2013). For example, essential prey such as calorie-rich caterpillars may develop too early or too rapidly during warm springs to meet requirements for parents feeding chicks (Perrins 1991, Buse et al. 1999, Reed et al. 2013). Reed et al. (2013) found that Great Tit females that arrived earliest to the Netherlands enjoyed several fitness benefits resulting from better synchrony with caterpillar emergence, although population-wide effects on fitness were not evident such as total number of recruits.

Focal Species

New World Flycatchers are members of the suborder Tyranni, which comprise 20% or over 1000 species, of the largest order of birds, Passeriformes (Gill 2006). Members of Tyranni that breed in North America undertake long migrations, overwintering in Mexico, Central and South America. All aerial insectivores in Canada and the USA are experiencing declines, especially since 1980 in northeastern North America (Nebel et al. 2010, Spiller and Dettmers 2019). A species of special concern is the Olive-sided Flycatcher (OSFL), a sit-and-wait predator of medium to large flying insects that has decreased an alarming and largely unexplained 78% across North America and 70% in Canada between 1970 and 2015 (Rosenberg et al. 2016). Long-term trend estimates were -2.6%/yr (credible interval of -3.3%/yr , -1.9%/yr) between 1970 and 2015, based on Breeding Bird Survey (BBS) data (Environment and Climate Change Canada, ECCC 2016) or -3.3%/year (-4.5%/yr, -2.4%/yr) between 1955 and 2015 (Sauer et al. (2017). OSFL was designated as "threatened" in 2007 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), is listed as Near Threatened globally (IUCN red list classification in 2012 and again in 2016, BirdLife International 2015), and is listed as a Bird of Conservation Concern by the U.S. Fish and Wildlife Service. It was placed on the Partners in Flight (PIF) watch list as "Yellow", with a priority to reverse declines (Rosenberg et al. 2016). Rates of decline may have slowed in recent years; the short term trend was -1.9%/year (-3.0%/yr, -0.7%/yr) between 2005 and 2015 (ECCC 2016, Sauer et al. 2017).

The Western Wood-Pewee (WEWP) is another long-distance migrant and aerial insectivore that has suffered declines in recent decades. BBS data reveal a trend of -1.4%/yr (-2.0, -0.89%/yr) in North America between 1966 and 2015 (Sauer et al. 2017). Within Canada, trends revealed much steeper declines, of -2.6%/yr (-3.6, -1.7%/yr) between 1966 and 2015 (Sauer et al. 2017) [or -2.2%/year (-3.0, -1.4%/yr) between 1970 and 2016 (A. Smith, ECCC *unpubl. data* 2017) and short term -2.4%/year (-4.2, -0.7%/yr) between 2006 and 2016, and (A. Smith *unpubl. Data*, ECCC 2017). Although relatively common and widespread in western North America, population declines of WEWP are steep in some regions, such as AB, YT and Alaska (Stehelin et al. 2020). Overall, declines across Canada and the USA have resulted in a cumulative estimated loss of 39% of WEWP between 1966 and 2016 (A. Smith *unpubl. data* 2017), although some estimates have been as high as 47% decline overall (Rosenberg et al. 2016).

I selected these two congeneric species, OSFL and WEWP, for a comparative study because they are closely-related, lessening variation in contributors to declines arising from phylogeny. My results may provide insight into particular vulnerabilities of similar species and inform effective management of remaining populations.

Summary of Key Potential Drivers of Declines

Habitat Loss

Non-breeding and stopover habitat: Habitat quality or quantity on overwintering areas, and habitat degradation therein, may potentially limit population sizes of migratory birds (Sherry and Holmes 1996). Because both the OSFL and WEWP have been steadily declining in many North American regions since approximately 1970, degradation and loss of overwintering or migratory stopover habitat is often cited as a potential cause (Altman and Sallabanks 2012). Diamond (1991 *in* Altman and Sallabanks 2012) estimated that a 39% reduction of South American winter habitat occurred between 1980 and 2000 for OSFL. In addition, overwintering range is proportionately smaller than breeding range because of smaller land mass available in tropical regions of the Americas, especially for tyrant flycatchers (Tyrannidae), with mean overwintering area only 42% of that used for breeding (Mills 2006).

Overwintering habitat quality and resultant body condition can greatly influence reproductive success of migratory songbirds on breeding grounds (Marra et al. 1998, Norris et al. 2004), as well as influence factors during migration, such as sex-specific patterns of migration and refueling (Paxton and Moore 2015) as well as mortality. The global populations of both OSFL and WEWP depend entirely on forests of the Tropical Andes of northern and western South America, an area experiencing significant conversion to agricultural crops and ranches (Davidson et al. 2011). Conservation efforts in that area have focused mostly on species of critically-endangered endemics (Davidson et al. 2011), not on the relatively small proportion of migrants in tropical bird assemblages. Loss of tropical dry forest reached the highest level globally in South America between 2000 and 2016 (Hansen et al. 2013). Rates of deforestation may be particularly high in western Colombia (Armenteras et al. 2006, Etter et al. 2006, Hansen et al. 2013); an area recently identified using data from geolocating devices as important for overwintering OSFL that breed in Alaska (Hagelin et al. 2014). Although geolocator data are not yet available for WEWP, occasional records of WEWP also indicate that they overwinter in areas of the Andean foothills of Colombia and Ecuador (Global Forest Watch 2019). The Northern Andes may be one of the most species-rich forests, even more so than Amazonia, and yet has estimated forest losses of 90 – 95% (Henderson et al. 1991). Brazil also may be an important overwintering location. Although rates of forest loss declined in Brazil between 2004 and 2011 (Hansen et al. 2013), primary forest losses have increased again between 2016 and 2018 and only about 12% of Brazil’s Atlantic Forest remains, and much of that in a matrix of agricultural and urban land uses (Ribeiro et al. 2009, Coelho et al. 2016). It is not yet known if the timing of deforestation coincides with the greatest declines in abundance for each species; however, declines appear to be steady and long-term since 1970, a pattern often associated with non-breeding habitat loss.

In addition to loss of overwintering areas, declines may be affected by processes at stopover sites critical for successful migration to breeding areas. Some of these stopover areas are comparatively small, and the entire population may depend on a single food source available within a limited time frame (Baker et al. 2004). All OSFL individuals fitted with geolocating devices in Alaska used two very small regions in Central America and southern Mexico during both southward and northward migration, and one very small region in Guatemala was used by all individuals during spring migration (Hagelin et al. 2019). In addition, migration is inherently risky, exposing birds to direct mortality from collisions, inclement weather events, and various types of land use at multiple sites. Mortality rates can be as high as 15 times greater during migration, as found for the Black-throated Blue Warbler (*Dendroica caerulescens*, Sillett and Holmes 2002). Migration timing can also be influenced by extent of refueling possible at comparatively small areas used as staging areas (Baker et al. 2004, Eikenaar and Bairlein 2014).

Alteration of breeding habitat in northern North America: Although the boreal forest of North America is considered one of the largest ecologically intact areas remaining globally, and has relatively low human population density, significant forest alteration from land use and climate change threaten this intactness (Hobson et al. 2002, Brandt et al. 2013, Gauthier et al. 2015, Stralberg et al. 2018a). Of the approximately 552 million ha classified as boreal forest in Canada, areas along the southern periphery have experienced steep increases in land use over the last century from forestry (especially between 1975 and 2005), increasing rates of energy sector development (mines, well sites), hydroelectricity (Brandt et al. 2013), agriculture, as well as changes to successional regimes from decades of fire suppression (Soja et al. 2007). Although forestry practices vary across the region and harvest rates have been relatively stable in Canada since the 1980s, approximately 11 million ha of boreal forest is harvested annually (National Forest Database 2015). Over three billion birds utilize the boreal forest of North America (Wells et al. 2018), but only 8.1% of the boreal forest in Canada is protected (Andrew et al. 2014). Targets of 17% conservation of terrestrial ecosystems in Canada have been established to meet commitments under the Convention on Biological Diversity, with much higher targets suggested for the North American boreal forest in recognition of significant potential to house future biodiversity (Langham et al. 2015), support ecosystem services, and for carbon sequestration (Carlson et al. 2009, Badiou et al. 2011, Stralberg et al. 2018a).

The boreal forest of North America has experienced dramatic increases in temperature since about mid-century (Zhang et al. 2019), with correlated changes to disturbance dynamics, such as increased fire intensity (Kasischke and Turetsky 2006, Soja et al. 2007), and changes to hydrologic systems, including disparate drying of wetlands and permafrost thaw, further impacting greenhouse gas cycles (Smith et al. 2005, Sannel and Kuhry 2011, Brandt et al. 2013, Andresen and Lougheed 2015). The sometimes long-lived and slowly reproducing boreal species, such as conifers, are particularly vulnerable to rapid paces of climate change (Andrew et al. 2014). These changes will likely impact the potential for the boreal region to provide habitat for forest-dependent species (Matthews et al. 2011).

Although birds are negatively influenced by some types of anthropogenic disturbance, they are positively influenced by others (Hutto 1995). For example, species distribution models for the Canadian boreal by Haché et al. (2014) demonstrated that linear disturbance negatively impacted predicted abundance of OSFL, whereas WEWP may be more abundant near linear disturbance, depending on pre-existing surrounding habitat (ABMI and BAM 2018). OSFL were predicted to be less abundant in agricultural and developed habitats than various types of open forest, shrub, and wetland habitat at the national scale (ABMI and BAM 2018). Although both species are found in forest disturbed by forest harvest, natural disturbances such as fire are associated with higher abundances in WEWP (Stehelin et al. 2020) and with higher breeding success in OSFL (Robertson and Hutto 2007).

Intensification of agricultural practices is a conservation concern on non-breeding and breeding areas, especially widespread use of pesticides, year-round tillage, increased use of fertilizers, and general increased demands on soil and arable land. As part of agriculture intensification, pesticide application has increased in southern USA, Central America and South America, possibly with direct physiological effects on birds (Goldstein et al. 1999), and removal of essential overwintering food (Nebel et al 2010).

In Alberta, land use from agriculture had a negative influence on predicted abundance of OSFL (-0.8%), with an especially pronounced negative influence on predicted abundance of WEWP of -34% in the prairie (south) region and -2.7% in the forested (north) region (ABMI and BAM 2018). This represents a large area with over 50% of the land in the prairie region classified as agricultural. Both OSFL and WEWP are associated with wet areas and riparian habitat (Sólymos et al. 2015; 2019, BAM and ABMI 2018, Stehelin et al. 2020), habitats almost invariably altered in agricultural areas.

Dependence of post-fire could have contributed to declining abundances of these species, because 97% of fires over 200 ha in size were suppressed in Canada between 1959 and 1997 (Stocks et al. 2002). Both species were found almost exclusively in post-fire sites in Saskatchewan compared to both unburned and burned and salvage logged forests (Morissette et al. 2002). Post-fire habitats may provide a complex matrix of burned or partially-burned material, allowing sit-and-wait predation tactics, as well as positivity influencing abundances of insects adapted to recolonize following fire (McCullough et al. 1998, Maser and Schowalter 2013b). Both the OSFL and WEWP, and many other species, increase in abundance following fire (Hutto 1995, Hobson and Schieck 1999, Smucker et al. 2005, Kirkpatrick et al. 2006, Schieck and Song 2006, Cahall and Hayes 2009, Gyug 2013). Despite an abundance of OSFL in post-fire regions (Altman and Sallabanks 2012, Smucker et al. 2005), nest loss was much higher (71%) in burned than in unburned areas (20%) in northwestern California (Meehan and George 2003). However, samples were collected only one-year post-fire (Meehan and George 2003). In addition, both species were found in many other habitats that were not classified as post burn (COSEWIC 2018, Stehelin et al. 2020). Abundance patterns following fire depend heavily on time since fire (Hobson and Schieck 1999), age of stand at the time of fire, fire severity (Smucker et al. 2005, Haney et al. 2008, Nappi and Drapeau 2009) and pre-existing forest edge (Meehan and George 2003). Fires are predicted to increase in area and intensity with climate change over the 21st century in North America; in particular, compared to global increases (de Groot et al. 2013, Flannigan et al. 2013), with largely unknown results of interactions with forestry practices.

Abundance of some aerial insectivores birds increases following extensive tree kill by insects, such as Spruce Budworm (*Choristoneura fumiferana*, Bemis and Rising 1999) and Mountain Pine Beetle (*Dendroctonus ponderosae*, Weber 2015a). However, insect outbreaks are increasing in magnitude and extent in the boreal forest with relatively minor changes to climate (Price et al. 2013), causing defoliation and novel disturbance levels, with unknown long-term impacts on insectivorous birds.

Impacts of forestry on abundance of OSFL and WEWP remain equivocal (ABMI and BAM 2018), and like impacts of fire, probably depend heavily on characteristics of remaining forest. A review by Hutto (1995) revealed that 60% of studies detected OSFL in early successional clearcuts (less than 10 years), 40% in mid-successional stages following clearcut (10 – 40 years old), whereas in post-burn areas, 74% were detected in early successional and 40% in mid successional burned forest, suggesting that both natural and anthropogenic disturbances are associated with higher densities of this species than other forest types. Selectively-logged forest attracted a higher density of males, but breeding success was reduced almost 50% compared to a recently burned area (Robertson and Hutto 2007), providing some evidence that this harvest method may have created an ecological trap. The correct cues for habitat such as trees for nesting and flowering herbaceous plants (McGrath et al. 2009, Hagelin et al. 2015) may be present, attracting males in search of territories in the first place, but predator abundance may be much higher than in naturally-disturbed habitat, causing high nestling mortality (Robertson and Hutto 2007). In addition, standing dead and old trees are under-represented in a selectively-logged forest compared to burned areas, potentially reducing the abundance of foraging trees.

Although ecological traps from selective logging or pesticide use may not explain potential declines in the northern boreal, removal of standing dead trees for fuel wood following a fire or insect kill (Schwab et al. 2006), is common in parts of North America and may create artificially attractive breeding habitat (Schmiegelow et al. 2006, Cahall and Hayes 2009). Salvage logging removes trees that may be essential habitat components for foraging and roosting for some species (Schmiegelow et al. 2006, Koivula and Schmiegelow 2007, Cahall and Hayes 2009).

Oil and gas and mining exploration, extraction and development have increased rapidly in magnitude and geographic reach in boreal Canada, especially between 1990 and 2009 (Brandt et al. 2013). Impacts on birds may include habitat loss, introduction of potentially invasive species, changes to abundance of brood parasites (Ludlow et al. 2015), chronic noise, changes to vegetation succession, and direct poisoning from by-products contaminating water bodies or other habitats (Bayne et al. 2005, Machtans 2006, Venier et al. 2014). Approximately 25,000 nests (median, range of 11,840 – 60,380) of 72 species of breeding birds were estimated to be lost annually to energy sector development in the Western Canadian Sedimentary Basin of the Canadian prairie provinces (Van Wilgenburg et al. 2013). Land use footprint classified as energy sector had a positive influence on relative abundance of WEWP (1.9%) in forested region of Alberta, although the influence of this sector was negative in the prairie region (BAM and ABMI 2018). The influence of this sector was negative on OSFL (-0.2%) in the forested region, with no data for the prairie region (BAM and ABMI 2018). Although the overall footprint for this sector of land use was historically relatively small (approximately 2%), it represents one of the fastest growing land use types in Alberta (Schieck et al. 2014).

Insect declines and pesticide use: It is estimated that 41% of insect species are declining globally, with 51% declining in North America (Sánchez-Bayo and Wyckhuys 2019). Of particular relevance for insectivores is the associated loss of 2.5% of global insect biomass per year (Sánchez-Bayo and Wyckhuys 2019). Bees and moths are groups that are particularly noted as declining in North America (Grixti et al. 2009, Potts et al. 2010, Sánchez-Bayo and Wyckhuys 2019). On the global scale, agricultural intensification may be a main driver of these declines, followed by a multitude and potentially synergistic mix of other factors including habitat loss, pesticide and other toxin application, unfavorable interspecific interactions, such as decreasing diversity in host or other plants, invasive species, and climate change (Sánchez-Bayo and Wyckhuys 2019).

As a sit-and-wait predator, OSFL may feed preferentially on large insects, such as beetles (Otvos and Stark 1985), flying Hymenoptera (bees and wasps), sallying from open perches to capture large flying insects (Altman and Sallabanks 2012). Hymenoptera have suffered dramatic declines, such as the 59% loss of honey bee (*Apis mellifera*) colonies in the USA between 1947 and 2005, from Colony Collapse Disorder (CCD), which is characterized by a sudden disappearance of most adult bees in a colony (Potts et al. 2010). In addition to agricultural intensification and changing pesticide use and climate change (Mullin et al. 2010), bee declines are driven by decreasing plant resources for bees and the spread of particularly virulent invasive parasites, such as the mite *Varroa destructor*, and the microsporidian parasite *Nosema bombi* (Alaux et al. 2010, Potts et al. 2010, Cameron et al. 2011, Gill et al. 2012).

Neonicotinoids were authorized for agricultural use in USA in 1994 (Goulson 2013, 2014). Exposure to neonicotinoid pesticides (e.g., Imidacloprid) may make bees more susceptible to pathogenic infection through a synergistic interaction: in the presence of the insecticide, bees cannot make an essential enzyme used in the sterilization of colony food (Alaux et al. 2010). In addition to being particularly toxic to bees (Gill et al. 2012), these recently-popularized insecticides influence non-target insects because they are water soluble and toxic at low concentrations (Main et al. 2014, Anderson et al. 2015). Use of neonicotinoids has increased rapidly in Canada to approximately 80% of the seed treatment market for crops such as wheat, soy, sugar beet and potatoes, and corn, although Health Canada (2018) has proposed a phase out of three types of neonicotinoids. The high environmental persistence of neonicotinoids in soil and wetlands suggests that aquatic insects may be impacted particularly (Main et al. 2014, Anderson et al. 2015). Many insects eaten by aerial insectivorous birds have aquatic larval stages. Because declines in aerial insectivores in North America commenced earlier than the widespread use of neonicotinoids, initial declines cannot be attributed to these pesticides, but they are likely contributing to continuing declines. Insectivorous birds and their prey are also influenced by organochlorine pesticides, even DDT (dichlorodiphenyltricholorethane), despite widespread bans in the 1970s in North America. Exposure to DDT was reported as recently as the 1990's, due to high environmental persistence (Klemens et al. 2000, Mora 2008, Nocera et al. 2012). In parts of Central and South America, "legacy" pesticides (such as DDT and other organochlorines) and newer classes of pesticides (neonicotinoids) may be applied simultaneously, with potentially cumulative effects. Insecticides such as neonicotinoids are likely impacting insectivorous bird populations in North America as they are in Europe (Goulson 2013, Goulson 2014, Hallmann et al. 2017).

Climate Change: Both focal species may be particularly vulnerable to impacts of climate change because of their long migrations, high latitude and terrestrial breeding range (exposing them to rapidly changing climate envelopes), and association with both early and late seral stages (ABMI and BAM 2018a,b). Changes to forest disturbance dynamics and hydrologic cycles from climate change may also influence their obligate insect food supply.

Stralberg et al. (2015b) predicted a decline in abundance of 38% of 80 species of boreal forest-breeding birds by 2040, with climate clearly implicated as a contributing factor in 58% of these declines, despite potentially disparate effects of land use and topography. Results of these comprehensive, boreal-wide modelling efforts suggested that OSFL may essentially disappear from the southern boreal in Canada, and increase (from zero) in some regions of the southern arctic by 2071, with small “refugia” or strong-holds of abundance remaining in YT, a small portion of northern BC and northern Quebec. Similarly, refugia were predicted for the WEWP in northern Quebec and central NWT (Stralberg et al. 2015b). With time lags from vegetation considered, the potential for refugia was contracted considerably for some species, such as WEWP (Stralberg et al. 2015a).

Despite significant recent efforts of modelling at broad scales (Haché et al. 2014, Stralberg et al. 2015a,b, Sólymos et al. 2017, ABMI and BAM 2018, Stralberg et al. 2018a), uncertainty about species responses to climate change and potential land use change remains greatest in northern regions of North America. Long-term time series of abundance data are sparse, and limited historic data exist to benchmark phenology of songbirds breeding in northern Canada prior to contemporary climate change. No studies of potential phenological adjustment to climate change or abundance of insects exist for either focal species prior to initiation of this work, except concurrent studies in Alaska on OSFL (Hagelin et al. 2014, 2019).

Overall Objectives and Chapter Breakdown

The main objective of this thesis is to advance understanding of potential drivers of decline for OSFL and WEWP through a multi-scale approach that addresses climate and habitat-related factors across northwestern North America, as well as local factors in southwestern Yukon. Most studies to date have examined drivers for decline at one scale (e.g., nationally - Haché et al. 2014, Sólymos et al. 2017, or regionally (Alaska, Hagelin et al. 2014, 2019). This is the first detailed study of the federally-listed species, OSFL (Schedule 1 of the Canadian Species At Risk Act, where it is listed as Threatened since 2007), considering multiple scales and climate scenarios, and the first regional or local study in northwestern North America of the vulnerable species, WEWP (not assessed by the Committee on the Status of Endangered Wildlife in Canada, COSEWIC; listed as species at risk under Alberta's Wildlife Act, 2015 and *sensitive* under the General Status of Alberta Wild Species 2010).

In Chapter II, I examine relative influences of various climate, landcover, topographical and disturbance variables on current abundance and distribution of each species across northwestern North America. I also examine historical interannual variability of abundance for regionally-specific trends and patterns between 1994 and 2014.

Chapter III is focused on predicting changes to distribution and abundance across northwestern North America from climate change, including uncertainty and bioclimatic velocity, within a baseline time period and two future time periods, and two greenhouse gas emission scenarios.

In Chapter IV, I provide baseline information about proximate causes of decline through phenological schedules, breeding success, and potential asynchrony between energetic demands of breeding birds and peaks of insect abundance occurring in local populations of southern Yukon.

In Chapter V, I synthesize knowledge gained through this work about potential contributors to declines of the two focal species and make suggestions regarding conservation potential for remaining populations.

CHAPTER II: DESCRIBING RELATIVE DISTRIBUTION AND ABUNDANCE OF OLIVE-SIDED FLYCATCHER (*CONTOPUS COOPERI*) AND WESTERN WOOD-PEWEE (*C. SORDIDULUS*) IN NORTHWESTERN NORTH AMERICA USING CLIMATE, LANDCOVER, DISTURBANCE, AND TOPOGRAPHICAL VARIABLES.

2.1 SUMMARY

Long-term data reveal regionally-specific declines in OSFL and WEWP, that may be particular pronounced in some regions of the northwest, from multiple factors including land use change, climate change, and insect abundance changes. Description of factors contributing to abundance is an important first step in management of declining species. I describe the distribution and abundances of the OSFL and WEWP, two aerial insectivorous birds in northwestern North America. Models were developed from 15,637 observations from point count surveys conducted between 1990 and 2014 where at least one individual of either species was detected. Abundances were selected by stratified number of observations at each site and an approximately equal number of absences were added. Stagewise models were then built using a suite of 37 climate, landcover, topographical and disturbance covariates combining both spatial (4-km scale) and spatiotemporal influences. I also included species-specific offsets for detectability. Model fit was generally quite high and error from sampling was low. Covariates describing landcover were most important in describing abundance, followed by those for climate and topography. Influences of individual covariates were mostly non-linear and specific to species, but overall they described mid-elevation habitats that were forested and complex topographically, characterized by intermediate temperature, high precipitation, and relatively long summer seasons. Habitat associations revealed relatively higher predicted abundances in open forest types, tundra, wet areas and riparian habitat, and old burns. Because results of other

projects reported declining trends for these species, I generated generalized additive models (GAMs) to examine historical patterns of interannual variability in abundance for my study area and time period (1992 – 2014). These analyses revealed declining but non-linear trends in some regions.

2.2 INTRODUCTION

Populations of aerial insectivorous birds in North America are declining, especially in species with long migration routes (Böhning-Gaese et al. 1993, Askins 1995, Nebel et al. 2010), probably in part from changes to distant overwintering areas. Climate change may also play a role in these declines, with unknown contributions relative to other drivers such as land use change and declines in abundance of their insect prey (Crick 2004). A first step toward better understanding characteristics and possible drivers of these declines is building environmental and climatic predictors to model distribution and abundance for affected species.

Species Distribution Modelling (SDM) includes a suite of modelling techniques to explain or predict distribution and abundance of organisms across a landscape (Elith and Leathwick 2009, Franklin 2013, Engler et al. 2017). SDMs correlate the presence or absence of a species at each location with environmental covariates (reviews: Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009, Peterson and Soberón 2012, Franklin 2013). This approach is also referred to as “ecological niche modelling”; a term thought to encourage more realism in model inputs and outputs (Peterson and Soberón 2012). The earliest known example of SDM dates back to 1924, from a study that examined the spread of an invasive cactus in Australia, with expansions to include computer-based modelling in the 1970s (Guisan and Thuiller 2005). Facilitated by advancements in computer and statistical sciences, the use of these models has increased exponentially since the 1990s (Guisan and Thuiller 2005, Peterson and Soberón 2012). Such efforts have since become important tools in biogeography, species conservation and management, land management, and evaluation of climate change impacts (Franklin 2013, Guillera-Arroita et al. 2015, Engler et al. 2017, Urbani et al. 2017). In addition, they contribute to multidisciplinary efforts, such as predicting regions suitable for agriculture under future climate change scenarios in calculations involving human carrying capacity (Beck 2013). However, the conservation or management objectives of modelling exercises have sometimes been eclipsed by the lure of novel and complicated techniques (Guisan and Thuiller 2005, Peterson and Soberón 2012), or suffered from a mismatch between data type and desired objectives (Guillera-Arroita et al. 2015).

Increasingly advanced SDM techniques have recently been facilitated by publicly-available geographic information system (GIS) data products and computer algorithms able to handle large datasets (Guisan and Zimmermann 2000, Franklin 2013). As SDM techniques grow in number and are used more frequently, an increasing number of authors are questioning conceptual frameworks used to establish and interpret results (Jiménez-Valverde et al. 2008, Peterson and Soberón 2012, Franklin 2013, Guillera-Arroita et al. 2015, Westwood 2016). Data and model design must meet modelling objectives appropriately (Guillera-Arroita et al. 2015). For example, presence-only datasets may generate predictions of potential niche but not necessarily realized niche for a species (see below).

There may be limits to dispersal that prevent some species from realizing predicted distributions from models; from intrinsic limits to mobility or geographical barriers (Peterson and Soberón 2012). Factors limiting species distributions are commonly abiotic but also include biotic effects such as intra and inter-specific interactions or anthropogenic effects on the environment (Elith and Leathwick 2009, Methorst et al. 2017). Complex interactions can be partially accounted for using absence data from seemingly-suitable habitat (Jiménez-Valverde et al. 2008), however, absence data can be difficult to obtain, especially at the large geographic scale of many SDM exercises.

SDM techniques alone are insufficient for extrapolation of future biogeoclimatic change, because they cannot predict distribution in novel environments (Peterson and Soberón 2012). However, applying models iteratively, with process data included (e.g., those reflecting ecophysiology, community dynamics, limits to dispersal, trophic dependency in "mechanistic modelling"; Trainor and Schmitz 2014) and augmenting results with targeted sampling, have the potential to strengthen predictive power considerably (Franklin 2013).

Application of SDM are numerous enough of late that four 'domains' of use for conservation were suggested by Guillera-Arroita et al. (2015): 1) management of invasive species, 2) management of threatened species, 3) spatial planning such as prioritization of areas for conservation, protected area networks, or quantification of biodiversity hotspots, and 4) ecological and biogeographical inference, including projections of distribution, abundance or species richness under future climate change scenarios (Chamberlain et al. 2013, Serra-Diaz et al. 2014, Distler et al. 2015, Engler et al. 2017). I focus mainly on the latter two applications in this thesis.

Data and model limitations

Correlative SDMs typically use one of three data types. *Presence* data, sometimes called *presence-background* data, includes only presence records of species and environmental variables relevant to modelling objectives (Guillera-Arroita et al. 2015). Large sample sizes and sampling considerations are particularly important to ensure sufficient signal to noise ratio for these data (Phillips et al. 2006, Merow et al. 2014). In addition to records of presence, *presence-*

absence data also includes locations where none of the species of interest were recorded (or absences), and *occupancy-detection* data, which includes, in addition to presence-absence data, information about the observation process, such as probability of detection given the environment, time to detection or from repeat visits (Guillera-Arroita et al. 2015). If detectability is constant across environments or if the relative detectability is known for a species in a particular environment, imperfect detection can be accounted for (using offsets) to achieve a relatively unbiased estimation of occupancy (Sólymos et al. 2013). Further information still can be obtained from datasets that include a metric of abundance in addition to presence. These could be termed *abundance-absence-detection* data, and this is the type of data I used for this study.

SDM data are often collected in a spatially biased manner, i.e. "sampling bias" (Peterson and Soberón 2012). Sampling is often limited in some areas, more complete in others, or sampling bias may also be inherent in a study design with narrow objectives. For example, more samples may be obtained based on accessibility, such as along or near roads, trails, or towns (Phillips et al. 2006, Merow et al. 2014). Sampling bias can change model results and interpretation considerably for some species, specific geographical space, and time periods (Stralberg et al. 2015b). Environmental features may be incorrectly identified as 'preferred' habitat, but instead are sampled at greater frequency based on accessibility. Comparisons between data collected near these features vs. away, can attempt to quantify some sampling bias (e.g., roadside bias; Haché et al. 2014). However, some habitat types may be unsampled altogether (Merow et al. 2014). Offsets, based on habitat type or likelihood of detection can help ameliorate, but never completely remove, sampling bias. However, uncertainty from sampling error can be quantified using bootstrapping methods.

Scale is a common theme in SDM, as grain/resolution and extent of scale both determine the efficacy and purpose of the analysis (Guisan and Thuiller 2005, Austin 2007, Cumming et al. 2014). For example at broad scales, such as global or continental in extent, climate may best explain distribution of organisms, but at narrower scales, such as hundreds of kilometers, topography, soil, water or nutrients composition may become more important (Elith and Leathwick 2009, Cumming et al. 2014). Too coarse resolution of climate data can miss important heterogeneity in microclimates, which could be especially important in topographically and climatically diverse regions of western North America (Wang et al. 2012, Wang et al. 2016). However, resolution may differ between species data and environmental predictors, a problem often arising from data availability (Guisan and Thuiller 2005, Austin 2007). Data choices by the researcher may impose scale unintentionally; again, data and variable selection in light of modelling objectives are important. In addition to careful variable selection, hiercharchial modelling techniques with nested structuring may separate variables based on scale, possibly ameliorating issues with disparate scales (see Elith and Leathwick 2009).

Species and environmental variates included in models are limited to the time period or space that they were collected, meaning that results only represent a ‘snapshot’ in time and space. An assumption is required that species are in equilibrium with their environment, which may not always be appropriate. Equilibrium in SDM occurs if a species occurs in all areas climatically suitable and is absent from those areas that are not (Araújo and Pearson 2005, Araújo and Rahbek 2006). Disequilibrium between climate and other environmental variables may occur with invasive species, or species with ranges predicted to alter because of climate change, or when land use changes are not incorporated into modelling procedures (Guisan and Thuiller 2005), as well as when interspecific interactions relating to density dependence are present, such as in predator-prey systems (Trainor and Schmitz 2014). Plants and birds were closer to equilibrium than reptiles or amphibians (Araújo and Pearson 2005, Munguia et al. 2012), suggesting that they may better track climate change through dispersal compared to other taxa. To address disequilibrium, error from extrapolation can be quantified and compared between spaces and times (Elith and Leathwick 2009), and SDM results can be linked to variables that describe change, such as predicted land use change (e.g., ABMI and BAM 2018a,b) or predictive vegetation layers (Rehfeldt et al. 2012).

Another important consideration in SDM is a relatively common problem of *spatial autocorrelation* of data, i.e. values that are close to each other exhibit more similarities than those further apart (Dormann et al. 2007). Results of these models may reveal strong aggregation of residuals in geographic space, which violates an important assumption of many statistical analyses: that residuals are independent (Guisan and Thuiller 2005, Dormann et al. 2007). This can lead to erroneous conclusions in hypothesis testing, such as a higher Type I error rate, e.g.: overestimating correlation between range size and climate variables (e.g., Boucher-Lalonde and Currie 2016). Aggregations may result from biotic processes such as impediments to dispersal, unforeseen biotic interactions (intra or interspecific), or from a relevant environmental predictor that is in itself spatially patterned and missing from the model (Guisan and Thuiller 2005). Possible solutions to spatial autocorrelation include resampling plots at greater spatial uniformity, addition of a missing key predictor, combining population dynamic or dispersal information with SDM to account for biotic processes (Guisan and Thuiller 2005), and using statistical techniques that can correct for some of the problems arising from spatial autocorrelation, such as generalised least squares (GLS), generalised linear mixed models (GLMM), or generalised estimation equations (GEE, Dormann et al. 2007). These techniques, and many others that are similar, fit a covariance matrix using the data and make no *a priori* assumption of normality (Dormann et al. 2007). Detection of spatial autocorrelation and quantification can be achieved through calculation of the Moran's *I* statistic, calculated using a matrix of distance weights (Dormann et al. 2007, Elith and Leathwick 2009). In addition, some constraint can be achieved through bootstrap sampling and accounting for sampling effort, such as stratified sampling (depending on which process is causing the spatial autocorrelation).

Selection of the suite of predictor variables used in models can also be a significant source of uncertainty in prediction (Romero et al. 2015), especially if relationships between variables change in the future. Again, careful variable selection can reduce this. Robustness of SDM can be quantified with the proportion of variance explained by the predictors, however, too many or redundant predictors may produce an overfitted model that describes random error or noise instead of underlying biological relationships (Guisan and Thuiller 2005, Peterson and Soberón 2012), leading to erroneous conclusions. For example, overfitting can overestimate niche differentiation among species (Peterson and Soberón 2012) and can exacerbate problems associated with spatial autocorrelation (Merow et al. 2014).

Various techniques are used to *constrain model complexity*, such as ensemble modelling, which involves combining multiple simple models into a single one using decision trees (bagging, random forests or boosted regression trees, e.g., Friedman 2001, Prasad et al. 2006, De'ath 2007, Elith et al. 2008, Merow et al. 2014). Classification and regression tree techniques are often used in exploration, description and prediction, and have the advantages of being able to handle various types of data (such as categorical, interval, and multivariate data), and are resilient to transformations of predictors and to missing values (De'ath 2007). However, results depend on criteria selected and straight-line functions may not be modeled well (Elith et al.

2008). Nonetheless, boosted regression trees have two advantages over traditional classification and regression trees: improved prediction and greater interpretability (De'ath 2007, Elith et al. 2008).

Despite limitations and with careful considerations of data type, predictor selection, and modelling objectives, SDMs can address complex, broad-scale and invaluable ecological questions that can inform a range of objectives in conservation understanding, planning, and decision making. Explanation of quantitative ecological processes, but also increasingly, accurate prediction are important, and timely, goals of SDM at broad and regional scales (Elith and Leathwick 2009). Nonetheless, traditional hypothesis testing using model development and selection have fallen short of achieving both simultaneously. Model selection techniques using information theory address relative model selection (Burnham and Anderson 2004), but fall short of ensuring accurate prediction and may not address explanation, depending on the models selected in the suite (Romero et al. 2015). Prediction has been improved greatly through learning algorithms and intense computation (De'ath 2007) using "machine learning" techniques (Elith et al. 2008) that take into account potential interactions between predictors, thus improving accuracy. The approach of machine learning differs from traditional statistics in that it uses algorithms to "learn" the strongest relationships between response and predictors, rather than starting with a candidate data model and estimating parameters from it (Elith et al. 2008). Boosting improves accuracy by repetition; for example, many vague rules are easier to find than a single accurate prediction rule. Boosting is different from other ensemble/averaging techniques (bagging, stacking and model averaging) because it is a forward, stagewise approach that retains the original model with each iteration. Boosted regression trees (BRTs) employ a binary approach of classification for each datum, weighting each response based on whether it was correctly or incorrectly classified. Incorrectly classified responses receive a higher weighting, thereby increasing the probability of them being correctly classified (De'ath 2007). Nonlinear responses and interactions are automatically accounted for in the large structuring of binary responses (Elith et al. 2008). The number of splits or size of the individual regression trees and associated prediction error can be used to assess interactions between predictors; for example, trees with two splits include only first-order interactions, those with three splits include up to second-order interactions (Elith et al. 2008).

Boosted regression trees have become more common in the ecological literature of late, and are useful when numerous individual trees are beneficial, many predictors are relevant and prediction is a goal; such as to unknown data locations (interpolation) or to grids (Elith and Leathwick 2009). BRTs have been used to predict various processes such as: the success of potentially invasive species (Carboni et al. 2016), seed desiccation responses (Wyse and Dickie 2018), avian diversity with various agricultural (vineyard) landscape characteristics (Steel et al. 2017), multispecies responses to climate change (Langham et al. 2015, Stralberg et al. 2015a, Stralberg et al. 2015b), projections of environmental suitability under various climate and land use scenarios for bat fauna in Mexico (Zamora-Gutierrez et al. 2018). BRTs, also called stochastic gradient boosting (Friedman 2002, De'ath 2007) have particular strength in specificity (the model's ability to predict a true absence of a species), as well as the proportion for correctly classified units, i.e. "accuracy" (Fielding and Bell 1997, Moisen et al. 2006). The Receiver Operating Characteristics (ROC; the ratio of true positive rates to false positive rates) and the area under this curve (AUCs) (Fielding and Bell 1997) were high (close to 1) as well for most species examined, indicating models perform well for correlation, explanation, and prediction (Moisen et al. 2006).

Regional modelling

Much SDM at the continental scale describes first order habitat selection based on primarily climate variables, whereas second order habitat selection may be influenced by vegetation predictors as well, such as in the selection of home-ranges for foraging and nesting requirements (Johnson 1980, Cumming et al. 2014). Recently improved spatial extent and resolution of species data and precision of geographical variables, combined with recent modelling techniques, have allowed relative contributions of predictors to be quantified at the continental scale (Cumming et al. 2014). However, responses of species to environmental predictors is unlikely to be linear, simple, or even equivalent across broad geographical areas (Merow et al. 2014), and not always in equilibrium across regional boundaries. A next step is to focus efforts on regional variation in habitat and localized climate associations for species of interest (White et al. 2011), to inform local conservation and management goals (Austin 2007). This is especially important because the greatest temperature changes from climate change between 2006 and 2015 globally occurred in the northern hemisphere, with northern North America warming more than double the global average (Allen et al. 2018). Predictions from all climate models agree that the boreal zone will increase in temperature for decades to come (Price et al. 2013). Vegetation communities typical of this ecozone with shift poleward (Alo and Wang 2008), and future community dissimilarity is predicted to be disproportionately high in projections for the boreal zone (and west, in particular) compared to the rest of North America (Langham et al. 2015). Regionally-specific habitat preferences for OSFL (e.g., Westwood 2016, COSEWIC 2018), also suggest that regional habitat and climate modelling is required for identifying essential habitat to inform the conservation and management of these species.

Northwestern North America has more limited bird abundance data compared to the eastern boreal regions (Barker et al. 2015), making predictive SDM techniques one of the only available methods to project and interpolate distribution and abundance under current conditions, and under conditions of predicted climate change. Results of many regional-based studies were compiled and adjusted for disparate sampling methodology to amass a broad-scale spatially-explicit avian data set by the Boreal Avian Modelling (BAM) research team (Barker et al. 2015), allowing greater ability to distinguish regional habitat preferences and relative contributions of climate versus land use factors (Cumming et al. 2010).

Broad-scale patterns can be used to generate hypotheses of processes at regional scales (e.g., White et al. 2011); for example, climate variability, such as within season temperature variability, which had largely negative effects on long-distance migrants, could influence insect abundance negatively (Cumming et al. 2014). Land cover and vegetation measures should be included in modelling exercises in addition to climate variables, because of a potential disequilibrium, in particular from land use changes and climate change (Cumming et al. 2014). Much of the disturbance to boreal forest in northwestern North America can be attributed to natural agents (fire and insect outbreak), more so than forest harvest (White et al. 2017) or broad-scale land use (Brandt et al. 2013), allowing for climate variables to be examined with fewer confounding effects from land use.

National-scale SDMs have been generated by BAM for OSFL, to identify critical habitat for this threatened species (Haché et al. 2014), and to delineate potential range shifts from climate change (Stralberg et al. 2015a). These model results predict a high relative abundance of OSFL in the western regions of Canada (Haché et al. 2014), further highlighting the importance of regional studies in the west.

Interannual variability in abundance

An important step in regional conservation and management is assessment of overall trends (Thompson and La Sorte 2008), and more specifically, interannual variability in abundance of sensitive species in the area of management interest, especially because both focal species in this study reveal evidence of declines both in the short and long term. Long-term trend estimates for OSFL in Canada were -2.6%/yr (credible interval of -3.3%/yr , -1.9%/yr) between 1970 and 2015 (Environment and Climate Change Canada, ECCC 2016) or -3.3%/year (-4.5%/yr, -2.4%/yr) from Sauer et al. (2017) for the period 1955 to 2015. Although almost every trend calculated from Breeding Bird Survey (BBS) data is one of decline, the magnitude of decline is very much regionally-specific (Sauer et al. 2017). For example, long term trends between 1966 and 2015, range from approximately -0.17 in BCR 11 (Prairie Potholes) to as steep as -4.77 %/yr in BCR 12 (Boreal Hardwood Transition) utilizing BBS data (Sauer et al. 2017).

Long-term trend estimates for WEWP between 1966 and 2015 were -1.4%/yr (-2.0, -0.89%/yr) in North America (Sauer et al. 2017). Declining trends were steeper in Canada: -2.6%/yr (-3.6, -1.7%/yr) between 1966 and 2015 (Sauer et al. 2017) or -2.2%/year (-3.0, -1.4%/yr) between 1970 and 2016 (A. Smith, ECCC *unpubl. data* 2017). Declines were pronounced in some regions, such as in Alberta, Yukon and Alaska (Stehelin et al. 2020). The steepest declines of all regions, political or BCR, occurred in BCR 6 (Boreal Taiga Plains) between 1966 and 2015 , with a trend of -4.9%/yr (-6.6,-3.2%/yr), and Alberta (which encompasses a sizeable portion of BCR 6), with a trend of -3.4%/yr (-9.5, -1.2%/yr, A. Smith *unpubl. data* 2017, Sauer et al. 2017).

Examining patterns in abundance over time using long term datasets with numerous contributors is fraught with problems arising from disparate data collection techniques, missing data, geographical non-independence of data (Fewster et al. 2000, Link and Sauer 2002, Bart et al. 2003, Humbert et al. 2009, Matsuoka et al. 2012, Sólymos et al. 2013, Knape 2016), the overdispersed nature of count data that often contains many zeros and small values (Link and Sauer 2002), and sometimes too short of time series to detect an overall trend (Sólymos et al. 2013). Linear regression techniques (often log-linear regression of counts over time, where the slope is the trend) have been used previously (Link and Sauer 2002, Bart et al. 2003), however trends in abundance are often not linear (Flemming et al. 2010), and rare or declining species may have large interannual fluctuations in counts. Improvements include consideration of random effects and fewer assumptions about underlying population growth models (Humbert et al. 2009), and inclusion of offsets for imperfect detectability of singing birds a (Matsuoka et al. 2012), such as the QPAD approach of Sólymos et al. (2013) and Ralston et al. (2015). Bayesian hierarchical modelling techniques have also been utilized for describing long-term trends from disparate data across years and locations (e.g., fit using Markov chain Monte Carlo methods, Link and Sauer 2002, and subsequent updates to techniques, Adam Smith ECCC). These are multi-level models that do not assume a prior distribution (Kruschke and Vanpaemel 2015). Birds of the boreal forest are dispersed widely across a vast and changing landscape, making prioritization of specific areas for conservation and regional trend estimation particularly challenging goals (Schmiegelow and Monkkonen 2002, Stralberg et al. 2018a). In the absence of long-term data with high sample sizes per site in the northwestern boreal region, interannual variability in abundance can help quantify fluctuations in abundance rather than long term trends *per se*.

Objectives

My two main objectives for this chapter were to 1) generate spatially-explicit density estimates for OSFL and WEWP based on a suite of landcover, climate, topography and disturbance layers, and associated biophysical attributes selected based on their likelihood of influencing the abundance of these species in northwestern North America between 1992 and 2014; and 2) investigate regionally-specific and temporally concordant patterns of interannual variability of abundance for these two species in northwestern North America.

2.3 METHODS

Study area

I chose a study area encompassing the northern and western region of North America, including much of Alaska, Yukon, western Northwest Territories, central and northern British Columbia and Alberta, corresponding to Bird Conservation Regions (BCRs, North American Bird Conservation Initiative) 4-Northwestern Interior Forest, 5-Northern Pacific Rainforest, 6-Boreal Taiga Plains and the northern region of BCRs10-Northern Rockies and 11-Prairie Potholes. This area extends from approximately 70° N, -160° W (on the North Slope in Alaska) in the northwestern corner to 50° N, -96° W (in northern Saskatchewan) in the southeastern corner (Fig. 2-1), encompassing approximately 2.3 million km^2.

The study area comprises mostly the boreal zone, defined as the broad, circumpolar vegetation zone of northern latitudes covered principally with forest, but also lakes, rivers and wetlands, and the hemiboreal subzone, defined as part of the temperate zone but transitional to the boreal, with overlap between boreal and temperate vegetation (Brandt et al. 2013, Price et al. 2013), and also includes the northern temperate forest of southern BC. The vegetation of the western boreal and hemiboreal is dominated by a few cold-tolerant tree species such as coniferous *Picea* spp. and shade-intolerant deciduous trees such as *Populus* spp., with tree density varying geographically (Brandt et al. 2013). Moisture gradients influence vegetation and also vary geographically across the region (decreasing from west to east, for example). The major processes that drive ecosystem dynamics in this region are fire, insects, and disease of vegetation, which all vary geographically and temporally (White et al. 2017). The boreal and hemiboreal zones of Canada provide numerous ecosystem services, such as food and water resources, climate regulation, carbon sequestration that has global significance (Gauthier et al. 2015) and other biogeochemical nutrient cycling (Brandt et al. 2013), to name a few. Although the Canadian boreal forest is considered relatively intact as an ecosystem, increasing land use and climate change threaten this state. Only 8% of boreal forest within Canada is protected (Brandt et al. 2013). Most disturbance (per unit area) is from fire in the western boreal (compared to harvest), however, climate change is impacting fire characteristics, and one impact is a slower recovery trajectory following fire (Kurz et al. 2008, Price et al. 2013, White et al. 2017). The area disturbed in western Canadian forested regions was approximately 9.9 million ha, or 7.5%, between 1985 and 2010, almost all from fire (>95%), except for the Montane Cordillera region (central and southern BC), in which most disturbance was from harvest (83% of 3.5 million ha disturbed, White et al. 2017). Most land use in this region is from forestry, energy sector exploration and development, mineral resource exploration and extraction, and hydroelectric energy development (Brandt et al. 2013). The annual area of forest harvest has decreased in the region since about 2005, although the vast majority of British Columbia is considered "commercial forest", or forest managed for forestry operations (Brandt et al. 2013).

Data sources

Bird data

I used abundance-absence data from the large BAM database (BAM 2019), which includes ~1.5 million bird detections from over 250,000 point counts conducted at more than 130,000 locations across North America, from between 1990 and 2014. Combined with on-road data contributions from the Breeding Bird Survey (BBS), this constitutes one of the largest and most spatially-extensive avian datasets in the world (Cumming et al. 2010, Barker et al. 2015).

In addition to data collection and management, BAM has developed statistical methods to account for several sources of heterogeneity that may influence results, such as different data collection or survey protocols, survey effort, as well as factors influencing detectability of birds (Sólymos et al. 2013, Barker et al. 2015). Raw survey counts often do not result in reliable estimates of abundance because a surveyor may not detect a bird. The probabilities are both < 1 that the bird was present and gave an auditory signal, p (available) or the bird may be present but was not detected because of habitat obscuring the noise, time of day, or distance to the observer (q, detected). Expected density then depends on these two factors (qp or detectability) as well as the area sampled (A), and the point level density (D) or "QPAD" (Sólymos et al. 2013). In addition, detectability is influenced by song type and vegetation, as well as date and time of sampling. Survey protocols vary in duration of counting time and point-count sampling radius (e.g., 50 m, 100 m or unlimited), which influences total counts considerably (Matsuoka et al. 2012). Using these measures as offsets unique to each species, observed relative abundances can be converted into consistent estimates of bird density as a function of various biophysical covariates. In addition, the combination of on- and off-road surveys in the dataset allows for calculation of roadside bias, or the probability that a species may be detected from a survey conducted on a road compared to the probability of that species being detected from a survey conducted off-road.

For this research I extracted 15,637 observations from the large BAM dataset, from point count surveys conducted at 7397 unique locations between 1990 and 2014, where at least one OSFL or WEWP was detected. Surveys conducted outside the boreal or hemiboreal zone were removed. Surveys conducted within a one-year period following a disturbance categorized as forest loss from land use (Global Forest Watch Canada 2014) were also removed, because the impacts of immediate land use would have been difficult to differentiate from other covariate impacts, such as those from climate change. To reduce the influence of geographical bias from uneven sampling, and to reduce the potential for pseudo-replication, abundance values were averaged across surveys conducted at the same site and year (1568 unique locations remained). Observations were grouped according to how many repeat observations from the same site occurred within the dataset (regardless of year). Observations included in models were selected according to the total available in each of these groups. Five points were sampled from each group that had more than 20 surveys and six points were sampled from each group with fewer than 21 surveys. A total of ~1,500 and ~2000 non-detections (surveys with abundance of zero) were included in each dataset for OSFL and WEWP, respectively, to balance detections (abundance) and non-detections (many more were available). A total of ~3000 and ~4000 (depending on run) measures of abundance or absence remained for OSFL and WEWP, respectively, for use in models (Fig. 2-1).

BAM also continually updates and manages a biophysical database with environmental covariates such as land cover and these were linked to each avian point-count location. For this study, I extracted several categories of land cover (vegetation categories), fire disturbance, topography, and one wetness variable.

Land cover

Nine land cover layers were chosen based on expected influence on abundance of species and minimal pairwise correlation between them. These selected land cover layers were download and adapted from 2005 North American Land Change Monitoring System (NALCMS; MODIS data; 250 m spatial resolution; Commission for Environmental Cooperation 2014) and included Temperate Needle, Taiga Needle Forest, Temperate Deciduous, Mixed Forest, Temperate Shrub, Shrub Lichen Moss, Grass Lichen Moss, Barren Lichen Moss and Wetland (names slightly modified from original layers from CEC.org). Land cover layers were resampled at 4 km resolution by D. Stralberg (Stralberg et al. 2015b), cropped to northwestern North America in ArcMap 10.4, then projected using the coordinate reference system commonly used by members of the BAM research team (Canadian Lambert Conformal Conic, ellps and datum WGS84, hereafter “CLCC”) in R (R version 3.5.1, R Core Team 2018).

Vegetation classes (categorical variables) were obtained and adapted from NALCMS (same source as above), the Land Cover Map of Canada 2005 (LCC05, 37 categories) using the land cover time series from 1985-2005, derived from MODIS 250 m spatial resolution data (Natural Resources Canada 2014). An interaction term between distance to road (d2road) and tree height was created as d2road x treeheight. Observations conducted on what was classified as Urban and Built-Up, Snow and Ice, and Rocky Outcrops from the LCC05 categorical system were removed from the dataset because of very low probabilities of bird presence. Specific land cover variables are summarized in Appendix 1, Table A1.

Disturbance

Fire categorical variables (fire size and year since fire) were obtained from the Canadian Wildland Database Fire Information System; Natural Resources Canada 2014). I obtained a forest loss layer from the 2000-2016 Global Forest Change database (Hansen et al. 2013), which represents a change from forest to non-forested state at ~30 m spatial resolution. Tiles for each 10 x10 degree were downloaded from Global Forest Change (Hansen et al. 2013), merged and resampled to 4 km resolution using ArcMap 10.4, and then projected to CLCC using R. Land use changes can alter predictions from SDM considerably (e.g., Methurst et al. 2017), however, broad scale anthropogenic land use change is not expected to have a large influence on abundance and distribution for much of the study area, therefore only one layer of land cover change (forest loss) was included in models.

A road covariate was included: distance to road, based on the perpendicular distance to road from each point count location (d2road). Another covariate was created (Road) based on extent of disturbance expected from road characteristics, such as pave status, width, as well as perpendicular distance from the road. These were highly correlated ($r > 0.9$) and contributed comparatively little to variation in abundance, so only one was included in final models (d2road).

Topography and Wetness

A combined topographic index (CTI 90), derived from a 4-km digital elevation model, was included as a surrogate for a wetness index (Higginbottom et al. 2018). I obtained a topography layer (Pacific Northwest Topography) from Data Basin (USGS TOPO30, Phil Nott, The Institute for Bird Populations) at 1 km resolution, resampled this to 4 km resolution, cropped it to northwestern North America in ArcMap 10.4, then projected it in R using CLCC (Appendix 1, Fig. A1).

Climate Data

I obtained spatially interpolated bioclimatic variables from the AdaptWest Project (Wang et al. 2016) for current climate conditions between 1981 – 2010 (ensemble of downscaled projections for North America), obtained from 15 Coupled Model Intercomparison Project phase 5 (CMIP5) models (AdaptWest Project 2015). I chose specific climate variables based on two criteria: expected influence on focal species during the breeding season, and relatively low correlation between variables. Correlation among variables was examined using correlation matrices in R. Climate layers included were: beginning of the frost free period (bFFP), mean annual radiation (MAR), mean summer precipitation (MSP), mean temperature of the warmest month (MWMT), number of frost free days (NFFD), summer heat moisture index (SHM) and average summer temperature from June to August (Tave_sm), precipitation as snow (PAS), and difference between mean temperature of the coldest month and mean temperature of the warmest month (TD). For consistency, climate raster layers were merged from 1 km to 4 km resolution using the "raster" package in R. I also created an "InsectOffset" variable by calculating the difference between the temperature that coincided with the maximum abundance of insect biomass in southern Yukon (see *Chapter IV*) in each breeding season, and the mean average summer temperature (Tave_sm) for each grid cell. Another variable was created to approximate the annual difference in temperature (MWMT) from the average temperature on date of first arrival dates for each species ("ArrivalTemp", *Chapter IV*). Temperature of first arrival may represent a constraint on breeding range at the northern edge of range for species breeding at northern latitudes.

Final datasets utilized in SDMs for each species were evaluated for potential spatial autocorrelation through examination of residuals from BRT models, as well as by calculating a non-parametric equivalent of the typically-used Moran's *I* test statistic (a Mantel test that uses a randomization procedure of two matrices, one for spatial differences between values and one for measured differences, and then examines differences between matrices across 2000 permutations (Dormann et al. 2007). Model residuals and Mantel tests did not indicate the presence of significant spatial autocorrelation ($P > 0.05$) for either species, unless more absences than abundance measures were included in datasets. Therefore, the number of absences was constrained to equal to or less than the number of abundances for each species.

Species distribution models

I defined an observation as a single measure of raw abundance per site per year, and selected observations based on the stratified sampling procedure described above (in *Bird Data*). Boosted regression tree techniques were deemed appropriate because of the wide variety of selected predictor variables with unknown interactive structure, the potential for non-linear relationships with the dependent variable, as well as the predictive strength in this technique. I developed boosted regression trees using the "gbm" package (Ridgeway 2010 – GBM: Generalized Boosted Regression Models, specified as a Poisson distribution) in R version 3.5.1 (and RStudio version 1.1.423) to explain and predict abundance of WEWP and OSFL using a suite of *a priori* selected climate, landcover and topographic predictors. Before performing BRT analyses, I determined the optimal settings of the three user-set model parameters, and the resulting optimal number of trees for prediction, using guidelines from Elith et al. (2008) and (Elith and Leathwick 2017).

Model performance was assessed using 10-fold cross-validation, during which ten groups of data were used to build ten models, each with a different group as a test dataset and the remaining nine as the training dataset. Predicted and observed values were then compared between each and quantified with a correlation value. I then performed 25 bootstrap iterations of each data resampling and modelling procedure. I also examined predictive ability to independent data using AUC (Area Under the operating Curve), which is normally conducted on binary response variables (presence/absence) but can be applied to the ability to distinguish between high and low abundance values using a threshold (Liu et al. 2009).

I estimated the optimal learning rate, tree complexity, and number of trees for boosted regression models using a subset of the data. I used reduction in deviance for prediction to independent data as an initial measure of performance. Optimal settings of these parameters are often determined iteratively, because the three elements selected by the user influence each other, with a trade-off between the number of trees, tree complexity and learning rate (and computing time needed, Elith et al. 2008). For example, decreasing the learning rate increases the number of trees necessary for prediction. The learning rate is the contribution of each tree to the model (and impacts speed of analyses). The tree complexity depends on interactions that are fitted, and these two parameters then determine the number of trees needed for prediction (Elith et al. 2008). Tree complexity, or number of nodes in the tree, should reflect the true interaction order being modelled, but this is almost always unknown at the onset of analyses. A greater interaction order is sometimes desirable, but with an increase in tree complexity, learning rate must be decreased (Elith et al. 2008). In addition, the advantage of lower predictive deviance wanes beyond a tree complexity of four, except for very large sample sizes (Elith et al. 2008).

Survey abundances were adjusted for detection probability using species-specific offsets, which are influenced by two component probabilities: 1) that a bird will sing or be visible at the time of the count p, and 2) that the bird was detected by the observer q. The (log) product of these two probabilities (log*pq*), gives an estimate of overall detection probability as a function of habitat (see *Bird Data* above).

The relative influence of each predictor variable was estimated based on the number of times a variable was selected for splitting, weighted by the squared improvement to the model and averaged (Friedman 2001, Elith et al. 2008). I utilized simplify function (gbm.simplify) to determine if dropping any (up to five) model covariates would improve predictive ability. Results indicated that dropping three covariates would improve model fitting and predictive ability. Three land cover covariates were dropped that were not contributing more than 0.1% of relative influence (Shrub_Lichen_Moss, Grass_Lichen_Moss, Barren_Lichen_Moss). The InsectOffset variable was also removed because it did not influence more than 0.1% in any single model. This resulted in models for current climate conditions that included 37 categorical or spatiotemporal and spatial predictors. Partial dependence functions with smoothing were created to visualize the influence of each individual predictor (other covariates were held at their means and no pairwise interactions were considered). To further assess covariate structure and relative influences, pairwise interactions were quantified and ranked according to importance.

Habitat Associations

I calculated associations with habitat by dividing predicted abundances from BRT models per habitat class (in the LCC05 land classification system) by the relative availability of that habitat class in the study area and then log-transforming these values. These continuous values were used in place of rank differences because using ranks can cause overestimation of both positive and negative habitat associations (Johnson 1980, Beyer et al. 2010). Results also did not differ between the two techniques.

Interannual variability in abundance

Interannual variability in abundance for the time period 1993 – 2014 was examined with generalized additive models (GAMs), using a log-link function based on a Poisson probability distribution. Bayesian techniques (e.g., Kruschke and Vanpaemel 2015, Adam Smith, ECCC, *unpublished data*) were deemed too complex for this investigation because multiple levels were not understood well enough for this first examination of interannual variability for a little-studied region and with a relatively short time series. In addition, in regional modelling exercises with limited long-term data, interannual fluctuations in abundance may be more important to examine than overall change in abundance. GAMs have smoothing procedures built in with model development for any non-factor explanatory variable (with user-estimated degrees of freedom, Wood 2004) and allow fit for any pattern, from straight lines to various nonparametric curves, and can therefore be utilized for assessing simple linear change, non-linear trends or interannual variation (Fewster et al. 2000, Flemming et al. 2010, Knape 2016). Overdispersion is an almost unavoidable problem with count data, arising from two principles: most organisms are not distributed randomly in the environment and many counts are "zero", causing variation in counts (variance) to be greater than the population mean (Harrison 2014, Hilbe 2017). The negative binomial distribution can be utilized as an alternative to Poisson when the variance exceeds the mean (refuting Poisson). However, I chose the Poisson over the negative binomial distribution because, although overdispersion was detectible, it was not large enough to require negative binomial – i.e., conditional variances were not greater than means within each polygon of geographical space (BCR) (Cameron and Trivedi 2013).

Raw abundances (including absences) were modelled as the dependent variable, while year, d2road and latitude, and one climate covariate (TD or DD01) were included as non-linear predictors with smoothing terms, and BCR and habitat class (LCC05) were included as factors. The number of absences was constrained to less than the number of abundances to reign in potential overdispersion (Flemming et al. 2010). Overdispersion was calculated as the sum of squared Pearson residuals divided by the sample size minus the number of parameters (Zuur et al. 2009, Hilbe 2017) and was deemed to be relatively low for each species (< 0.7 for OSFL and < 1.0 for WEWP). Species-specific offsets from variation in detectability were included for each species (see section on *Bird Data* above). I chose degrees of freedom (df) of 9 - 16 for the smoothing functions, increasing df until desired detail and complexity in smoothness was achieved to meet research objectives (Fewster et al. 2000): in this case, an interest in examining interannual variability rather than overall trends. The unbiased risk estimator was used to compare several different versions of models, selecting the best of the group via backward stepwise selection (Flemming et al. 2010). Only a limited number of potentially important variables (such as latitude, habitat class, distance to road, year and one climate covariate) were included, because my objective was to examine the impact of year on interannual variability, not an exhausted assessment of relative influences of predictors, which I had already completed using BRTs. I then ran an Analysis of Variance (ANOVA) on factors of the GAMs to examine and compare influences of these variables. Model performance was assessed by examining residuals, R^2 values and deviance explained. I used the “mgcv” package in R to develop and run these models (Wood 2004).

Percentage change in the abundance index (I) between 2010-2014 (t_2) and 1994-1999 (t_1) was calculated as $(It_2 – It_1)/It_1$ *100% (Fewster et al. 2000) for each BCR. Population changes were considered to differ significantly if the confidence intervals did not overlap, and to indicate significant change overall, if the confidence interval did encompass the point 0. For comparison to results of other studies, I also calculated a percent abundance change per year, calculated as the mean annual rate of change in abundance using mean abundance values per BCR.

2.4 RESULTS

Model evaluation

For boosted regression tree model building using a Poisson distribution under current climate conditions, including both categorical and continuous predictors, a learning rate of 0.01 for both OSFL and WEWP, tree complexity of three, a bag fraction of 0.5 (which was the default), resulted in the lowest predictive error for sample sizes used (average n = 3542 for OSFL and n = 4070 for WEWP). The bag fraction sets the percentage of the data that is drawn at random, which improves accuracy, speed and helps reduce overfitting of models. This step model (using GBM.step version 2.9) resulted in models with a mean of 4978 and 7824 trees for OSFL and WEWP, respectively, coinciding with the minimum predictive deviance for the chosen tree complexity and learning rate (for example, a minimum of 1000 trees was recommended for similar data, Elith et al. 2008, Appendix 2, Fig. A2). The mean total deviances were 0.40 and 0.32, mean correlation values were 0.73 and 0.70, and mean correlation to training data values were 0.84 and 0.82, for OSFL and WEWP, respectively. A coefficient of variation from sampling error across bootstrap runs, calculated as the average standard deviation divided by mean predictive correlation in predictions was 0.017 or 1.7% for OSFL and 0.0160 or 1.6% for WEWP, suggesting that error from sampling was relatively low.

AUC (above and below median predicted abundance per 4 km pixel) was 0.96 and 0.94 for OSFL and WEWP, respectively. These metrics suggest that sampling bias was adequately controlled, and that variables selected could adequately distinguish between abundance above and below the median predicted abundance. Predictive deviance for all trees is plotted in Appendix 1, Fig. A1, and is minimized at the optimal number of trees.

Relative contributions of covariates

As combined groups of covariates, “landcover” (vegetation categories and landcover layers) contributed the most to the variation in prediction of abundance for OSFL (49.4%, Table 2-1), followed by climate variables (26.4%) and then “topography” (topographical raster layer, tree height, elevation, slope and CTI) had a combined influence of 15.8% on abundance of OSFL. Disturbance variables (roads, forest loss, fire size, and fire year) contributed 10.3%.

Habitat (vegetation) categories based on the LCC05 vegetation system had the largest relative influence on abundance of OSFL of any single variable (23.4%), followed by the influence a modified vegetation classification system based on NALCMS (Commission for Environmental Cooperation 2014, “NALC1”, 17-levels, 13.7%, Table 2-2). Single variables with the largest relative influences were a Temperate Needle layer (4.6%), elevation (4.2%), BCR (4.0%), and topographical layer (3.8 %, Table 2-2). The highest ranked climate covariates were DD01 (3.5%) and MSP (3.4%, Table 2-2). When it was included, an interaction term between road and tree height was ranked very highly among predictors (road*tree, ~7.9%). A variable that indicated the presence of roads was also selected often and ranked quite highly (3.4%), as was CTI (2.7%) and slope (2.5%). It is important to note that in different runs of models, the order of importance and percent of relative contribution of different covariates sometimes differed slightly. Results presented are an “average” of 25 bootstrap iterations. Interestingly, the covariate Year varied between iterations of models for OSFL, contributing from a minimum of 0.66% up to a maximum of 4.5%.

For WEWP, “landcover” contributed a combined 42.7%, followed by climate variables (39.1%), followed by “topography” (14.1%) and disturbance covariates, which contributed 7.61% to the variation in distribution and abundance (Table 2-1). Habitat (vegetation) categories based on the LCC05 vegetation system had the largest relative influence on WEWP abundance of any single variable (22.3%), followed by the influence of the NALC1 vegetation classification system (10.5%, Table 2-3). The four climate layers (TD, DD01, NFFD, and MSP) had the next highest influences (Table 2-3). Start time of surveys had a relatively large influence (3.8%), suggesting that disparate methods of survey methodology may be contributing sampling error (despite the inclusion of species-specific offsets for detectability). The highest ranking landcover layer was Temperate Deciduous (2.6%). The presence of roads had a high relative influence (3.6%), as did elevation (3.5%) and latitude (3.1%). When included, the interaction between road and tree height (road*tree) contributed 5.1%.

Partial dependence functions indicated that variation in the predicted abundance of OSFL was heavily influenced positively by the Temperate Needle layer until close to 90% cover, after which it decreased rapidly (Fig. 2-2.3). Although response curves were not linear, predicted abundance of OSFL was generally influenced heavily by elevation (Fig. 2-2.4). Peak predicted abundance occurred between approximately 0 and 1000 m asl. The relationship with topography indicated a complex, non-linear relationship, with most values peaking at the higher end of the range (Fig. 2-2.6). Slope positively influenced abundance until a certain level, after which it declined rapidly (Fig. 2-2.10). For climate variables, the smoothing function for DD01 indicated a high influence at the lower range of DD01, followed by a rapid decline at very high values (Fig. 2-2.9). The influence of MSP was also non-linear, but with smoothing seemed to peak and then decline across the data (Fig. 2-2.11). CTI revealed a complex non-linear relationship with fitted values, but possibly a decline across most values of the data (not shown). Fitted functions of models decreased with increasing bFFP and NFFD initially, and then stabilized, followed by an increase (not shown). d2road had a negative influence on abundance (not shown). Year had a complex bimodal influence on abundance, with a peak between approximately 1994 and 1998, followed by a dramatic decline between 1999 and 2006, and then a smaller increase between 2007 and 2011 (not shown). The influence of BCR was relatively high (ranked 5th overall, Table 2-2) and indicated a relatively low predicted abundance in BCRs 6 and 11, although sample sizes for BCR 5 were generally quite small (~75 observations depending on run). When an interaction between road and vegetation height was included, it positively influenced the abundance of OSFL (not shown).

Overall, relative influences of covariates and partial dependence functions indicated that predicted abundance of OSFL was highest under the following conditions: high levels of Temperate Needle forest, low to intermediate elevation (0 – 1000 m asl), complex topography (topography, slope, and CTI were all important), intermediate levels of DD01, low to medium levels of MSP, low bFFP (early spring and high NFFD), and high levels of PAS.

Partial dependence functions indicated that predicted abundance of WEWP was influenced heavily by TD and peaked at intermediate levels (Fig. 2-3.3). The influence of increasing DD01 was generally negative, with a steady decline in predicted abundance as DD01 increased (Fig. 2-3.4). The partial influence of NFFD was large, but difficult to characterize, with two peaks across the data (Fig. 2-3.5). As MSP increased, it had a negative influence on abundance of WEWP, followed by a slight increase (Fig. 2-3.6). Start time of surveys influenced the abundance of WEWP, peaking between 500 and 1000, suggesting that species-specific offsets possibly did not eliminate the influence of sampling times and imperfect detection (not shown). Slope showed a peak of fitted function at the lower levels, followed by a decline, but most values were at the lower end of the range (Fig. 2-3.8). MAR showed a complex, possibly bimodal pattern, although most values were at the higher end of values and showed a slight decline as MAR increased (not shown). SHM revealed a peak in the intermediate range, followed by a decline. The function for a temperate deciduous layer was non-linear, but generally increased rapidly and then stabilization (not shown). WEWP predicted abundance was positively influenced by d2road. Elevation had a negative partial effect on models for WEWP, with most occurrences between 400 and 750 m asl. CTI influenced WEWP abundance positively (not shown).

The influence of year was bimodal, with a peak in early years of data collection, followed by a decrease, with lowest values between approximately 2001 and 2008, and a temporary peak in 2010 (not shown). Vegetation height had a negative influence on abundance of WEWPs from 10 – 15 m, after which it stabilized at a low relative abundance (not shown). When included, an interactive covariate, road*tree (a relationship between tree height and the presence of roads) had a positive partial effect on WEWP abundance, but then declined at very high values (Fig. 2-3.4).

BRT models overall suggest WEWP abundance was highest in regions with low to medium seasonality (TD), low DD01 (relatively cool regions overall), but with relatively high NFFD (longer summer season), low to moderate MSP, low to moderate slope, moderate to high MAR and low SHM (both indicating relatively low to moderate heat conditions), close to roads, at mid-elevation (500 – 1000 m asl) and where a temperate deciduous forest layer was present.

Pairwise interaction sizes in models for OSFL were generally quite low, but the highest level of interaction occurred with several covariates paired with the Mixed Forest landcover layer: for example, between Start Time and Mixed Forest (Fig. 2-4A). This was probably related to greater detectability at earlier start times compared to later. Interaction size was also relatively high between a climate variable (DD01) and Mixed Forest, as well as between bFFP and Mixed Forest (Fig. 2-4B, C). Mixed Forest also had a relatively high level of interaction with Year (Fig. 2-4D), suggesting relative predicted abundances in this landcover layer depended on year. Slope and a landcover layer (Taiga Needle Forest) also revealed a measurable degree of interaction (Fig. 2-4E).

Pairwise interaction sizes in models for WEWP were also relatively low, but the highest level of interaction occurred between latitude and NFFD (Fig. 2-5A). The second highest interaction size was found between DD01 and PAS, suggesting that predicted abundance found for PAS was dependent on how many days were above 0ºC (Fig. 2-5B). A relatively high interaction was also evident between d2road and Start Time, (Fig. 2-5C). Start Time and the Mixed Forest layer also revealed a detectable level of interaction (Fig. 2-5D), possibly from changes to detectability in different levels of vegetation. Pairwise interactions revealed a relatively low, but consistent relationship across iterations of models between vegetation height and the presence of roads in prediction of distribution in both species (not shown). This may indicate that, although roads influence abundance, this depended highly on the height of the surrounding vegetation.

Habitat Associations

Overall, the land cover classes with by far the highest predicted abundance of OSFL, as determined from BRT models, were areas with coniferous forests, shrub, tundra and wetland. I collapsed 37 LCC05 categories into 19 for ease of visualization and interpretation. For example, I combined categories 3,4, and 5, which all described closed tree evergreen canopy (but differing in age of trees and whether the evergreen forest was mixed with deciduous (Appendix 1, Table A1) and categories 6,7, and 8, which all described evergreen forest of medium density (but differing in understory). The habitat classes with the highest predicted abundance of OSFL (not taking into account availability of each habitat class) were medium density evergreen forest, mixed open, tundra shrub, low density evergreen forest and lichen tundra (Fig. 2-6). Taking the relative availability of each class in the region into account, the habitat classes with the highest predicted abundance of OSFL were low density evergreen, tundra shrub, lichen tundra, lichen spruce bog and old burns (Fig. 2-6). The largest differentials (or negative difference between predicted abundance and predictive abundances constrained by availability), occurred for low density evergreen forest, tundra shrub and lichen tundra, suggesting preferential association occurred for these habitat types.

The highest relative abundances of WEWP were spread across several land cover categories, but were highest in vegetation classes that described open areas with low vegetation cover, and wet areas. Using the collapsed LCC05 classification system, the highest predicted abundances of WEWP were found in mixed closed forest and medium density evergreen forest, deciduous open, mixed open, and cropland. When the availability of each class was taken into account, the highest relative abundances were found in riparian habitat, mixed open, tundra, wetlands, grassland, and burns (recent and old, Fig. 2-7). The largest differentials occurred in riparian, tundra, and wetlands and old burns, suggesting a positive association occurred. A large negative difference occurred for cropland, suggesting that a much lower predicted abundance occurred when availably of the habitat class was considered. It should be noted that whether a survey was conducted on or off-road impacted these habitat associations, especially for deciduous and mixed vegetation types (T. E. Stehelin, *unpublished data*).

Interannual variability in abundance

A slightly declining linear trend is visible overall for both species, although abundances revealed high variation between years (Fig. 2-8). Declines were particularly noticeable for OSFL in BCRs 4 and 10 (Fig. 2-9). For WEWP, a declining trend was particularly visible for BCRs 4 and 11 (Fig. 2-9). A total of 5781 abundance measures between 1994 and 2014 were used in GAMs for OSFL, and 7457 for WEWP. Mean number of records per year was 251 (range 89 - 368) for OSFL and 428 (range 71 – 668) for WEWP. All diagnostic plots were indicative of relatively poor to moderate fit of GAMs to data. R^2 values averaged across bootstrap replicates were 0.36 and 0.31, and deviance explained was approximately 37% and 35%, for OSFL and WEWP, respectively. The "trend" or pattern of abundance index over time fit by models for OSFL (with smoothing) can only be described as "fluctuating": an overall trend is not readily apparent (Fig. 2-10). However, some peaks in abundance can be seen between approximately 1997 and 2000 and then possibly again between 2007 and 2008. WEWP abundance also did not show an obvious pattern over time, but reveal some peaks between approximately 1998 and 2000 and then somewhat again in 2003 (Fig. 2-10).

Despite the non-descript appearance of smoothing factors in models, year was significant in explaining interannual variability in abundance for OSFL ($x^2 = 80.7$, $n = 5781$, $P < 0 .001$). A smooth term for latitude was also significant in predicting the abundance of OSFL ($x^2 = 116.4$, $P < 0 .0001$, Fig. 2-10), as was a smooth term for the climate covariate DD01 (x^2=177.5, $P < 0 .0001$), and for perpendicular distance to roads (x^2=63.5, $P < 0 .0001$), with lower predicted abundance with increasing proximity to roads. BCR was also a significant factor in models for OSFL ($x^2 = 187.3$, $P < 0.001$), but habitat class was not ($x^2 = 1.3$, $P > 0.05$).

Year was also significant as a smooth term for WEWP ($x^2 = 34.8$, n = 7457, $P < 0.001$, Fig. 2-10). A smooth term based on latitude was highly significant ($x^2 = 185.0$, $P < 0.001$) and indicated that the relative index of abundance for WEWP peaked at intermediate latitudes (Fig. 2-10). A smooth term based on perpendicular distance to roads was also significant (x^2=60.8, $P <$ 0 .0001), and was difficult to interpret because most values for distance to roads were close to 0 or -1, but examination of predicted values directly from model results indicated that abundance was higher in closer proximity to roads for WEWP. A smooth term for the climate covariate TD was highly significant in predicting abundance for WEWP (x^2=361.6, $P <$ 0 .0001). BCR was a significant factor in models for WEWP ($x^2 = 93.8$, $P < 0.001$), but habitat class was not ($x^2 = 1.0$, $P > 0.05$).

The abundance index decreased significantly in BCRs 4 and 10 for OSFL, whereas BCRs 5, 6 and 11 did not change significantly from zero (Fig. 2-11). The abundance index decreased in all BCRs examined for WEWP (4, 10 and 11), except for BCR 6, in which confidence intervals overlapped slightly with zero (Fig. 2-11). It is important to remember that these changes in abundance can be interpreted as change for only the region and time of data collection, i.e. only for northwestern North America, and only between the years selected for these comparisons: 1994 - 1999 and 2010 - 2014. An approximate overall trend between 1993 and 2014, calculated using percent abundance change per year (also with overly simplistic assumptions of continual linear trends), was -2.35%/year for OSFL (95% CI -2.44, -2.26) and -1.57%/year for WEWP (-1.69, -1.44) for all BCRs combined in the study area.

2.5 DISCUSSION

Relative contributions of covariates

Vegetation categories can be used to predict a comparatively large proportion of the variation in distributions and relative abundances of OSFL and WEWP at the scale examined here. Both the LCC05 and the NALC1 classification systems of vegetation had a large relative influence on model results. Although climate may describe first order habitat selection at broad geographic scales (Jimenez-Valverde et al. 2011), the influence of vegetation should not be ignored because of the potential for decoupling between vegetation and climate covariates, from land use or climate change, in future scenarios (Cumming et al. 2014). Decoupling may be particularly relevant in this region for species such as WEWP, given that seral stage analyses suggested a time lag of 30 – 60 years between vegetation and climate change was the most likely scenario for this species (Stralberg et al. 2015b). It is interesting that broad ordinal categories of vegetation classes (LCC05 and NALC1) were selected so frequently in models and explained much of the variation. Bayne et al. (2010) also found that broad vegetation categories (when combined with remotely sensed forest data) could adequately predict abundance of most boreal forest birds, even when compared with models that included detailed vegetation surveys.

This importance of vegetation in determining distribution is inherent for many migratory bird species that breed in temperature regions (Matthews et al. 2011). While their overall range is large, and some micro-habitat requirements can be quite specific, they utilize a relatively wide range of forest types when examined at a broad geographic scale. Complex forest heterogeneity required for foraging or nesting could be provided at the microhabitat scale by a variety of processes, such as various forms of disturbance in the boreal forest (fire, flooding, forest harvest, insect outbreaks, linear disturbance for energy exploration and development, and forestry). The non-linear relationships between predictors and abundance (e.g., Figs. 2-3, 2-4), may be indicative of some of these potentially complex micro-habitat requirements. As an individual covariate in models, the Temperate Needle layer had a relatively large influence on the distribution and abundance of OSFL, with a relatively stable relationship across many levels of cover, followed by a dramatic decrease at very high levels of cover (although most data were in the lower range). This pattern likely reflects an association with coniferous forest; however, a high density of trees would be inappropriate because of a lack of open areas for sit-and-wait foraging of flying insects.

Covariates that described multi-dimensional space, such as elevation, slope, topography, and latitude, were important in predicting relative abundances of these species. Topographical covariates (topography layer, slope and CTI) contributed greatly to variation in distribution and abundance of OSFL, in particular, because of the potential relationship between slopes and moisture pooling. Complex topography has potential to create many microhabitats, promoting insect diversity and abundances (Spence et al. 2008). As part of this complexity, surface moisture pooling would occur in areas with variation in slope (and elevation) and support relatively higher abundances of hygrophilous insects. Topographical features and edge may also protect insects from wind (Whitaker et al. 2000). These results highlight the importance of including three-dimensional space in modelling exercises aimed at explaining and predicting abundances of species (Stehelin et al. 2020). ABMI and BAM (2018b) also found that predicted density of WEWP peaked at lower levels of slope and then declined as slope increased to relatively high levels, probably because provision of novel microhabitat structure wanes with steeper slopes (above 15 degrees). Results of habitat models conducted for a status report for WEWP in Alberta (Stehelin et al. 2020) indicated that surrounding wet-water (open wetland, bogs, fens and open water at a 1-km^2 scale around points) predicted three times the abundance of this species when increased from 0% to 100%.

Although ranked lower than vegetation layers and categories, climate variables as a group also contributed highly to explaining the distribution and abundance of these species, reflecting the relatively large geographical area included in models, and northern edge of current range for both of these species, constraining distribution. Climate constrained distribution has been found for many bird species breeding in North America (Jiménez-Valverde et al. 2011). While results were generally similar, climate variables as a group contributed more towards WEWP distribution and abundance than for OSFL, probably because it is a more southern-breeding species, with areas of central Yukon and Alaska representing the northern edge of the current breeding range for this species. Climate variables such as TD, DD01, NFFD, and MSP had a large influence on distribution of WEWP, reflecting cold temperature constraints on distribution. However, as the climate variable DD01 increased, it had negative influence on distribution and abundance of WEWP in the region, suggesting that regions with long periods of warmth in summer (days over 1 degree) may not necessarily support high abundances. The influence of TD peaked at low to intermediate values, suggesting that seasonality was important, but with well-defined limits at both extremes. Overall influences of these climate variables on predicted abundances suggest that, despite being at the northern area of their range, predicted abundances of WEWP were relatively higher in cool conditions, which has implications for a region predicted to change disproportionately with climate change. For OSFL, the highest ranking climate variables were DD01, followed by MSP, predicting the highest relative abundances at intermediate levels for both, followed by decreases at very high levels of each, also suggesting that relatively cool regions with intermediate levels of moisture may support the highest densities of this species. A relatively early beginning of the frost-free period also predicted relatively high abundances, and could also be beneficial for early season insect abundance. In general, moderate climate covariates (relatively cool, somewhat moist, but with an early start of the frost-free period) would likely be associated with abundant insects, especially in combination with complex topography that could allow moisture pooling. Somewhat differently from what I found here, but not unsurprising given differences in spatial extent of analyses, climate variables such as climate moisture index ranked very highly relative to landcover covariates in a national-scale modelling exercise on OSFL by Haché et al. (2014).

The relative influence of disturbance was comparatively small for both species, probably reflecting the relatively small area of anthropogenic disturbance within a large study area. However, the influence of roads (distance to road) alone was relatively large for a single variable (especially for WEWP), and was negative for OSFL and positive for WEWP. The influence of roads/linear disturbance on abundance of the OSFL is equivocal. Roadside surveys may overestimate the abundance of the species, and yet abundance was invariably lower near roads according to a national study (Haché et al. 2014). Roads may be attractive to species that are associated with edge and open forests, but roadsides may represent sub-optimal habitat, and be impediments to movement of some insects (Andersson et al. 2017). Roads, especially small roads, may create openings in forest and may not have a negative impact on abundance of WEWP in areas that are relatively undisturbed to begin with, such as much of the study area considered here.

Fire variables were less important than expected in explaining distribution and abundance for both species, given that both species are described as fire-dependent (Hutto 1995, Morissette et al. 2002, Robertson and Hutto 2007, Haney et al. 2008). Haché et al. (2014) found that fire ranked highly in predicting abundance of OSFL in Canada, and was associated with higher abundances. Fire variables available for inclusion here (fire year, fire size) may not have been sufficient to capture specifics surrounding fire influence, such as the impact of fire severity or age of stand at the time of fire (e.g., Smucker et al. 2005). The forest loss layer also captured impacts of fire, because it included any process that removes forest (Hansen et al. 2013). However, while the relative influence of this covariate was certainly measureable, it was not large (~2% for both species) compared to the effects of other covariates.

Interaction size was high between several climate variables (DD01, bFFP) and Mixed Forest landcover layer for OSFL, indicating that predicted abundance in this landcover layer may depend on climate and possibly geography. Mixed Forest was more prevalent in the southern part of the study area (T. E. Stehelin, *unpublished data*), influencing predictions of abundance in this type of forest in an interactive manner with climate. Mixed Forest also had a high interaction level with year, possibly because mixed forest changed with either climate change or land use in the southern portion of the study area over the course of the study period (1994 – 2014). Taiga Needle Forest layer also interacted with slope, corroborated by observations of OSFL territories in southern Yukon that often occur on slopes (see *Chapter IV*).

Pairwise interaction sizes in models for WEWP were highest between latitude and NFFD, probably due to the dependence of this climate variable on geography. NFFD would be less of a constraint at lower latitudes. An interaction between DD01 and PAS for WEWP suggests that predicted abundance for PAS, although generally positive, was dependent on temperature and, thus also probably related to latitude. PAS may be a more important source of precipitation in some regions that are relatively dry. A relatively high interaction was also evident between d2road and Start Time, suggesting that abundance at certain distances from roads is influenced by start time of surveys. This may reflect lower accessibility of more distant surveys from roads, and resultant increased travel times to reach and survey areas, but is a factor that could be addressed in future survey design.

The selection of absence data could have introduced some error (akin to sampling error), because all absence data can be considered “pseudoabsence” data. Organisms could be absent because of negative habitat selection, or due to a suite of other factors such as anthropogenic disturbance, extirpation, or a barrier to dispersal into an area (Peterson and Soberón 2012), or were actually present and not detected despite the use of offsets for detectability. However, only a limited proportion of this study area can be considered disturbed, and habitat classes very unlikely to be occupied were removed, such as Snow and Ice and Rocky Outcrops. Samples acquired immediately following anthropogenic disturbance were also removed from the dataset prior to analyses.

Habitat Associations

Both OSFL and WEWP were predicted to occur across a wide variety of habitats and vegetation classes, but most categories of relatively high predicted abundances described open forest and a preference for wet areas. Abundance of OSFL was predicted to be highest in vegetation categories that described low density open forests with wet understory or wet forest, either dense or sparse riparian areas, and in forested areas regenerating from old disturbances and in old burns. Without taking into account the availability of the habitat class, medium density evergreen forest supported relative high abundance, however, this effect was overshadowed by much higher predicted abundance when low density evergreen forest was available. Similarly, both tundra shrub and lichen tundra were occupied with relatively low frequency, until the availability of that class was taken into account, and then the predicted abundance appeared to be much higher. However, the area for these vegetation classes was relatively small overall (1.25%

of the area for these two combined), inflating results. Nonetheless, these results do suggest that although they may be found in some areas at relatively high predicted abundances (such as medium and high-density evergreen forest), these habitat classes are not necessarily preferred. Open forest with a well-developed shrub layer and poorly drained soil would likely support high densities of insects. OSFL is associated with forest edge in many areas (Hutto 1995, Altman and Sallabanks 2012) and open forests and regenerating old disturbance would likely provide heterogenous habitat with forest edges. My results indicated a high predicted abundance in Sub-Boreal Pine-Spruce biogeoclimatic zone of BC, which exemplifies these habitat associations: mid-high elevation, relatively dry with numerous lakes and wetlands, and a high potential for fire and insect outbreaks (Meidinger and Pojar 1991). It is important to note that this was not an exhaustive assessment of habitat preferences by these species, and did not take into account many context dependent factors that likely influence whether an animal is present in a habitat class or not, such as a clear behavioral preference or avoidance, knowledge of, or access to, available habitat types, conflicting demands on habitat needs, and relative fitness across habitat types (Johnson 2007, Beyer et al. 2010). These techniques often require targeted studies to determine patch-level scale behavioral and fitness measurements of relative habitat quality to incorporate in resource selection function models (Johnson et al. 2004)

My results of habitat associations are in agreement with those of others. Openings and edges are important to this species according to many authors (e.g., Westwood 2016, COSEWIC 2018), although there are regional differences in processes that create these openings. Haché et al. (2014) found that conifer stands, especially those with relatively taller trees, supported the highest densities of OSFL, followed by shrubby areas, recent burns and wet areas at the national scale, emphasizing that a mosaic of regionally-specific heterogenous habitat, often near edge, may be considered critical for this species. Also at the national scale, Sólymos et al. (2018) found that the highest expected density of OSFL males was in a Coniferous Sparse class, followed by Coniferous Dense and Shrub, Wet dense and Wet sparse, Mixed Sparse and Open Coniferous forest, again suggesting that complex forest structure is important. Density was found to be negatively influenced by forest canopy height in mixed forest or wet habitats, but in coniferous forest density was positively associated with canopy height, suggesting that a complex association with tree age may also occur. The dependence on coniferous forest (of late seral stages in particular) is concerning, as tree dynamics are changing concurrently with climate change in Canada, with movement of forest-tundra ecozones northward and to higher elevations (Danby and Hik 2007), and increased tree mortality and slower tree growth expected (Zhang et al. 2015). In British Columbia and Alaska, OSFL was found breeding in wet coniferous forests, often adjacent to bogs or disturbed and harvested areas (J. Hagelin (Alaska), A. Norris (BC) *pers. comm*). In central and Eastern Canada, OSFL is similarly often found in open forests, including harvested forest, if tall mature trees are retained during the harvesting procedure (Westwood 2016, COSEWIC 2018).

Predicted abundances of WEWP were highest in riparian habitat, mixed open forest, tundra, wetlands, grassland and burns, with a potential “preference” (or largest differential) in riparian, tundra, wetlands and old burns. These habitats are generally open, with edges and wet areas, providing foraging opportunities from standing vegetation in a mosaic of open and forested areas, and with well-developed shrub layers and water for larval stages of flying insects, and therefor likely to support high densities of insects. WEWP was also found in riparian areas of the USA (Heath et al. 2010), and predicted abundance increased almost 3-fold with surrounding wet areas or water in Alberta (Stehelin et al. 2020). Others have also noted the prevalence of this species near edge (Bemis and Rising 1999). I found that the abundance of WEWP was high in cropland, but when this was constrained by availability, this was much reduced, suggesting that although they are found there, they may not prefer this habitat type. Mixed closed and medium density evergreen forests also supported high predicted abundances, but these were much reduced when the availability of those habitat classes were taken into account. Surprisingly, this was also true for open deciduous forest. Many authors describe WEWP utilizing deciduous forest for nesting in other regions (e.g., Beaver and Baldwin 1975, in Colarado; Cannings et al. 1987 in British Columbia; Hutto 1995 in northern Rocky Mountains; Heath et al. 2010, in high elevation eastern Sierra Nevada of California; Weber 2015b in BC).

In modelling conducted for a status report for this species in Alberta (Stehelin et al. 2020), we found that predicted densities were highest in young forest, such as larch, black spruce and pine, followed by wet grassland, then young seral stages of deciduous forest, upland spruce and mixedwood forest. Predicted abundances were relatively low in wet shrub, swamp and cultivated areas. Although results are not directly comparable (LCC05 categories do not explicitly describe age of vegetation), these results are similar in that open forest is likely important, whether that open structure is created by young (or mixed) ages of trees, edge, wetness or mixed-species forest. At the national scale, the highest expected densities of WEWP were found in shrub, followed by open, dense coniferous forest, open deciduous, and mixed open forest (Sólymos 2016, 2017). Late-stage deciduous habitat supported high predicted abundances, but that this was much reduced when the availability of that land cover category was taken into account (Sólymos 2016, 2017).

These predictive results also suggest that old burns may be preferred over recent burns (although both were predicted to be used); however, my results did not rank post burn areas as particularly high among the suite of land cover categories selected. Both species were positively associated with recently-burned habitat in other regions (OSFL: Meehan and George 2003, Hutto 1995; WEWP: (Hutto 1995, Kirkpatrick et al. 2006, Schieck and Song 2006, Cahall and Hayes 2009), although these associations depended on fire severity, between fire interval, and time since fire (Smucker et al. 2005), as well as pre-existing forest edge (Meehan and George 2003). Sólymos et al. (*unpublished data*) found that predicted abundance was bimodal with fire, peaking at 0-10 and then again at 50+ years since fire for OSFL.

Although forest harvest was not examined specifically in these analyses, WEWP generally show declines following fire harvest, although the response depends heavily on harvest type (Hutto 1995, Schieck and Song 2006), and forest age at time of harvest (Stehelin et al. 2020). A negative effect of harvest was obvious in young seral stages, but essentially disappeared by 60 – 80 years of stand age (Stehelin et al. 2020).

Future modelling exercises could improve upon these results with the inclusion of possible constraints due to interspecific interactions – such as with important prey (Trainor and Schmitz 2014), and associations with specific species of trees in forested habitats (Matthews et al. 2011). Results from preliminary investigations into phenology and community dynamics suggest that OSFL may feed their young large insects, such as members of the order Odonata, in southern Yukon (see *Chapter IV*), and members of orders Coleoptera and Hymenoptera in other regions (Otvos and Stark 1985, Altman and Sallabanks 2012). Inclusion of this potential dependency, combined with broader geographical sampling, could fine tune predictions of distribution and abundance and inform potential conservation efforts for this species.

Interannual variability in abundance

Examination of mean abundance within each BCR and year revealed wide interannual variation, but overall declines for both species between 1992 and 2014 (e.g., Figs. 2-9, 2-10). These declines were specific to geographical area (BCR) but not vegetation class. Relatively simple calculations of population change between two time periods (1994 – 1999 and 2010 and 2014) in each BCR revealed declines, especially for WEWP (BCRs 4,10 and 11 and BCRs 4 and 10 for OSFL, Fig. 2-11). Results of GAMs detected a highly significant effect of year, despite that predicted values from models did not reveal obvious trends with year for either species between 1992 and 2014. These models only explained approximately 35% of the variation in abundance for both species, suggesting that covariates other than the ones considered were contributing a substantial portion of the variation in the annual abundances of these two species. Of the somewhat limited variation explained by models, much was explained by BCR category, one climate variable, distance to roads, and latitude, more so than by year, suggesting that interannual variability in abundance is more dependent on geography and other covariates or factors not included. Geographically-specific land uses may be influencing annual abundances, and a metric of land use change and type should be included in future analyses. Because both species are dependent on flying insects, interannual variability in abundance may also be influenced by local climatic conditions (and subsequent availability of prey), creating a geographically-specific pattern. For example, insect populations at high altitudes may be particularly vulnerable to increasingly dynamic weather patterns occurring with climate change (Urbani et al. 2017). Although models were assessed for overdispersion, the variation in abundance was small, with values of 1 and 2 for many locations. All models were re-run using an index of abundance (calculated as abundance divided by the maximum abundance within each BCR) instead of raw abundances, and were also re-run utilizing a negative binomial distribution (which can constrain impacts of overdispersion), but results and variation explained were very similar.

Limitations from fewer available data in the northern boreal make it difficult to detect trends, especially in species that are forest-dependent, uncommon, and those that show a negative road-side bias, all of which apply to OSFL (Matsuoka et al. 2011, this study). Interannual variability in abundance is reportedly large in many bird populations, from local environmental fluctuations, density-dependent factors, non-breeding ground and migration factors, and even unexplained random variation (Knape 2016). Inclusion of non-linear models, smoothing, and separation of long- and short-term trends may help complete the complex picture of trends or interannual variability in abundance. Twenty years is short for assessment of long-term trends in abundance. Matsuoka et al. (2011) determined using simulation that over 40 BBS routes (that are mostly on-road surveys) per year would be needed for OSFL in order to detect a declining trend of 50% over a 20-year period with 80% statistical power. The data I used for the present analysis did not always meet this criterion (ranged from only 3 to 235 surveys by both year and BCR). However, I also analysed data without including the factor BCR (to increase sample size within each year), and the overall results were similar. Despite inherent limitations of data or methodologies, assessments of trends are essential criteria used in very broad-scale management decisions, such as International Union for Conservation of Nature (IUCN) Red List Categories for extinction risk (Knape 2016, Rueda-Cediel et al. 2018).

The relatively straightforward calculations of changes in population size - comparing two time periods (Fewster et al. 2000) - may be preferable over GAMs for these data because they are not as reliant on large sample sizes. They do, however, by nature of their simplicity, assume that the two time periods selected for comparison are indicative of trends over time, changes are linear, and patterns are similar across the geographic space of the data.

An overall trend was not detected for OSFL by Haché et al. (2014) between 1997 and 2013 using a similar dataset as used here (BAM data), but at the national scale. A declining trend was detected for OSFL in the northeastern US by Ralston et al. (2015) between 1989 and 2013 (-4%/year, 95% confidence interval -5% to -2%). Although not directly comparable because of survey type (mostly on-road) and methodological differences, BBS data reveal declines for OSFL in many eastern jurisdictions, such as the reported trend of -4.8 %/yr (-5.8,-3.7%/yr) in BCR 12 (Boreal Hardwood Transition) between 1966 and 2015 (Sauer et al. 2017). Most species dependent on spruce-fir forests showed declines (e.g., Canada Jay, *Perisoreus canadensis*), compared to fewer non-obligate spruce-fir species (Ralston et al. 2015). Declines may be more pronounced in eastern North America (Nebel et al. 2010, Sauer et al. 2017), and data were more comprehensive, allowing for detection of overall trends (Ralston et al. 2015). Sample sizes per survey location in Ralston et al. (2015) were much higher than mine, allowing investigators to remove cases with fewer than 50 detections and less than 8 years of observations. All aerial insectivores (including OSFL) were found to be declining between 1966 and 2006 (especially long distance migrants), and declines interacted with location (between aerial insectivorous assemblage and with each of latitude and longitude), revealing a strong geographical gradient of greater declines in northeastern North America (using BBS data, Nebel et al. 2010). For two BCRs in eastern Canada (Boreal Hardwood Transition and Atlantic Northern Forest), 17 species of aerial insectivores, OSFL included, showed consistent and marked declines following the year 1980, possibly from a multitude of cumulative stressors encountered along long migratory routes, such as pesticides (legacy and "new" classes, Goldstein et al. 1999), and agricultural and industrial land use intensification in Southern USA, Central America and northern South America (Nebel et al. 2010). In addition, migration is inherently the riskiest part of the avian annual cycle (e.g., Sillett and Holmes 2002), attributed in part to severe weather such as strong winds and inter-annual variation in precipitation and consequently in vegetation in non-breeding areas e.g., from the El Niño/Southern Oscillation phenomenon, ENSO (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005, Wilson et al. 2011). Many migrants rely on critical stopover sites (Hagelin et al. 2019), which if altered can have disastrous consequences on long-distance migrant populations (Baker et al. 2004).

The WEWP is declining overall in Canada according to assessments utilizing BBS data (ECCC 2017, Sauer et al. 2017), with particularly pronounced declines in Alberta, Yukon and BC. For example, BCR 4 revealed a decline of 3.9%/year between 2006 and 2016 (-8.4 to 0.10, 95% confidence interval, A. Smith, *unpublished data*, ECCC 2017). Because of the more southern distribution of WEWP compared to OSFL, they may experience greater impacts from land uses that occur in the southern boreal, such as agriculture and alteration of riparian habitat (impacted by both agriculture and urbanization), and to a lesser extent from forestry (Stehelin et al. 2020). These impacts could be exacerbated by known stresses from long migration, such as land use changes (forest loss especially), severe weather events and ENSO fluctuations, and agriculture intensification in distant, non-breeding areas. Sólymos (2016) reported a predicted percent annual change of over -5% per year for WEWP in Canada. A longer time series of overall abundance change, and more data per geographical location (BCR), is needed for this species.

Conclusions

Vegetation and landcover were important overall in both explanation and prediction of distribution and abundance for OSFL and WEWP, in part because of the extent of scale selected for this study, and also potentially because of regionally-specific habitat associations. Both species exhibited strong associations with habitats that were open, with multi-aged (and multi-species) forests and surface water. Covariates that described complex topography also predicted relatively high abundances of both species, highlighting the importance of three-dimensional space in descriptive modelling. Roads had a complex and species-specific influence on abundance of these species, providing, overall, a complicated picture with possible cumulative impacts of forest disturbance.

Higher predicted abundances for both species in cool, moist conditions that could be influenced by rapidly changing climate in the region raise concerns. Overall trends were not readily apparent in model results, but despite low sample sizes for assessment, declines were detectable using simple abundance comparisons between two time periods, and year was a significant factor influencing annual abundances. More information is needed on factors affecting interannual variability in abundance for these species and the extent to which such variability translates to trends in species abundance.

2.6 Tables

Table 2-1. Relative contributions of groups of predictor variables from boosted regression tree models for the Olive-sided Flycatcher and the Western Wood-Pewee between 1992 and 2014 in northwestern North America.

Predictor Group	Mean Relative Contribution %	
	OSFL	WEWP
Vegetation, Landcover	49.4	42.7
Climate	26.4	39.1
Topography	15.8	14.1
Disturbance	10.3	7.61
Geography (Latitude and Bird Conservation Region)	7.70	3.27

Table 2-2. Relative contributions of single predictor variables for boosted regression tree models for the Olive-sided Flycatcher between 1992 and 2014 in northwestern North America. See Appendix 1 Table A1 for definitions and sources of variables.

Predictor	Mean Relative Contribution (%)	Predictor	Mean Relative Contribution (%)
LCC05	23.1	SHM	2.25
NALC1	13.7	Temperate Shrub	2.18
Temperate Needle	4.58	Forest Loss	2.11
Elevation	4.18	Road	2.06
BCR	4.04	Fire Year	2.02
Topography	3.76	Mixed Forest	1.83
Start time	3.76	Tave_sm	1.52
Latitude	3.66	Fire Size	1.36
DD01	3.51	Temperate Deciduous	1.34
Slope	3.42	Vegetation Height	1.29
MSP	3.37	MWMT	1.08
CTI	3.14	HAB_NALC2	1.03
bFFP	3.02	Wetland	1.03
NFFD	3.00	ArrivalTemp	0.90
PAS	2.92	Taiga Needle Forest	0.55
MAR	2.83	Temp pre 1995 offset	0.49
d2Road	2.70	Year of Forest Loss	0.07
TD	2.62	“Northern”, north of 59	0.01
Year	2.44		

Table 2-3. Relative contributions of single predictor variables for boosted regression tree models for the Western Wood-Pewee between 1992 and 2014 in northwestern North America

Predictor	Mean Relative Contribution (%)	Predictor	Mean Relative Contribution (%)
LCC05	22.3	Topography	2.36
NALC1	10.5	Forest Loss	2.23
TD	7.18	Temperate Needle	2.21
DD01	6.46	Tave_sm	2.18
NFFD	4.64	Year	2.09
MSP	3.82	Vegetation Height	1.71
Start time	3.81	Fire Year	1.34
Slope	3.80	Temperate Shrub	1.06
MAR	3.62	MWMT	1.00
SHM	3.59	ArrivalTemp	0.95
Road	3.59	Fire Size	0.80
Elevation	3.54	HAB_NALC2	0.68
Latitude	3.13	Temp95	0.57
d2road	3.08	Wetland	0.56
PAS	3.04	Taiga Needle Forest	0.36
CTI	2.71	Year Loss	0.15
bFFP	2.62	BCR	0.13
Temperate Deciduous	2.61	"Northern", north of 59	0.01
Mixed Forest	2.42		

2.7 Figures

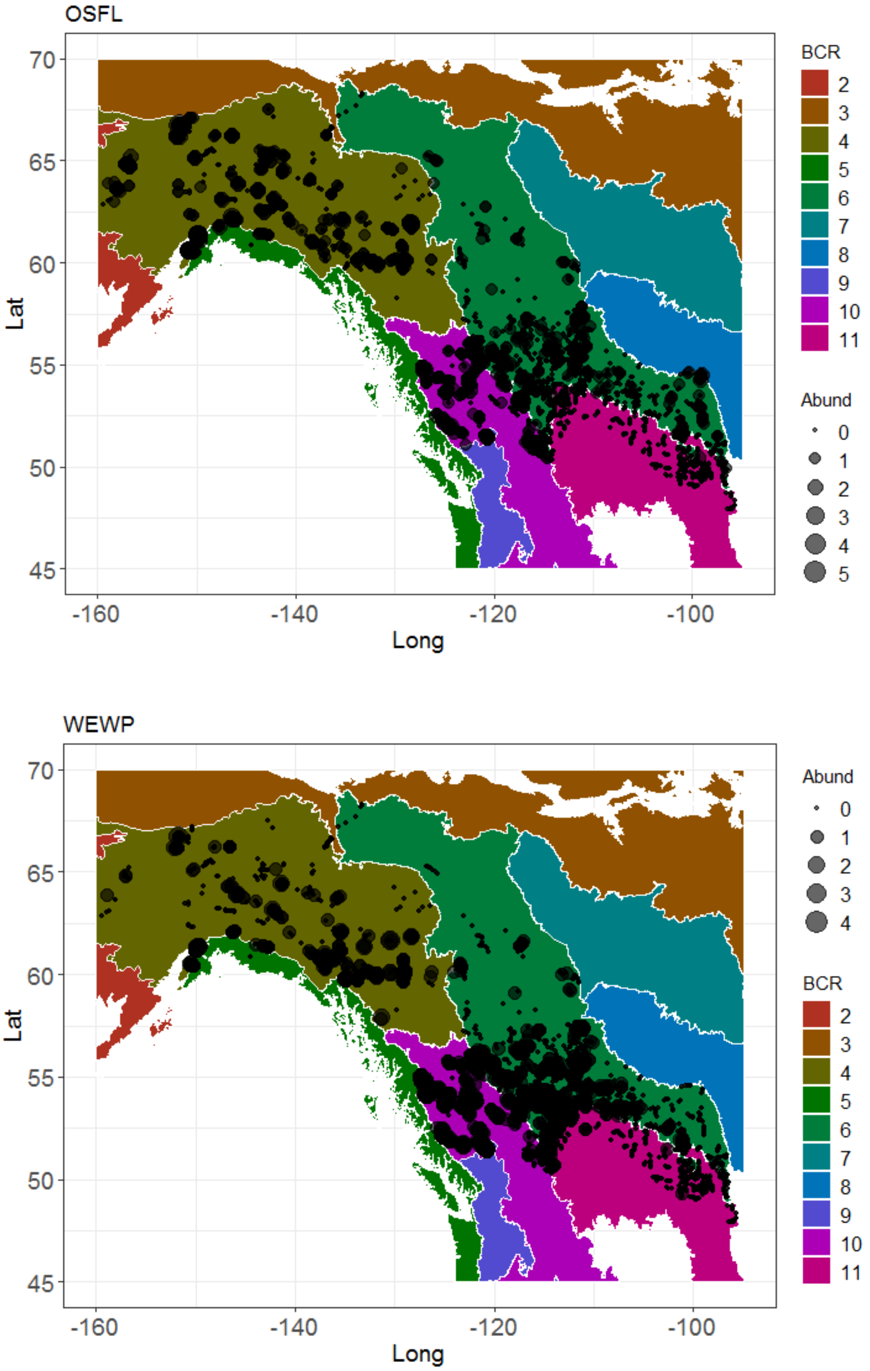
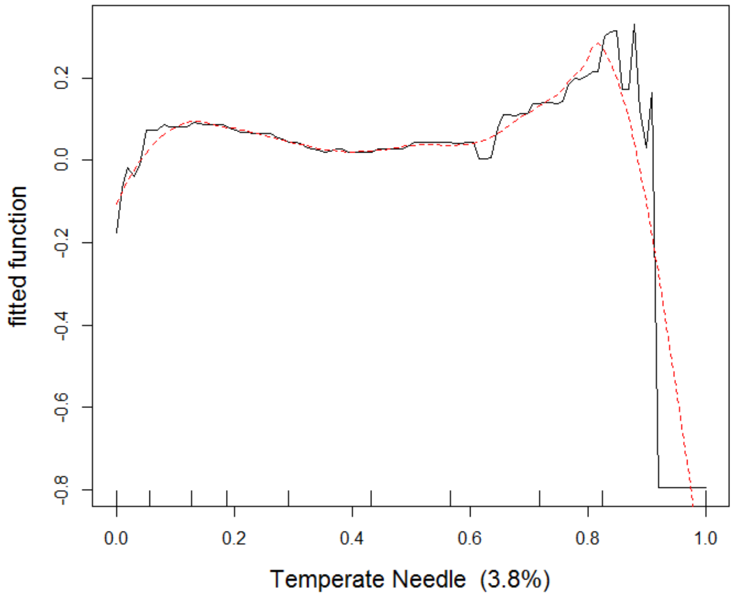


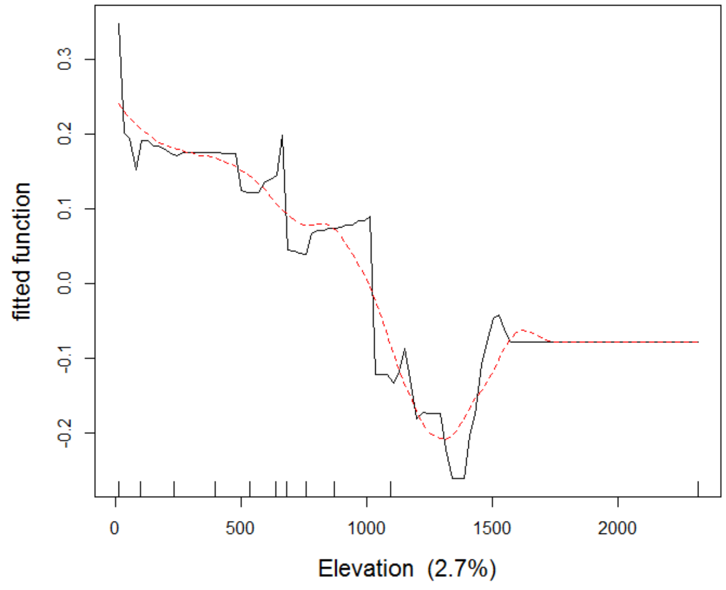
Figure 2-1. Study area and abundance – absence data locations and number of birds at each point used in analyses for the Olive-sided Flycatcher (OSFL, top) and the Western Wood-Pewee (WEWP, lower) from the BAM database. Bird Conservation Regions (North American Bird Conservation Initiative) are shown in colors with white outline.

Figure 2-2. Highest-ranking partial response variables contributing to predictions of distribution and abundance for the Olive-sided Flycatcher between 1992 and 2014 in northwestern North America from boosted regression tree models. Smoothing functions are shown with a dashed line (while other covariates were held at their means). The number at the top indicates mean rank of covariate importance (see Table 2-2).

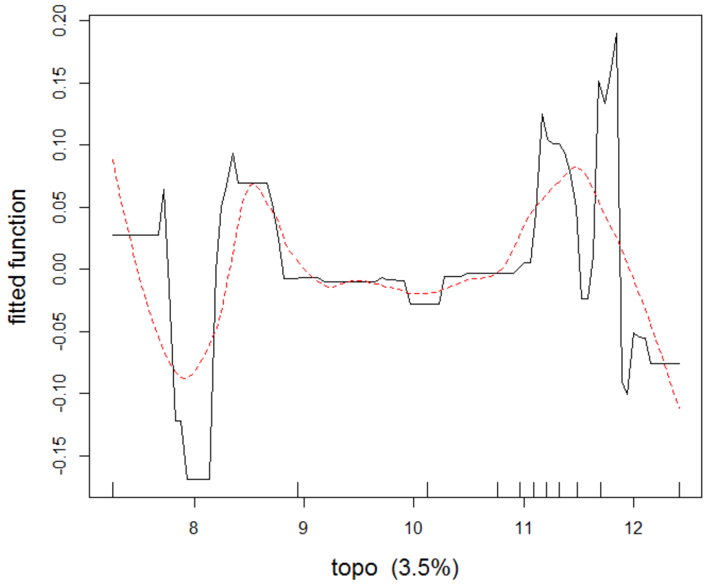
OSFL - 3



OSFL - 4

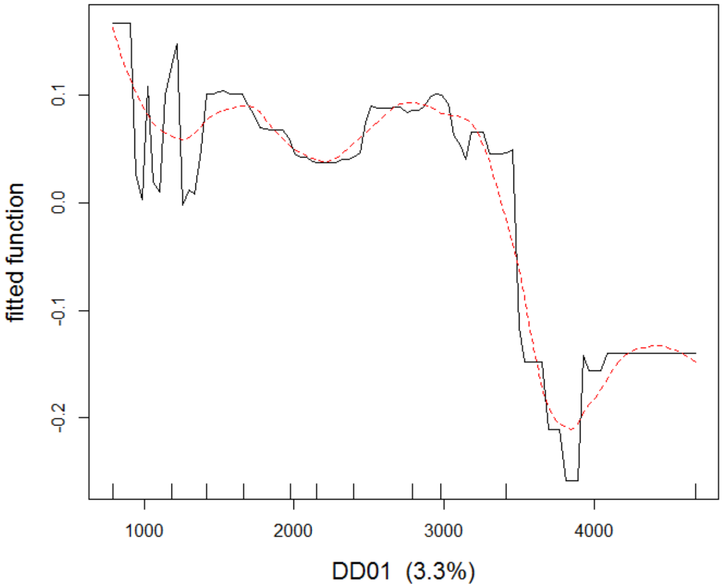


OSFL – 6



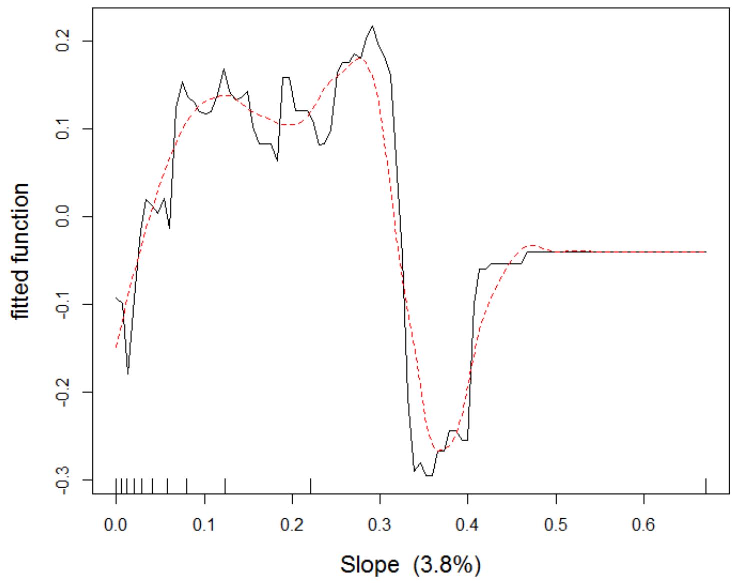
fitted function
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
8
9
10
11
12
topo (3.5%)

OSFL – 9



fitted function
0.1
0.0
-0.1
-0.2
1000
2000
3000
4000
DD01 (3.3%)

OSFL - 10



OSFL - 11

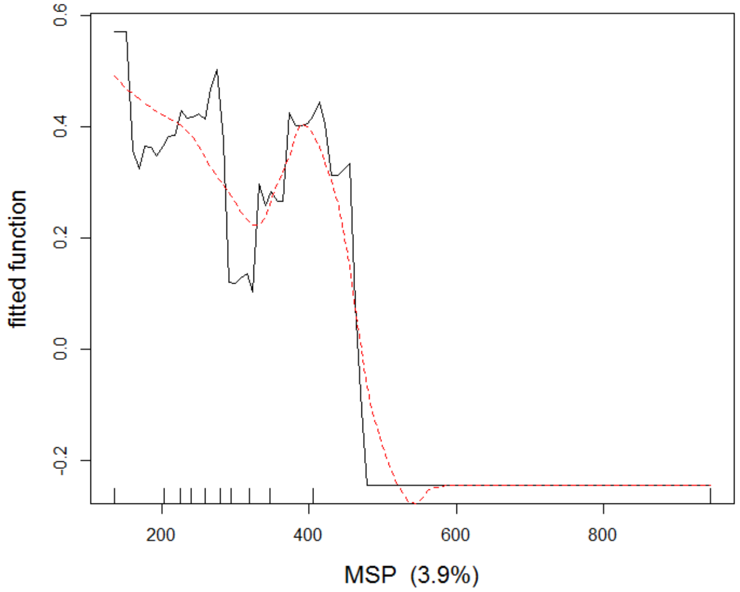
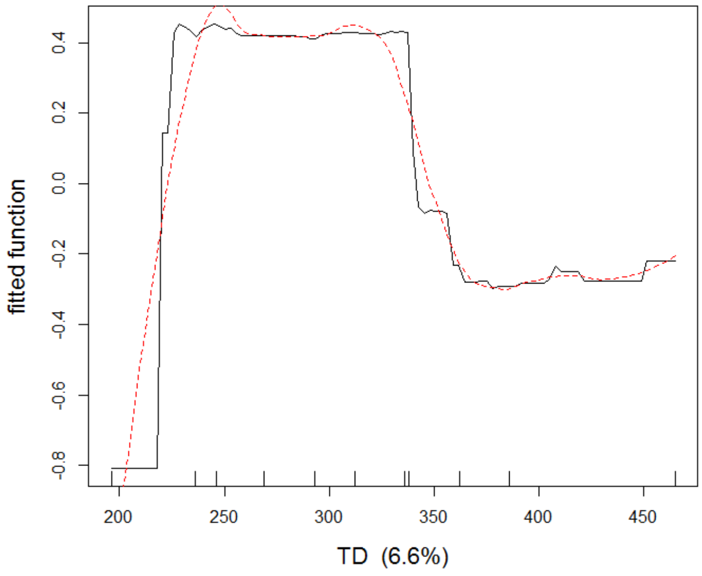
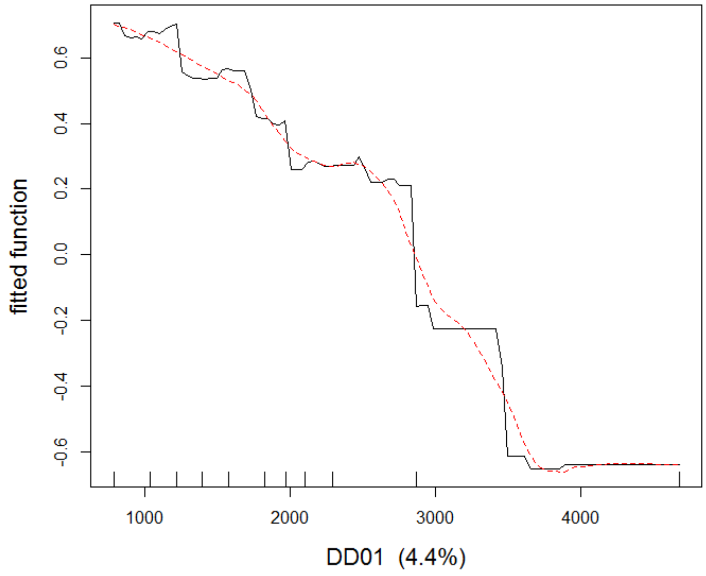


Figure 2-3. Highest-ranking partial response variables contributing to predictions of distribution and abundance for the Western Wood-Pewee between 1992 and 2014 in northwestern North America from boosted regression tree models. Smoothing functions are shown with a dashed line (while other covariates were held at their means). The number at the top indicates mean rank of covariate importance (see Table 2-3).

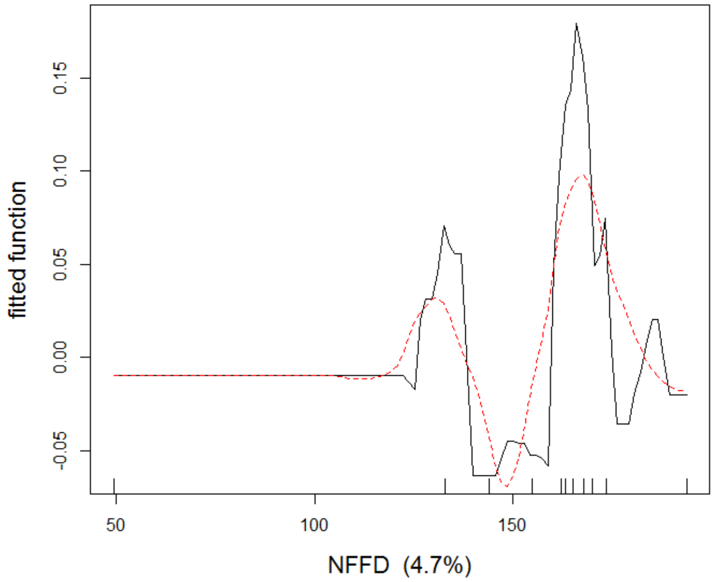
WEWP - 3



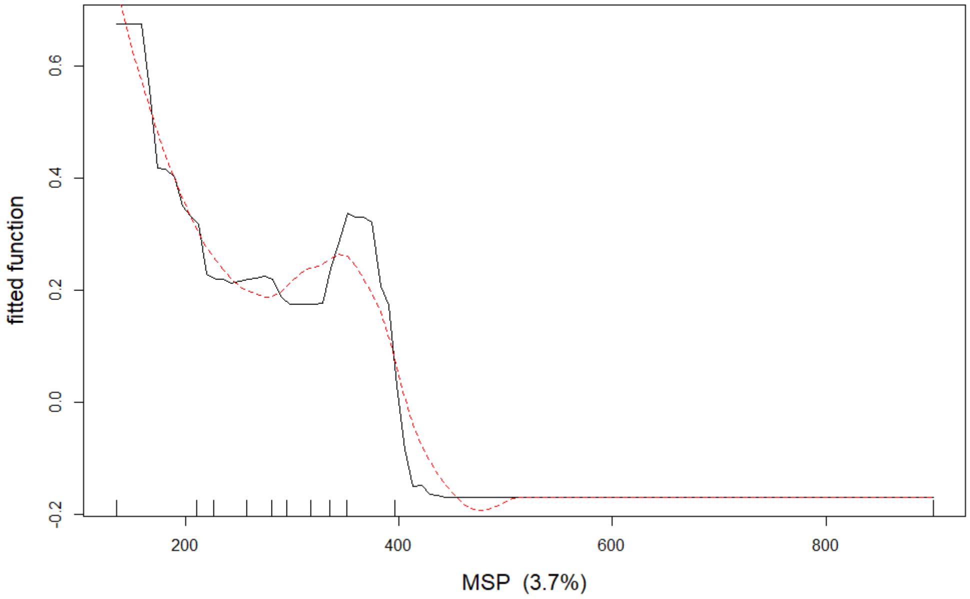
WEWP - 4



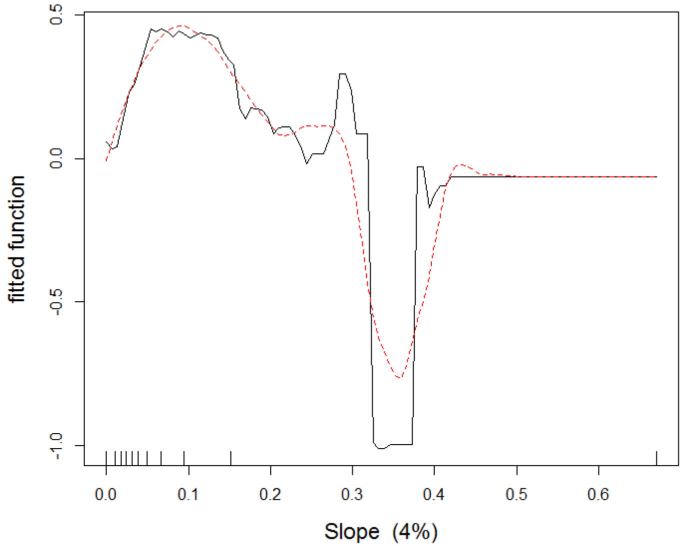
WEWP – 5


fitted function
0.15
0.10
0.05
0.00
-0.05
50
100
150
NFFD (4.7%)

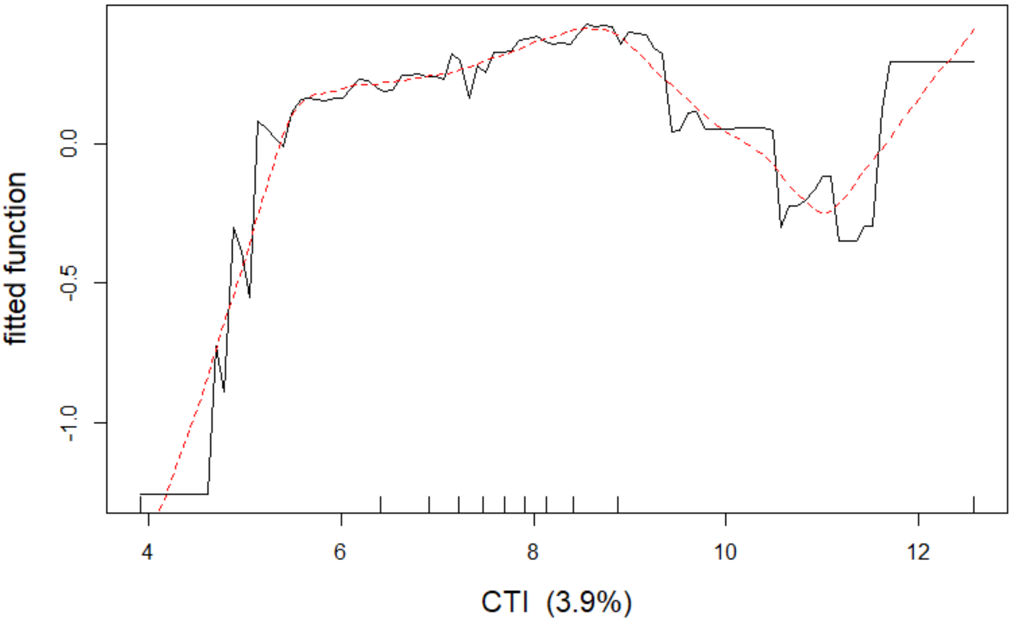
WEWP – 6


fitted function
0.6
0.4
0.2
0.0
-0.2
200
400
600
800
MSP (3.7%)

WEWP – 8



WEWP – 16



WEWP – 4 (some runs only)

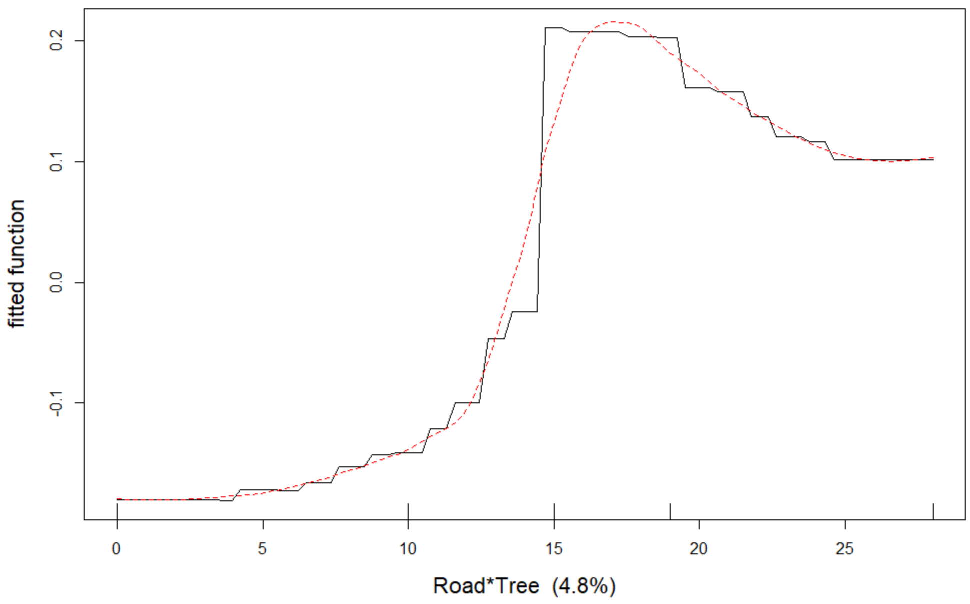
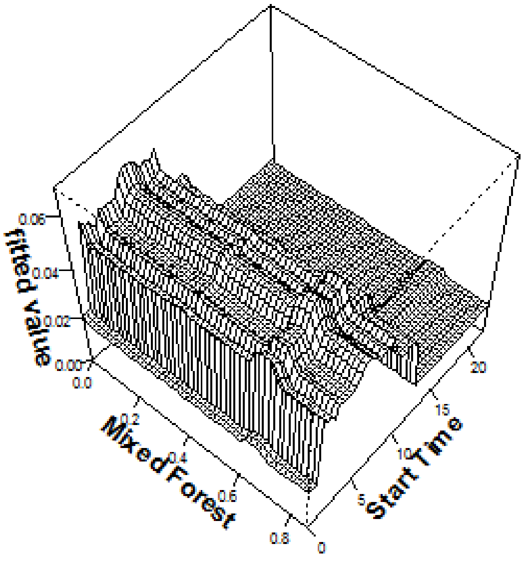
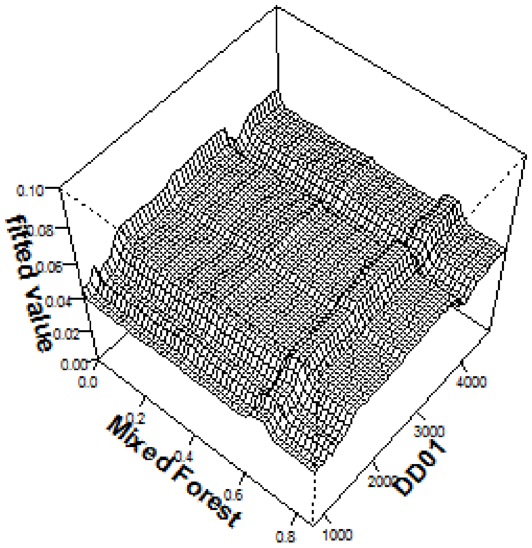


Figure 2-4A - E. Pairwise interactions between covariates with the highest-ranking interaction sizes for Olive-sided Flycatcher from boosted regression tree models for the Olive-sided Flycatcher between 1992 and 2014. A - Mixed Forest and Start Time, B - Mixed Forest and DD01, C - Mixed Forest and bFFP, D - Mixed Forest and Year, E – Slope and Taiga Needle Forest.

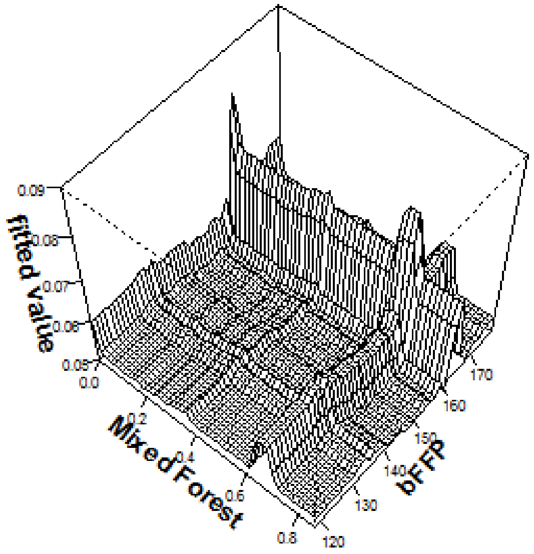
OSFL - A



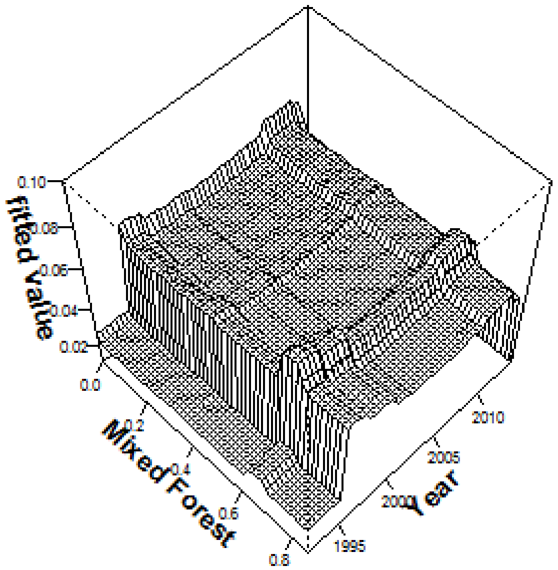
OSFL - B



OSFL – C


0.09
0.08
0.07
0.06
0.05
fitted value
0.0
0.2
0.4
0.6
0.8
Mixed Forest
120
130
140
150
160
170
bFFP

OSFL – D


0.10
0.08
0.06
0.04
0.02
fitted value
0.0
0.2
0.4
0.6
0.8
Mixed Forest
1995
2000
2005
2010
Year

OSFL – E

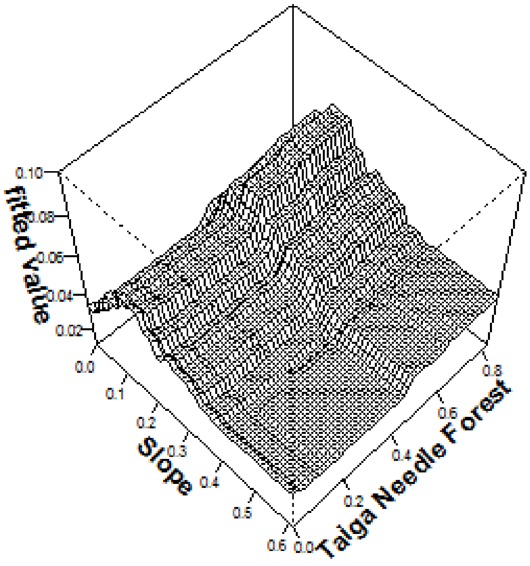
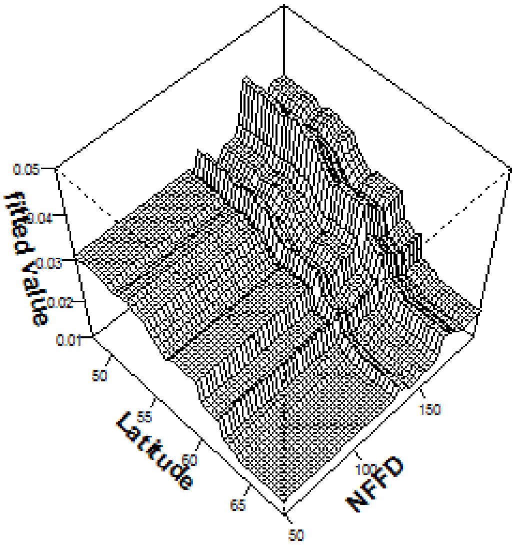
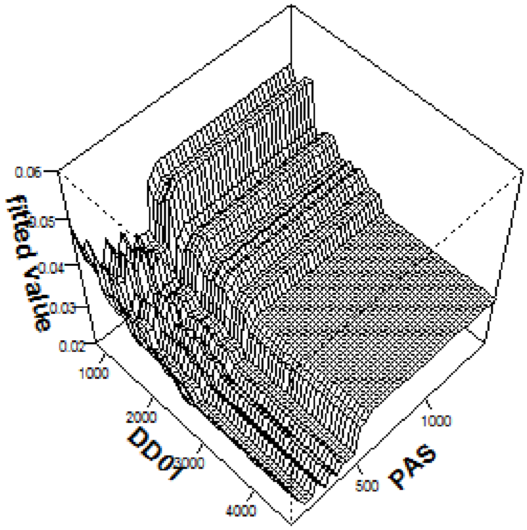

fitted value
0.10
0.08
0.06
0.04
0.02
Slope
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Taiga Needle Forest
0.0
0.2
0.4
0.6
0.8

Figure 2-5A - D. Pairwise interactions between covariates with the highest-ranking interaction sizes from boosted regression tree models for the Western Wood-Pewee between 1992 and 2014. A - Latitude and NFFD, B - DD01 and PAS, C – d2Road and Start Time, D - Mixed Forest and Start Time.

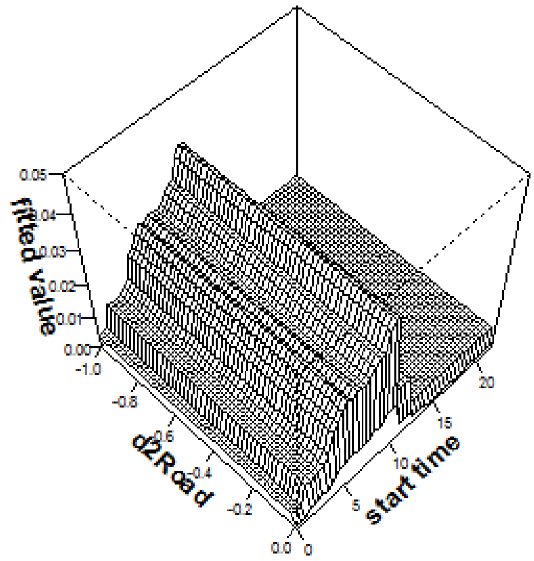
WEWP - A



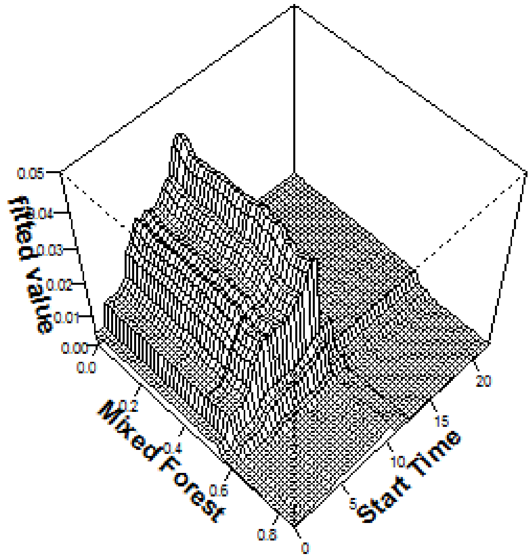
WEWP - B



WEWP – C


0.05
0.04
0.03
0.02
0.01
0.00
fitted value
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
d2Road
0
5
10
15
20
start time

WEWP – D


0.05
0.04
0.03
0.02
0.01
0.00
fitted value
0.0
0.2
0.4
0.6
0.8
Mixed Forest
0
5
10
15
20
Start Time

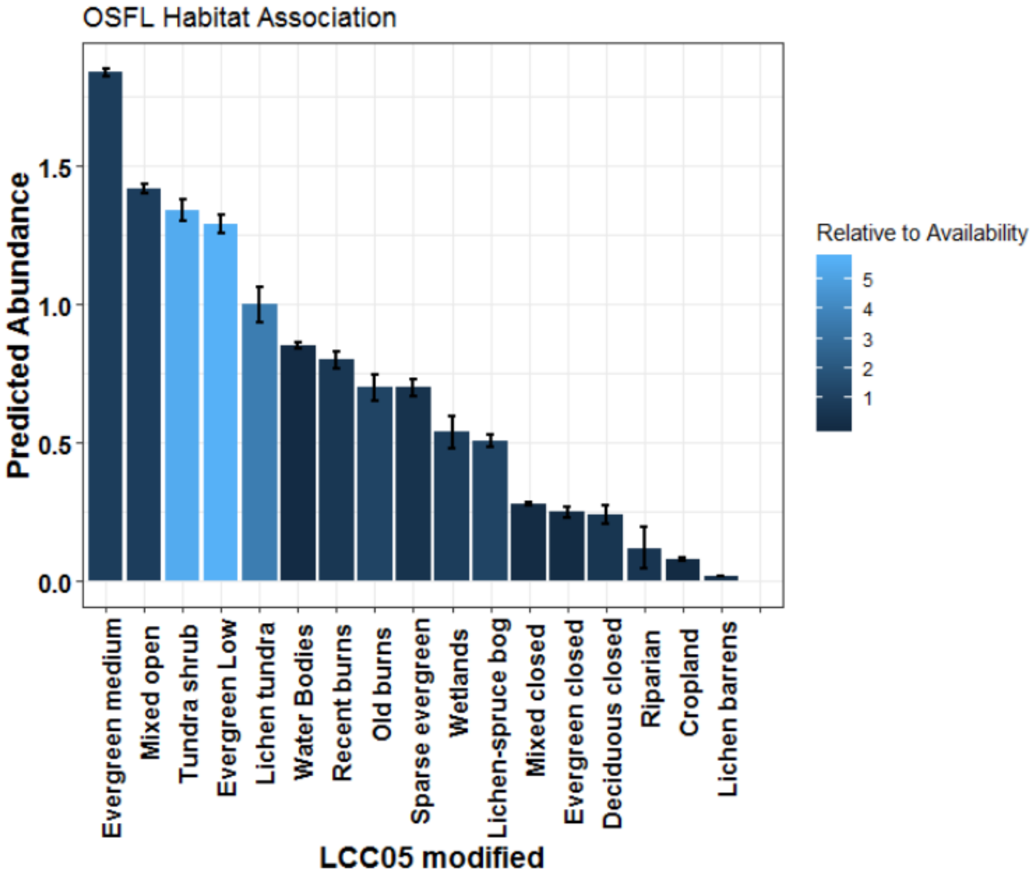


Figure 2-6. Predicted relative abundances of the Olive-sided Flycatcher in each vegetation class. Land Classification Cover Map of Canada 2005 categories were collapsed into 17 and relative abundances were calculated relative to vegetation class availability in the study region (lighter fill color indicates higher association relative to availability of each class).

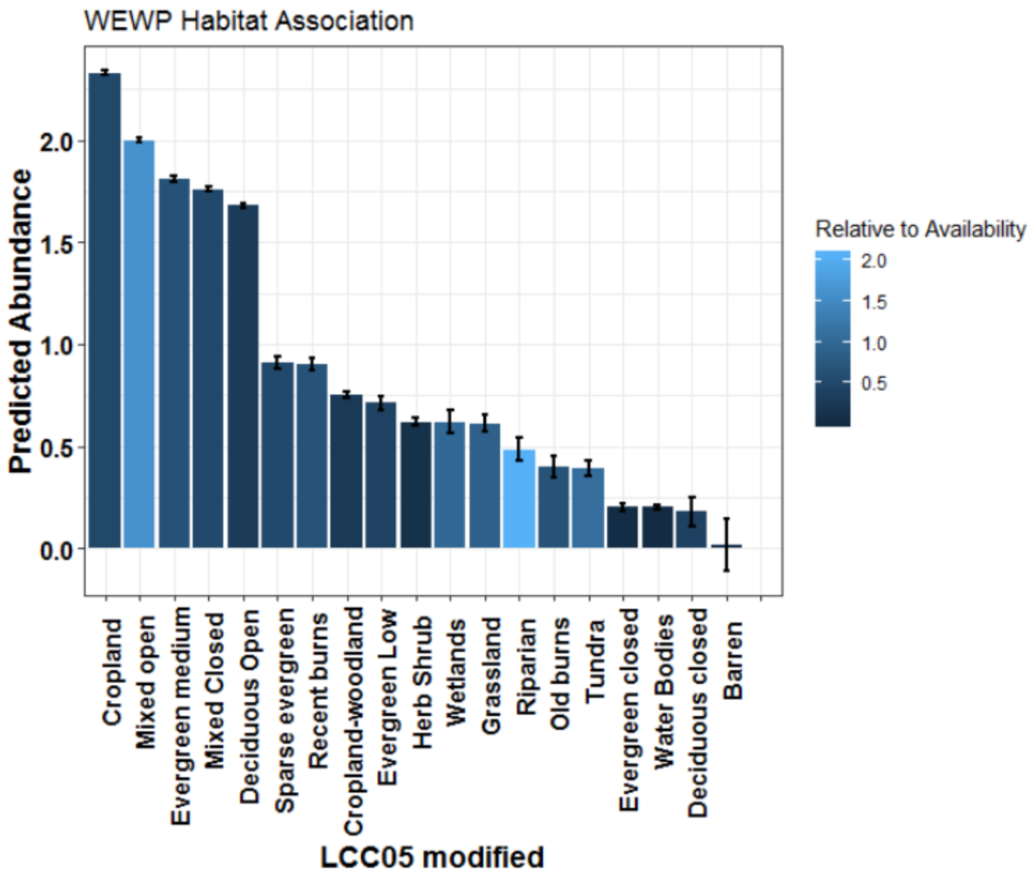


Figure 2-7. Predicted relative abundances of the Western Wood-Pewee in each vegetation class. Land Classification Cover Map of Canada 2005 categories were collapsed into 17 and relative abundances were calculated relative to vegetation class availability in the study region (lighter fill color indicates higher association relative to availability of each class).

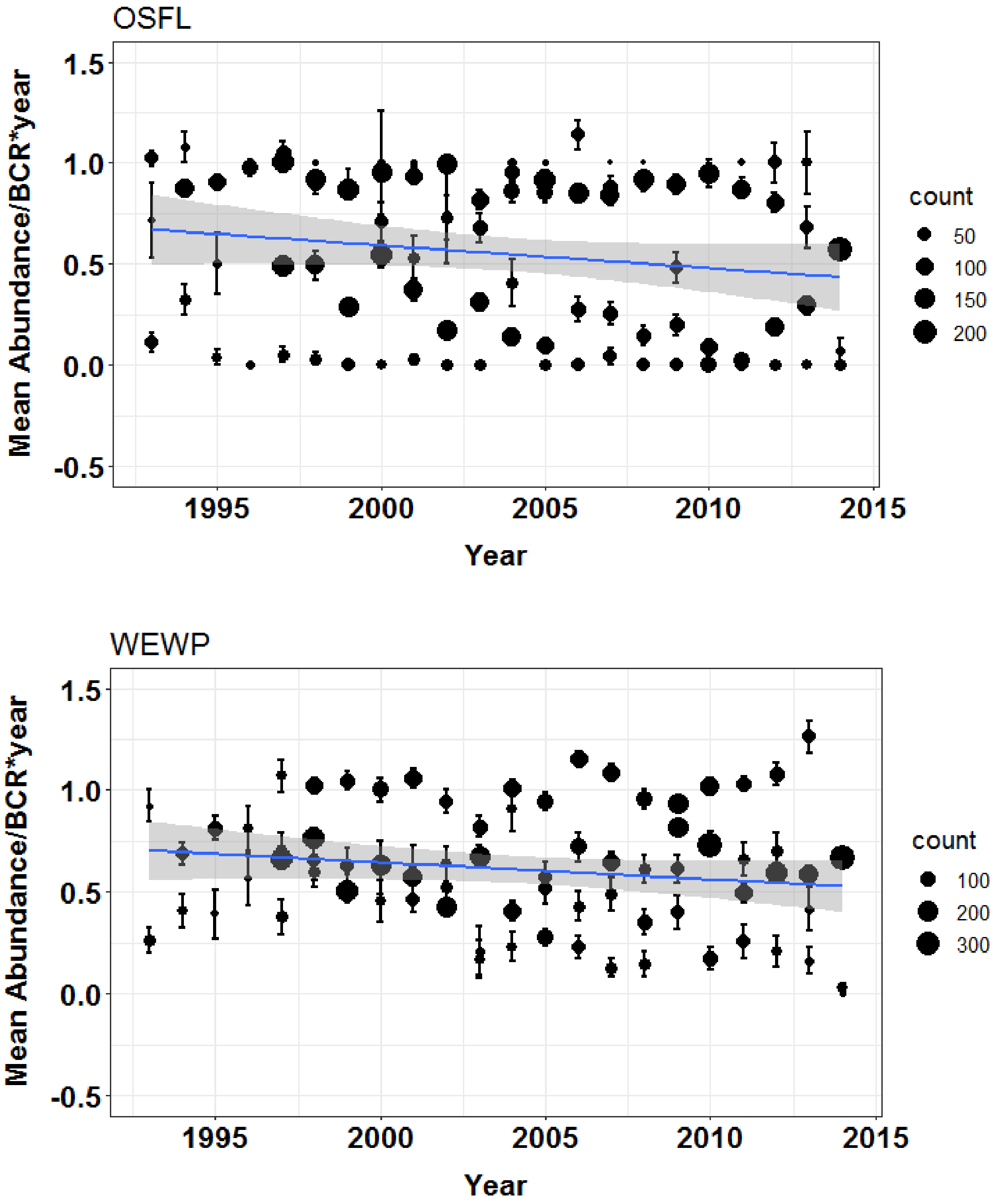


Figure 2-8. Mean abundances of the Olive-sided Flycatcher (OSFL, upper panel) and Western Wood-Pewee (WEWP, lower panel) per year and BCR between 1993 and 2014. Count of observations was mapped onto size of dot. Vertical bars indicate ± 1 SEM and the shaded area represents 95% confidence intervals on a linear model (for visualization only).

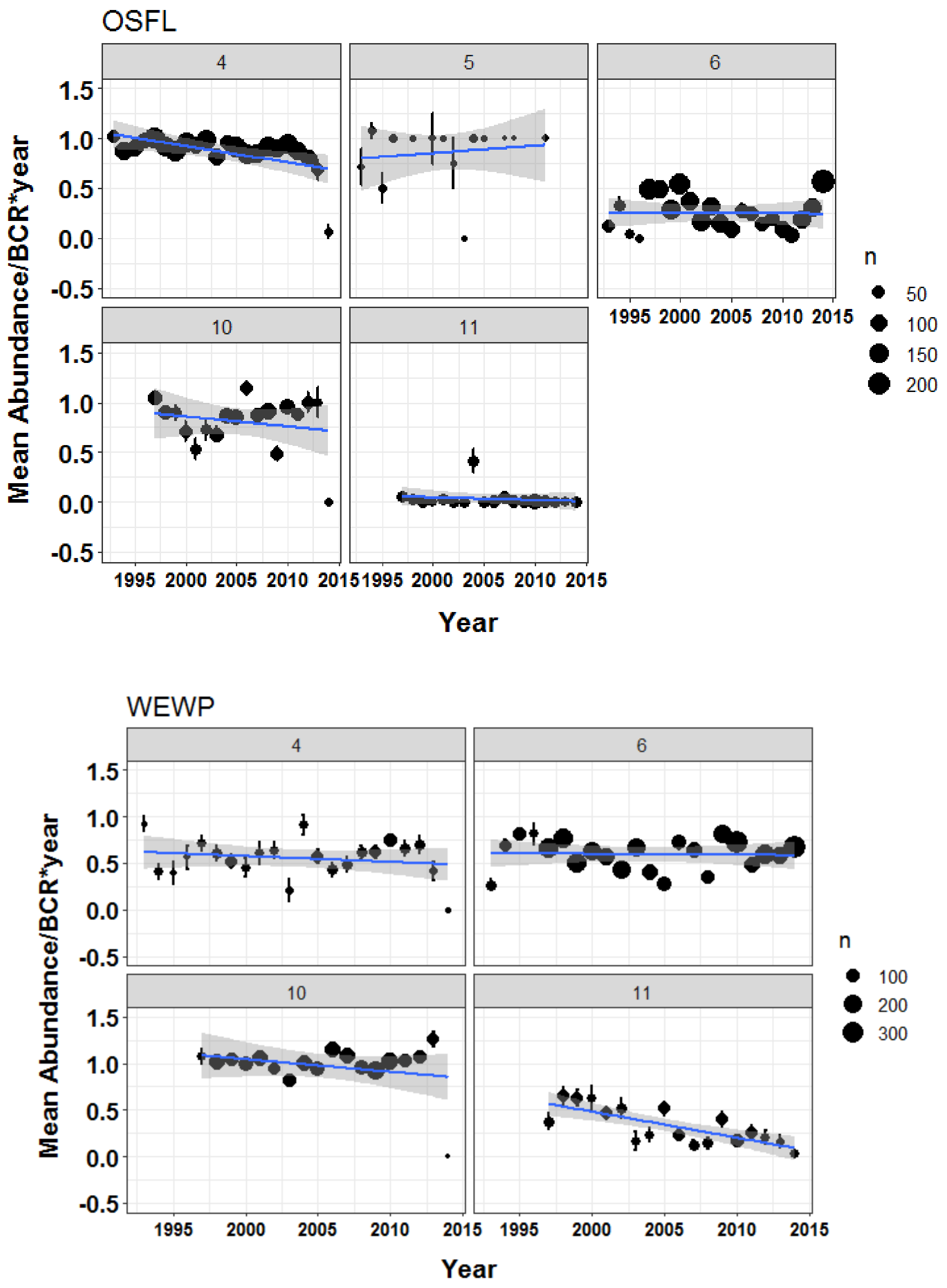
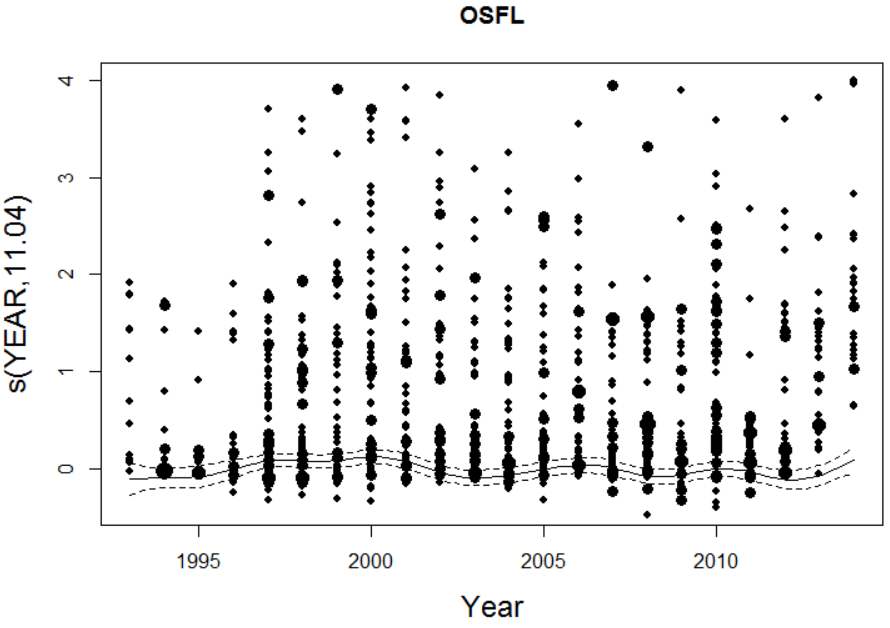
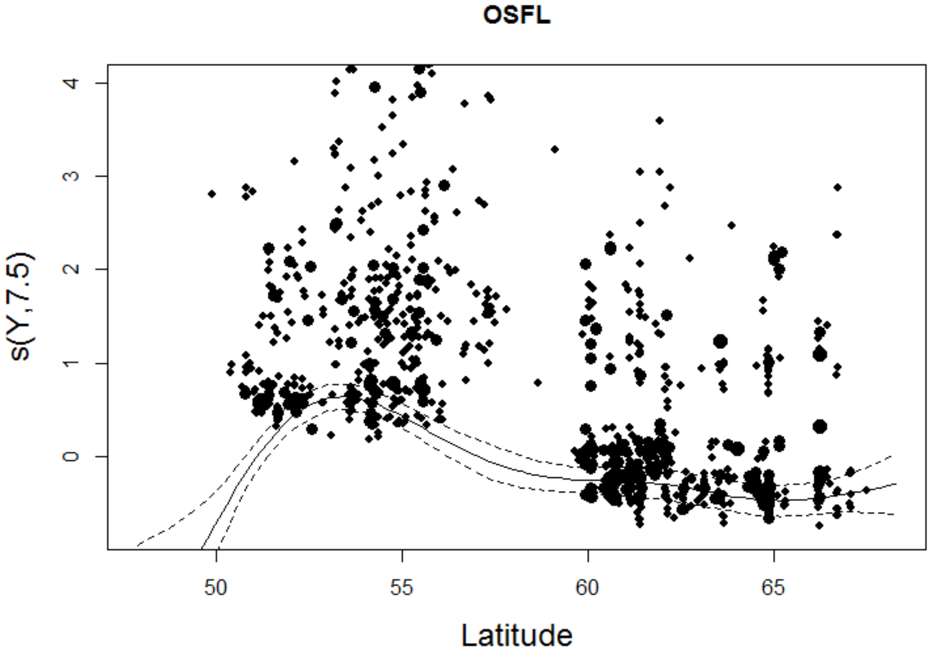
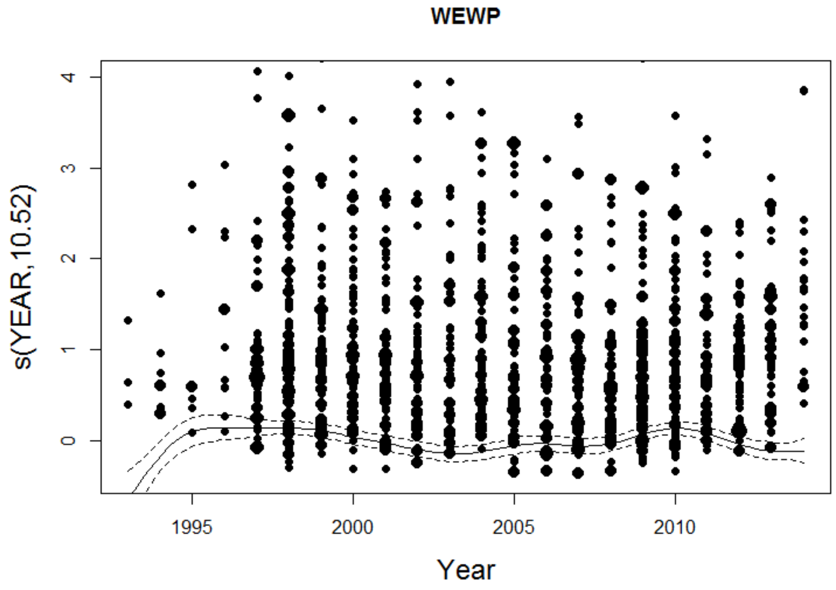


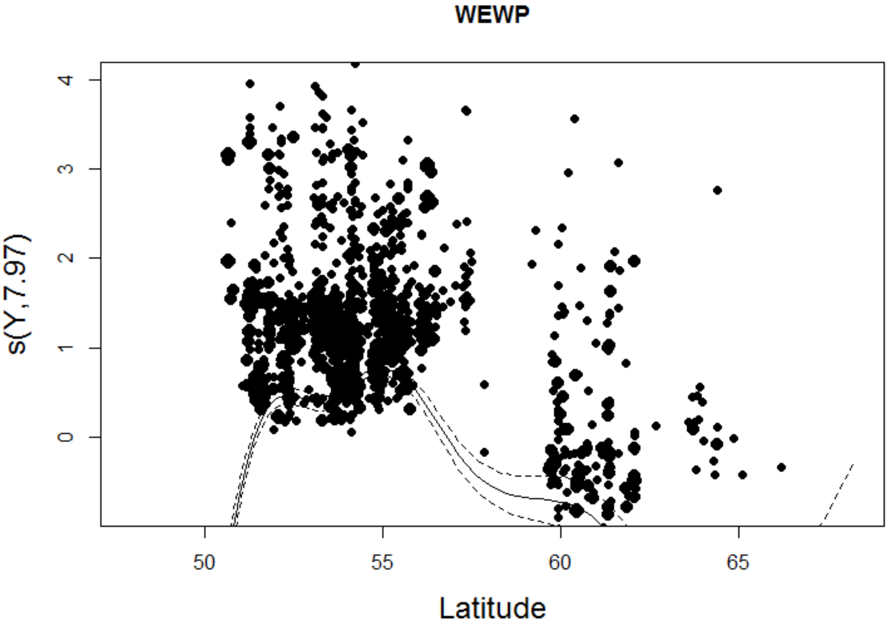
Figure 2-9. Mean abundance of the Olive-sided Flycatcher (OSFL, upper panel) and Western Wood-Pewee (WEWP, lower panel) within each BCR shown separately. Counts of observations are mapped onto size of dot, vertical bars indicate ± 1 SEM, and shaded area represents 95% confidence intervals on a linear model (for visualization only).

Figure 2-10. Smooothing functions for effects of continuous variables used in generalized additive models describing interannual variability in abundance of the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP, species indicated above each plot), dashed lines are 95% Bayesian confidence intervals (Wood 2004).






WEWP
s(YEAR,10.52)
4
3
2
1
0
1995
2000
2005
2010
Year


WEWP
s(Y,7.97)
4
3
2
1
0
50
55
60
65
Latitude

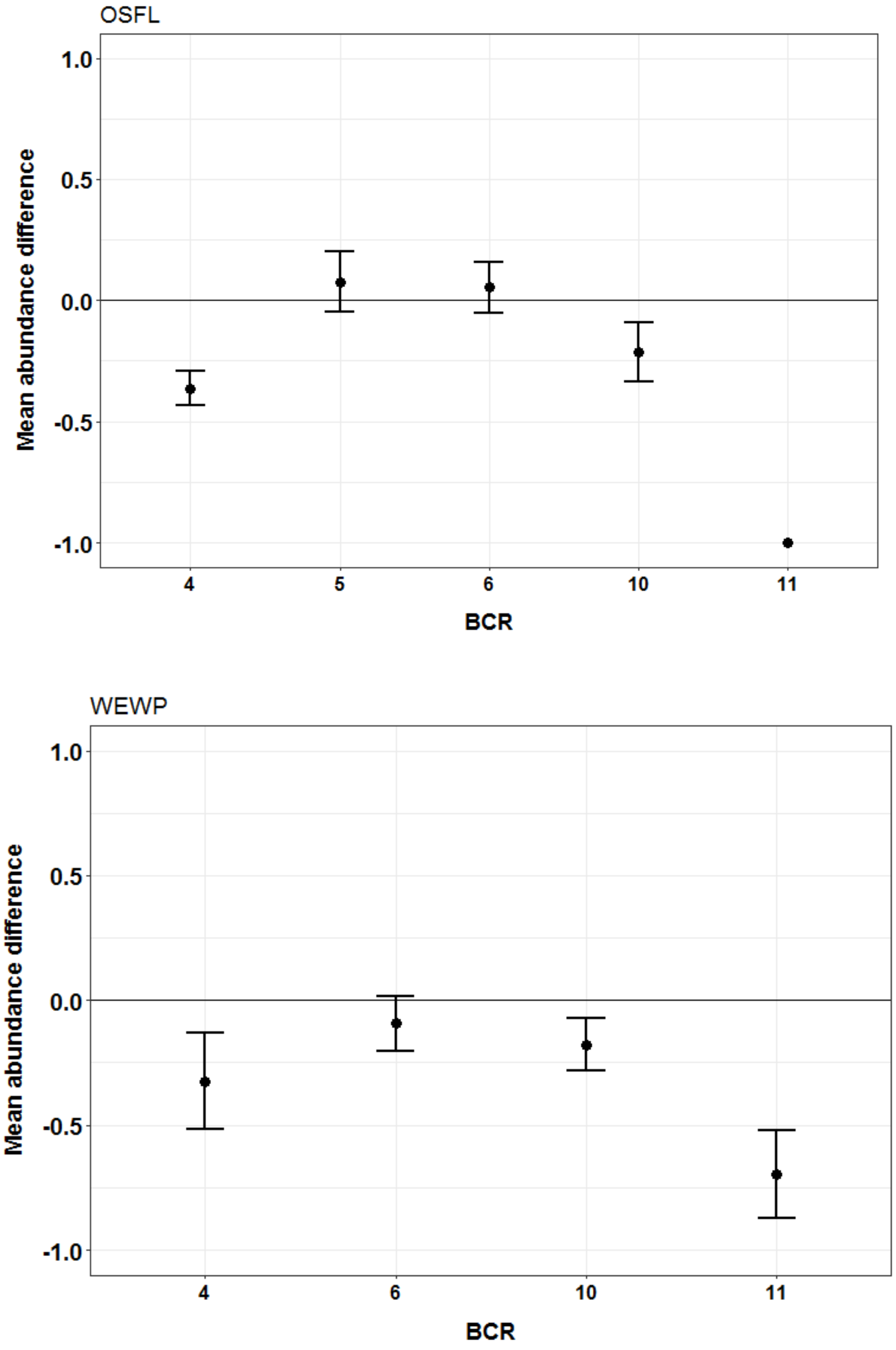


Figure 2-11. Differences between mean counts between the periods 1994 – 2000 and 2010 – 2014 within each BCR (shown with 95% confidence intervals) for the Olive-sided Flycatcher (OSFL, top panel) and Western Wood-Pewee (WEWP, lower panel).

CHAPTER III: PRESENT AND FUTURE DISTRIBUTION AND ABUNDANCE OF OLIVE-SIDED FLYCATCHER (*CONTOPUS COOPERI*) AND WESTERN WOOD-PEWEE (*C. SORDIDULUS*) IN WESTERN NORTH AMERICA; AREAS OF GAIN AND LOSS AND POTENTIAL FOR DISPERSAL

3.1 SUMMARY

The rapid pace of climate change in northern terrestrial regions of North America necessitates the identification of areas of importance for conservation planning. The pace of climate change and correlated impacts on predicted distribution and abundance is heterogeneous across geographic space, and specific to species. Thus, identification of potential microrefugia from climate change is a promising conservation approach for migratory birds that utilize the boreal forest to breed, as well as other species that depend on these systems. I developed BRT models to predict abundance of two long distance migrants (OSFL and WEWP) in northwestern North America, using climate conditions under a baseline scenario (30-yr time increments, 1981 – 2010, median of 1995), and two future time periods: 2041-2070 (median 2055) and 2071 – 2110 (2085). I explored future scenarios using two greenhouse gas concentration scenarios (RCP 4.5 and 8.5). Predicted abundances were mapped on to grids at 4 km resolution and compared between scenarios and species. Results were used to assess bioclimatic velocity, and to identify areas of potential habitat gain and loss in the region between the baseline and future scenarios. Projections to grids revealed relatively high predicted abundances as well as high bioclimatic velocity in terrestrial, montane (relatively high elevation) regions in central BC, northern BC and Yukon. Overall abundance (population size) and the amount of area considered ideal habitat (areas supporting an abundance greater than the baseline mean) declined between the baseline and future time periods, in particular for OSFL. Results for WEWP revealed increases between

the baseline and future scenarios under the RCP8.5 scenario. Future projections and range change analyses indicated that some isolated areas in the region have potential to provide macrorefugia from climate change for these two species, but there are serious reservations about potential impediments to dispersal. Areas of gain were concentrated in remote areas such as the far northwestern and northeastern parts of the study area. Large and contiguous areas of potential loss were evident throughout much of central Alaska and north-central Yukon for both species, but would likely have more impact on OSFL because this species has a more northern distribution than does WEWP.

3.2 INTRODUCTION

Losses to bird populations in North America have been attributed to forest alteration for agriculture in breeding and non-breeding areas, and other land use changes. However, widespread and long-term declines of some avian species, including those seen in areas with low levels of anthropogenic land-uses such as the northern boreal forest (Gauthier et al. 2015), also implicate climate change as a potential explanatory factor. Few studies have examined the link between climate and these declines at a sufficiently large scale to minimize noise from localized influences (exceptions include Anders and Post 2006, Wilson et al. 2011, McClure et al. 2012, Cumming et al. 2014). This is surprising given that mean temperatures in northern Canada (north of 60°C latitude) increased by 2.3°C, or three times the national average, between 1948 and 2016, with the greatest change occurring in western Canada (mostly in BC, Alberta, Yukon, NWT and western Nunavut) and during the winter months (Zhang et al. 2019). Projections for future climate change in northern Canada were as high as 6°C or more by late 21st century (IPCC 2014); however, this level has already been reached for mean winter temperatures in some regions of Yukon and NWT (Zhang et al. 2019). Climate can determine geographical distribution and abundance of organisms at broad scales, and changing climates are causing disruption to these patterns on a global scale. Climate variables contributed 77% of the variability in distribution of 98 species of Canadian boreal birds (Cumming et al. 2014). Each degree of warming is predicted to cause a non-linear increase in bird extinctions of over 100 species globally by 2100 (Sekercioglu et al. 2008).

In addition to temperature changes, northern and western Canada experienced increased precipitation between 1950 and 2007; in some areas by 40% or more, whereas central and southern Canada experienced a mixture of decreased and increased precipitation (Brandt et al. 2013). Annual precipitation increased by 32.5% in northern Canada between 1948 and 2012, compared with 18% for Canada as whole, but declined slightly in southcentral Canada (Zhang et al. 2019). Future projections for precipitation are more variable than those for temperature, but all models agree on predicted increases of moisture in the west and eastern regions of Canada in all future time periods examined, especially in the northwestern boreal forests, with increases ranging from 10% - 25% by 2100 (Price et al. 2013). Despite this, precipitation increases may be more modest than temperature increases, and this, combined with increasing fire intensity (and poorly understood interactions with insect disturbance), could transform boreal forest into a drier climate space occupied by the woodland or shrubland biome by late 21st century (Scheffer et al. 2012, Gauthier et al. 2015).

Increasing temperature and precipitation are predicted to cause expansion of the boreal forest northwards and upwards in altitude, replacing tundra and alpine habitats with forest (Gilg et al. 2012, Walker et al. 2012). However, boreal forests, although reaching further north at the expense of tundra habitats, are predicted to decrease in tree density, and the climate and rainfall envelope currently occupied by Canadian boreal forest may be replaced by one associated with shrubland by 2100 (Price et al. 2013), or with grassland or deciduous forest (Rehfeldt et al. 2012). Of particular concern in northwestern North America is the near complete replacement of the two dominant biomes of Yukon and much of Alaska (Alaska Subarctic Conifer Forest and Alaska Alpine Tundra) with Canadian Taiga by the time period 2086 – 2095 (Rehfeldt et al. 2012). Another change of note in Canada is the projected encroachment of grassland (Great Plains Grassland) biome from central Alberta to the Alberta/NWT border by 2090 (Rehfeldt et al. 2012). Some biomes must shift in their entirety to inhabit the same climate envelope they do today, i.e. there is no overlap between future and present predicted distribution of the biome, such as for the subalpine forests of BC (Rehfeldt et al. 2012). It is unlikely that vegetation associated with these biomes can keep abreast of climate change (Svenning and Sandel 2013, Stralberg et al. 2015a).

The changing temperature of the boreal forest will also impact disturbance dynamics, such as fire intensity (Kasischke and Turetsky 2006), and hydrologic systems, including disparate drying of wetlands and permafrost thaw, further impacting greenhouse gas cycles (Smith et al. 2005, Sannel and Kuhry 2011, Brandt et al. 2013, Andresen and Lougheed 2015). Globally, boreal forests sequester about 20% of the world's carbon as a significant carbon sink (Pan et al. 2011, Gauthier et al. 2015). The sometimes long-lived and slowly reproducing species of the boreal zone, such as conifers, are particularly vulnerable to rapid paces of climate change (Andrew et al. 2014). Predicted and documented impacts on birds depending on forested habitat for breeding in North America are dramatic. Suitable breeding habitat in the eastern USA, including vegetation information, is projected to change with predicted climate change by at least 10% by 2100 for almost 90% of bird species modelled (99 - 131 of 147 species, depending on GCM and climate change scenario modelled, Mathews et al. 2011). Ranges of these 147 species also had a mean projected shift in center of habitat of 98-203 km, most to the north (Matthews et al. 2011).

Altitudinal and elevational distributional shifts were predicted with changing climate for almost all 80 species of Canadian boreal birds modelled, shifting on average 18 m higher in elevation and 3 degrees North and West by the year 2100 (Stralberg et al. 2015b). The velocity of species exposure to climate change is likely increasing (Serra-Diaz et al. 2014). Devictor et al. (2008) demonstrated a steep linear increase in community temperature index between 1989 and 2006 in France, which corresponded to a 91 ± 11 km northward shift in the bird community; however, this adjustment to climate change lagged behind the climate shift by 182 ± 53 km. Organisms are thus being exposed to novel temperature envelopes, with unknown consequences to life history and community dynamics.

Climate velocity is the speed at which an organism (or group of organisms) must move to keep abreast of climate change (Loarie et al. 2009), and can be used to describe *ex situ* refugia – or areas outside of the current range that will remain relatively stable under future climate change (Carroll et al. 2015, Stralberg et al. 2018b). However, these simple velocity measures use a ratio of temporal over spatial rates of climate change, and can be improved upon with species-specific model information, improving both realism and specificity of predictions (Carroll et al. 2015). For example, most species will respond to a suite of factors, not a single climate variable, and these factors may be regionally-specific (Serra-Diaz et al 2014). Bioclimatic (or biotic) velocity, in turn, predicts species-specific changes to range over time (Serra-Diaz et al. 2014), and is sometimes referred to as a “gradient approach”. In contrast, an “analog approach” uses metrics describing the shortest distance(s) from current climate conditions that species would need to move in future time periods to occupy areas with similar climate conditions (a “forward velocity") or, it can be calculated "backward" to identify multiple locations according to their refugia potential, placing more emphasis on sites valuable for broader biodiversity conservation, rather than species-specific approaches (Carroll et al. 2015). These approaches; analog in particular, have recently become central to broad-scale conservation planning for future climate macrorefugia for multiple species and conservation of biodiversity in areas of rapidly changing climate (Stralberg et al. 2018b), and have produced disparate and sometimes unexpected results across approaches (e.g. see Carroll et al. 2015). For example, some of the direst predictions involve species and communities of the Amazon basin and Central America with narrow thermal tolerances, endemics with narrow ranges, and small population sizes (La Sorte et al. 2014, Carroll et al. 2015).

Impacts of climate change on birds at broad geographic scales are often species-specific, but typically predict overall decline. In addition to habitat losses (mostly to agriculture), and deliberate poisoning, climate change has contributed to the estimated decline of 85-95% of the insectivorous Rusty Blackbird (*Euphagus carolinus*) since 1966, and likely caused a 143 km northward shift in its range (Greenberg and Matsuoka 2010, McClure et al. 2012). Climate warming and land uses have desiccated and degraded necessary wetlands to support this species (Greenberg et al. 2011).

Long-distance migrants may suffer population declines from climate change to a greater degree than short-distance migrants, possibly because they do not adjust phenology to the same degree as other groups of birds (Miller-Rushing et al. 2008, Laaksonen and Lehikoinen 2013). Population decline has occurred as a consequence for inadequate adjustment to timing of reproduction with climate change for long-distance migrants breeding in Europe (Saino et al. 2011). In addition, habitat availability is projected to decrease more for long-distance migrants than short-distance migrants or residents in eastern USA over this millennium (Matthews et al. 2011). Forest species are also at greater risk compared to many in other habitat guilds, because climate change has contributed to tree mortality globally (Allen et al. 2010), and is projected to further alter forest dynamics and tree density (Allen et al. 2010, Matthews et al. 2011). Change in migration date was the only significant predictor of many factors explaining population declines of 100 European bird species between 1990 and 2000, whereas in an earlier time period (1970 – 1990), other factors were better predictors, such as body mass and a dependence on farmland habitat (Møller et al. 2008). In addition to long-distance migrants, aerial insectivores have been identified as an avian group particularly susceptible to impacts of human-induced climate change (e.g. Sillett et al. 2000, Both and Visser 2001). Aerial insectivores have been declining since 1980, especially in north and northeastern North America (Nebel et al. 2010).

Species distribution models have become important tools in conservation and management of sensitive or threatened species (Franklin 2013, Guillera-Arroita et al. 2015, Engler et al. 2017, Urbani et al. 2017). Results of detailed SDM with the most comprehensive data available can identify areas of relatively high abundances of vulnerable species at present and under future scenarios, and potentially provide information regarding potential refugia from climate change (Noss 2001), here akin to large-scale or “macrorefugia” (Ashcroft et al. 2010). These are habitats that can support future abundances of species under changing climates (both *in*- and *ex-situ* refugia, or within present range or outside), assuming dispersal is possible, which is generally a realistic assumption for migratory birds as a relatively mobile taxon (Tingley et al. 2009, Carroll et al. 2018), and that habitat characteristics such as vegetation can support the species (Stralberg et al. 2015a). For example, Environment and Climate Change Canada (ECCC) had a mandate to complete a recovery strategy for species that are listed as threatened within five years of the listing (such as the Olive-sided Flycatcher listing in 2016 as "schedule A threatened"), prompting a nation-wide modeling exercise to identify critical habitat for the species (Haché et al. 2014). Several agencies and organizations have called for higher levels of protected area to adequately protect biodiversity and/or vulnerable species under present and future threats of anthropogenic land uses and climate change (e.g. 17% of terrestrial areas conserved in Canada by 2020, Convention on Biological Diversity, International Boreal Conservation Science Panel), making SDM exercises paramount in prioritization of areas for conservation (Stralberg et al. 2018a). The conservation applications of SDM are high priority for adequate conservation of biodiversity in the face of changing climates (Stralberg et al. 2018a, b, Langham et al. 2015).

Appropriate use and utility of SDM

Demand is growing for mapped predictive products for conservation and land management, and uncertainty in prediction can increase with extrapolation into future times or spaces, making careful technique and links to ecological principles critically important (Elith and Leathwick 2009). A large body of literature on techniques and tools of modeling techniques make it difficult for managers, field biologists and non-specialists in modeling to keep abreast of advantages and disadvantages of different modeling methods (Austin 2007, Guisan et al. 2013). Predictions of SDM need to match metrics; inputs will differ considerably if the desired prediction is likelihood of occurrence or Area of Occupancy, a criterion used in assessment of IUCN Red List (IUCN 2012, Guillera-Arroita et al. 2015), relative abundance, potential distribution, realized distribution, prediction into future climates or places, or some measure of fitness. In a recent review of prediction metrics by Westwood (2016), 23% of 128 published studies reported incompatible predictions for the data type used, and many (68%) did not include an expression of uncertainty. Application of results of these models could lead to erroneous conservation or management decisions (Pearson et al. 2006). Choice of model algorithm can also influence predictions, and again should be selected with data type and limitations well-considered (Pearson et al. 2006). Uncertainty in predictions under various climate change and emission scenarios, and different climate modeling procedures, needs to be assessed and reported for sources of potential error to allow useful interpretation (Stralberg et al. 2015b). The importance of complete disclosure of uncertainty and model limitations cannot be understated: uncertainty in SDMs used to identify critical habitat for a rare species could lead to social and economic conflicts over land use, resulting in costly measures to intervene at one extreme, or to species extinction at the other (Guisan et al. 2013). Output metrics also need consideration, because a once very common procedure to convert all output metrics into binary responses (yes or no response) can diminish the usefulness of model results in several ways; one of which is a lack of recognition of imperfect detection (Guillera-Arroita et al. 2015).

An important source of uncertainty in applications of SDM to climate projections is from selection of General Circulation Models (GCMs) used to simulate the response of climate to changes in atmospheric greenhouse gas emissions (Stralberg et al. 2015b). GCMs have inherent uncertainty from difficult-to-predict climate and weather patterns (Allen et al. 2000), such as the influence of clouds and radiative effects, changes to hydrological flow, such as disappearance of ponds, and the potential for positive feedback between different systems (Price et al. 2013). Nonetheless, GCMs are based on similar three-dimensional representations of the global atmosphere and oceans and the transfer of energy within and between them (Price et al. 2013), and they generally perform well for the Northern Hemisphere (Scherrer 2011). Almost all predict that the greatest warming will occur at high latitudes (Alo and Wang 2008). Models are often combined as averages into ensembles, to take advantage of varying strengths of difference approaches; however, non-independence and diminishing new information occurs after a certain number of contributing models (Pennell and Reichler 2011, Fernandez et al. 2019). Of the four most utilized emission scenarios established in 2000 by an IPCC special report on emissions scenarios (Price et al. 2013), recent emissions have already exceeded those one commonly–used A2 (Low) scenario (to 9.9 GtC/yr produced from fossil fuels with net atmospheric growth of CO_2 of 4.7 ± 0.1 GtC/yr, Le Quere et al. 2018). Global atmospheric CO_2 concentration reached 413 ppm at the time of writing (January 2020), an increase of 66% over pre-industrial levels (Le Quere et al. 2018). Uncertainty from GCM in model predictions can increase into the future, but all agree that warming will continue until the minimum year of 2040, because most of the warming occurring until then is from emissions that have already occurred (Price et al. 2013).

Extrapolation or predicting values in unsampled locations or times such as future climate scenarios has been identified as a serious source of uncertainty in SDM (Peterson and Soberón 2012, Franklin 2013, Merow et al. 2014). Because SDM results are based on the assumption of equilibrium, extrapolation into new times or climate envelopes faces challenges (Guisan and Thuiller 2005, Franklin 2013). The assumption of equilibrium is not always accurate with populations in newly acquired habitat, such as invasive species, or those dispersing in response to changing climates, or altering distribution in response to local land use. In addition, SDMs essentially describe a realized niche for a species, or a reduced set of predictions from the fundamental niche, because of interactions with other species such as competition, predation, parasitism, or impediments to dispersal (Guisan and Thuiller 2005, Elith and Leathwick 2009). Inter-specific interactions and entire community food web dynamics do not necessarily occur in similar ways or simultaneously in the new space or climatic envelope, adding uncertainty to climate change projections (Matthews et al. 2011, but see Hof et al. 2012, Arctic Fox). Dispersal is also difficult to estimate, unless species-specific data are available on dispersal capabilities and fitness in new habitats (Methorst et al. 2017), which is rare. Studies at smaller geographic scales, such as regional modelling efforts, can help ameliorate some of the challenges with non-equilibrium conditions (Austin 2007).

Extrapolation into unknown climate envelopes or locations can be further improved using mechanistic approaches that include community dynamics (Hof et al. 2012) or using linkages between outputs of modeling exercises (Buckley et al. 2010, Buckley et al. 2011, White et al. 2011, Franklin 2013). Naujokaitis-Lewis et al. (2013) compared future projected distributions with climate change and associated uncertainty using the results of five SDM projections as layer inputs in a metapopulation dynamics model for the Hooded Warbler (*Setophaga citrina*). In a relatively complex approach, requiring detailed species-specific data on physiology, dispersal distances, and projected land use, Methorst et al. (2017) incorporated thermal metabolic optima in climate-based SDM to predict future distribution of the Ortolan Bunting (*Emberiza hortulana*) in Europe, and then refined projections using projected land use change and dispersal ability of the species.

Further utility of SDMs will require tighter links to ecological theory in areas such as dispersal and migratory processes, population dynamics, source-sink dynamics, and more detail on biotic interactions, such as the inclusion of competition with other species (Guisan and Thuiller 2005). Interdisciplinary use of products of SDM, such as by biogeographers and social scientists, has grown slowly, possibly because SDM researchers have not always disseminated their work in way that could be understood by non-specialists. New techniques include disentangling relative effects of different land uses from each other, and from climate, on abundance of individual species and communities of birds, to inform conservation and land management in the face of changing climate and continued pressures from land use (e.g. for Danish birds, Bowler et al. 2018).

Little guidance is also available on how results of modeling exercises can guide conservation decision making: a review of SDM literature found that less than 1% of published papers on SDM between 1992 and 2011 were specifically targeted at conservation decisions (Guisan et al. 2013). Illustrative examples of direct links to utility exist in grey literature, such as identification of critical habitat for persistence or recovery of threatened species, which is required by law in Canada (e.g. Haché et al. 2014), and in selection of area for reserves (Heinrichs et al. 2010). Areas that supported exceptionally high diversity of plants and animals in northeast New South Wales, Australia were identified in part using results of SDM, for exclusion from logging (Ferrier et al. 2002). It will become increasingly important for SDM researchers to make results and products less esoteric for interdisciplinary researchers, managers and the public, to increase uptake of SDM products in conversation planning under climate change.

Despite these limitations, SDM represents one of the only tools available for assessing impacts of climate change and land use on species distribution, range and abundance at multiple geographic scales. In future projections under climate change scenarios, the signal of climate change exceeded the data noise from other sources of error for most species of the North American boreal, providing robust predictions for conservation (Stralberg et al. 2015b). Management recommendations for ecosystems of low climate stability, but with relatively high vegetation intactness, such as northern North America, include maintaining vegetation intactness, including dispersal pathways, identifying areas of potential climate refugia, and monitoring species that may be particularly vulnerable to climate change (Watson et al. 2013). A logical next step is regional modeling to corroborate results of continental-scale techniques and identify geographically-specific contributions to distribution. Regional model results on target species or groups of species will inform local conservation and management objectives. This is essential in northern North America, a region that experienced more than double the global average in warming between 2006 and 2015 (Allen et al. 2018), with temperatures in the boreal zone predicted to continue to increase for decades to come (Price et al. 2013).

Boosted regression trees (BRTs) have particular strength in specificity, accuracy and interpretation when applied to species distribution modelling. BRTs are applicable for modelling exercises involving many predictors of varying types, and prediction to unknown data locations (interpolation) or to grids is a desired outcome (Elith and Leathwick 2009). Examples of BRT application include measures of environmental suitability under various climate and land use scenarios (Zamora-Gutierrez et al. 2018), predicting outcomes of invasive species (Carboni et al. 2016), avian diversity in various agricultural landscapes (Steel et al. 2017), multispecies responses to climate change, as well as in projections of potential refugia (Langham et al. 2015, Stralberg et al. 2015a, Stralberg et al. 2015b).

Results of many regional-based studies were compiled and adjusted for disparate sampling methodology to amass a broad-scale, spatially-explicit avian data set by the BAM research team (Barker et al. 2015). These data are utilized here to generate regional models for two vulnerable bird species in northwestern North America under current and predicted climate conditions.

Objectives

My specific objectives in this chapter were to:

1) generate spatially-explicit density estimates for OSFL and WEWP based on landcover, topography, disturbance, and current climatic conditions, and for climatic conditions in two future time periods under two climate change scenarios;

2) use spatial projections to map predicted distribution and abundance for both species under current climatic conditions, and two future time periods under two climate change scenarios;

3) use density estimates to generate abundance (population size) estimates for current climatic conditions and two future time periods under two climate change scenarios;

4) assess uncertainty for these predictions of abundance and map predicted sampling error for current and future scenarios;

5) estimate bioclimatic velocity for these two species in northwestern North America under these two potential climate change scenarios, and to

6) estimate northern range boundary and range filling, and projected large-scale differences between current extent and two future time periods under two climate change scenarios.

3.3 METHODS

Study area

My study area encompassed the northern and western region of North America, including much of Alaska, all of Yukon, western NWT, northern and central BC, western Alberta, corresponding to Bird Conservation Regions (BCRs, North American Bird Conservation Initiative, 4 Northwestern Interior Forest, 5 Northern Pacific Rainforest, 6 Boreal Taiga Plains and the northern region of BCRs10 Northern Rockies and 11 (Prairie Potholes). From approximately 70° N, -160° W (on the North Slope Alaska) in the northwestern corner to 50° N, -96° W (in northern Saskatchewan) in the southeastern corner (Fig. 2-1), this encompassed an area of approximately 2.3 million km^2.

The study area included boreal and hemiboreal zones, defined as the broad, circumpolar vegetation zone of northern latitudes covered with mostly forest, lakes, rivers and wetlands and vegetation, and the area transitional to the boreal with overlap between boreal and temperate vegetation (Brandt et al. 2013, Price et al. 2013). The vegetation of the western boreal and hemiboreal is dominated by cold-tolerant *Picea* spp. and deciduous trees (e.g. *Populus* spp.), with tree density varying geographically (Brandt et al. 2013). Moisture gradients influence vegetation greatly and also vary geographically across the region (decreasing from west to east for example, Brandt et al. 2013). The major processes that contribute to disturbance dynamics are fire, insects, and disease, and to a lesser degree in the northern boreal, land use changes (White et al. 2017). See *Chapter II* for a more complete description of the study area.

Data sources

Bird data

I obtained abundance-absence data from the BAM database (see *Chapter II*). I collected 15,637 observations of point count surveys where at least one OSFL or WEWP was detected between 1990 and 2014, in 7397 unique locations, to develop models. Surveys conducted outside of the boreal or hemiboreal zone were removed (1568 unique locations remained). A total of ~1,500 and ~2000 non-detections (surveys with abundance of zero) were included in each dataset (respectively for each species). A total of ~3000 and ~4000 (depending on run) measures of abundance or absence remained for OSFL and WEWP, respectively, to use in models (Fig. 2-1). Observations included in each iteration of models were averaged across surveys conducted at the same site and year, and selected in a weighted bootstrapping procedure according to how many were available for each group and location (irrespective of year). This was done to limit geographical bias and possible autocorrelation arising from unequal numbers of samples across geographic space.

Climate and land cover layers were chosen based on expected influence on abundance of the two species (as well as lowest pair-wise correlation values with other similar predictors, e.g. Pearson correlation values of $|r| < 0.7$ (Dormann et al. 2013). Although BRTs handle correlated variables without changing results markedly, multicollinearity can increase error in extrapolation (Dormann et al. 2013), and make general interpretation more difficult. Nine land cover layers were chosen and adapted from 2005 North American Land Change Monitoring System (NALCMS; MODIS data; 250 m spatial resolution; Commission for Environmental Cooperation 2014). I obtained a forest loss layer from Global Forest Change for 2000 to 2016 (Hansen et al. 2013) and a topography layer (Pacific Northwest Topography) from Data Basin (USGS TOPO30, Phil Nott, The Institute for Bird Populations 2018). I obtained spatially interpolated bioclimatic variables from the AdaptWest Project (Wang et al. 2016) for current normal (“baseline” of 1981 – 2010, median of 1995), and two future time periods: 2041-2070 (median 2055) and 2071-2100 (median 2085) were chosen with high (RCP8.5, Representative Concentration Pathways) and comparatively low (RCP4.5) greenhouse gas emission concentrations for each. Ensemble projections were downscaled and then averaged across 15 Coupled Model Intercomparison Project phase 5 (CMIP5) models (corresponding to the 5th IPCC Assessment Report for future projections) that were chosen to represent major clusters of similar models (Wang et al. 2016). RCP4.5 and RCP8.5 were considered medium and high greenhouse gas concentration scenarios, with CO_2 levels predicted to reach peaks of ~650 ppm and ~1370 ppm (radiative forcing levels of 4.5 W m^{-2} and 8.5 W m^{-2}) by 2100 respectively (Riahi et al. 2011, Thomson et al. 2011, van Vuuren et al. 2011). RCP4.5 is a stabilizing scenario (before 2100), and for realization would require major shifts to electricity use, the use of lower emission energy technology, carbon capture and geologic storage technology (Thomson et al. 2011). RCP8.5 does not assume stabilization, but rather a continued use of fossil fuels at similarly increasing rates as occurs currently (Riahi et al. 2011), but it may overestimate the availability of these fossil fuels.

I chose the following climate variables: frost free period (bFFP), mean annual radiation (MAR), mean summer precipitation (MSP), mean temperature of the warmest month (MWMT), number of frost free days (NFFD), summer heat moisture index (SHM) and average summer temperature from June to August (Tave_sm).

All raster layers were resampled at 4 km resolution and cropped to northwestern North America in ArcMap 10.4, then projected using the CRS commonly used by members of the BAM research team (Canadian Lambert Conformal Conic, CLCC, ellps and datum WGS84) in R (R version 3.5.1, R Core Team 2018) for consistency. Raster layers were combined into a raster stack using the “raster” package in R.

I examined and quantified spatial autocorrelation using residuals from BRT models and using a non-parametric equivalent of Moran’s *I* test statistic: a Mantel test that uses a randomization procedure of two matrices; one for spatial differences between values and one for measured differences, and then examines differences between matrices across 2000 permutations (Dormann et al. 2007). Both patterns of model residuals and Mantel tests did not indicate the presence of significant spatial autocorrelation ($P > 0.05$) for either species in various scenarios and data subsets.

I developed boosted regression trees using the “gbm” package in R (Ridgeway 2010 – GBM: Generalized Boosted Regression Models, specified as a Poisson distribution) utilizing R version 3.5.1 (and RStudio version 1.1.423) to explain and predict abundance of WEWP and OSFL using a suite of *a priori* selected climate, landcover, topographic raster and one disturbance layer, using optimal user determined settings with guidelines in Elith et al. (2008), updated in 2017 (Elith and Leathwick 2017). In addition to data collection and management, BAM team members have developed statistical methods to account for several sources of heterogeneity that may influence occupancy detection, such as different data collection or survey protocols, survey effort, as well as environmental factors influencing detectability of birds (Sólymos et al. 2013, Barker et al. 2015), culminating in the “QPAD” approach of Sólymos et al. (2013). These species-specific offsets for imperfect detection, based on habitat type, time and other factors during surveys, were included in the modelling procedure as correction factors for raw survey counts. Predicted abundances determined from models were then mapped onto grids for seven climate, six landcover layers, one topography, and one disturbance layer for each scenario in R.

Projected distribution and relative abundance

BRT models were fitted to future climate projections (two time periods, 2041-2070 and 2071-2100, and two emission scenarios) to predict abundance and distribution across the study area. A baseline period of 1981-2010 was used for comparison (hereafter referred to as the “1995”, “2055”, and “2085” time periods to represent the median year). Total projected abundance was calculated by multiplying the predicted density estimates per 4 km grid cell by the size of the grid cell (1600 ha) for each cell, and then summing these predicted values across all cells for a projected estimate of total number of males in the study area for each species. I generated 25 bootstrap iterations of sampling procedures and models for each species under each time period and each climate change scenario, for a total of 250 boosted regression tree models. I estimated sampling error using the coefficient of variation (standard deviation of the mean) across bootstrap samples and plotted these to grids for a spatial representation of sampling uncertainty.

I calculated Cohen's *d* statistic to quantify uncertainty (similar to an effect size) for projected changes by comparing mean abundances (difference between means) divided by the pooled standard deviation in each future time period compared to the baseline period (Cohen 1992, Stralberg et al. 2015b).

Ideal habitat and bioclimatic velocity

For a rough estimate of variation in "ideal" habitat to support each species across scenarios (within the study area, not entire range), I calculated the proportionate area that exceeded an abundance threshold, defined by the mean abundance of each species (per pixel) under baseline conditions during the time period 1995. These were summed and divided by the total number of pixels considered in analyses under each scenario (to create a proportion).

In order to examine and describe potential changes to temperature regimes that species are predicted to be exposed to in the region (Loarie et al. 2009), I calculated a species-specific climate velocity index by determining the change in abundance (from BRT predictions) between a future and baseline time period, per time period (in years), and then dividing this change by the local spatial gradient (range of abundance per area in km^2, Serra-Diaz et al. 2014, “bioclimatic velocity”). These velocity indices were then plotted to grids for visual interpretation.

Refugia

In order to examine spatial distribution of potential losses and gains, I used predicted abundances from BRT model results to predict future range gains and losses. Data from rasters from all scenarios were reclassified using the mean abundance from the baseline period (below the mean was 0 and above the mean was 1) to allow comparisons and calculations among multiple rasters (and for ease of visualization). I then used these predictions to calculate the relative “losses” and “gains” in areas of high and low predicted abundances (similar to Matthews et al. 2011) between the baseline time period and one future time period. I also calculated rough extent estimates of these gains and losses by summing cell counts within each category. Gains are one method of several (see Ashcroft 2010, Keppel et al. 2015) that can be used to estimate refugia, or more specifically, areas of macro-refugia from climate change within suitable habitat.

Vegetation layers were held constant and only climate layers were used in future projections for these models, adding some potential error to predictions due to assumed decoupling. Presumably, however, vegetation will keep abreast of climate change to some degree, making future vegetation layers only partially decoupled from climate. Therefore, I developed and ran a second set of models using only climate layers (and one topography layer) for comparison. I estimated gains and losses using the intersection between two rasters for WEWP to simulate a 30 – 60 year time lag from vegetation change using these climate-only models to allow comparisons (Stralberg et al. 2015b). No time lag (0 years) from vegetation change was considered most likely for the OSFL, so the core area predicted for 2085 was used and compared to the baseline to assess relative changes in abundance across the study area for this species.

3.4 RESULTS

Projected distribution and relative abundance

For models used for prediction to grids under baseline and future climate conditions correlation values averaged 0.67 to 0.68 and averaged deviance was 0.46 and 0.44 for OSFL and WEWP, respectively (Table 3-1). Projections onto grids using seven current (baseline) climate, five landcover layers, one disturbance layer and one topographical layer revealed a high relative predicted abundance of OSFL in the north and western regions of the study area (Fig. 3-1A). The central and southern interior of BC and south-central Yukon had particularly high predicted relative abundances of OSFL. Relatively higher predicted abundances followed the north-south axis of Rocky Mountain mid-high elevation areas, but low abundances were predicted in the very high elevation areas of the Rocky Mountains, such as areas that would be mostly snow and ice or rock (see Appendix 1, Figure A1 for the topography layer used). Areas in the far north, along the arctic coast, and the northwestern NWT, also revealed relatively low predicted abundances of OSFL (Fig. 3-1A). Projections for future climate scenarios revealed relatively high predicted abundances of OSFL in interior regions, in a very similar overall pattern to those of the baseline scenario, with high abundances predicted for central BC and interior Yukon, except that predictions were much reduced in the far north, such as in the Beringia Boreal ecoregion of Alaska (Nowacki et al. 2001), and central Yukon, under the high emission scenarios. Riparian areas were clearly visible, with higher predictive abundance than surrounding areas. Areas that retained high relative predicted abundances under future climate scenarios were central Yukon and central British Colombia. The geographical layers that explained the most variation in predictions to grids for OSFL under the baseline climate conditions were topography, MSP, Temperate Needle, MAR, and bFFP.

Regions with relatively high predicted abundance of WEWP under current (baseline) climate conditions were restricted to interior BC, the southern Yukon, south and central Alberta, and southwestern Saskatchewan (Fig. 3-1B). Regions of relative low predicted abundance of WEWP were areas of very high elevation (mountainous regions of western BC and western Alberta) and the far north and much of northern NWT (Fig. 3-1B). Terrestrial areas of mid-elevation and riparian areas were clearly visible, supporting relatively higher predicted abundances of this species (Fig. 3-1B). Predicted distribution and abundance of WEWP was greater in the southern portion of the study area compared to the north, possibly reflecting a near edge of northern range in the northwestern boreal.

Future projections for both time periods and under both climate change scenarios revealed a more restricted area of high relative abundance (areas of high predicted abundance were smaller) for WEWP, especially in the far northern regions of central Yukon and Alaska (Fig. 3-1B). Riparian areas remained clearly visible, with higher predictive abundance of WEWP than surrounding areas in future scenarios. Areas that retained relatively high predicted abundances in future scenarios were mid-elevation regions in central BC (Fig. 3-1B). Negative differences between baseline and future projections for OSFL were most visible in interior terrestrial areas of low elevation, but also some areas of mid-elevation in south-central BC for OSFL (Fig. 3-1C). Negative differences for OSFL were also readily apparent in Alaska under the High emission scenario (Fig. 3-1C). Negative differences for WEWP were most obvious in the southern portion of the study area, such as interior southern BC and Alberta (Fig. 3-1C). Most positive differences occurred in northern BC and southern Yukon for this species. Surprisingly, more positive than negative differences were evident over the entire study area for the 2055 high emission scenario for WEWP, prompting further investigation using a “gains and losses” strategy of analyses (see below).

Total projected abundance (population size within the study area) was 9.39 million OSFL males (8.39 – 10.4, 95% Confidence Interval) and 1.39 million WEWP males (0.88 – 1.91, 95% CI) under baseline conditions, i.e. current climate, topography and landcover conditions. Mean projected abundances of OSFL declined between the baseline and both future time periods, for both emission scenarios (Fig. 3-2, Table 3-1). Differences were significant across these scenarios ($F_{4,120} = 7.63$, $P < 0.001$), with pairwise differences occurring between the baseline and 2085 high emission scenario, between the 2055 and 2085 high emissions scenario, and the 2085 high and low emissions scenario (Tukey tests, $P < 0.05$). Mean total projected abundance of WEWP increased between the baseline and the 2055 time periods for both emission scenarios, and then decreased between the 2055 and 2085 time periods for the low emission scenario, and increased between 2055 and 2085 time periods for the high emission scenario (Fig. 3-2, Table 3-1). Differences were highly significant across scenarios for WEWP ($F_{4,120} = 243.5$, $P < 0.001$), with pairwise differences between the baseline and all other scenarios, and between the 2085 high and low emission scenario (Tukey tests, $P < 0.05$).

Uncertainty in predictions from sampling error was generally low across bootstrap runs for both species (Fig. 3-3). Regions of relatively high uncertainty occurred in far northern regions (e.g. arctic of northern NWT) and in high elevation regions in the west for both species. These areas would correspond to regions of sparse sampling (regions of the far north) or likely very low probabilities of occurrence (high elevation regions were probably dominated by snow and ice conditions). Uncertainty decreased between baseline/current and future scenarios for high emission scenario for OSFL, and remained relatively similar between baseline/current and all future scenarios for WEWP (Fig. 3-3). Although not directly comparable between species, uncertainty appeared lower for OSFL than for WEWP. Cohen's *d*, which is a measure of overall effect size, ranged from ~5.91 – 6.58 for OSFL, and from 0.99 – 1.58 for WEWP, when mean abundances were compared between future and baseline scenarios (Table 3-1). Values of Cohen's $d > 1$ are considered to have a greater signal-to-noise ratio for the differences between climate scenarios (Stralberg et al. 2015b).

Ideal habitat and bioclimatic velocity

The percent of the area (of pixels) that was considered ideal habitat climatically, or habitat that supported a density of males over the mean value from the baseline period, remained essentially the same or decreased between the baseline time period and future scenarios for OSFL (Fig. 3-4). The average decline in OSFL was 8.7%, with the largest decline of 19.8% occurring between the baseline and the 2085 time period under a high emission scenario (Fig. 3-4). For WEWP, the percentage of ideal habitat declined under the low emission scenarios (by 5.1 and 5.8% for 2055 and 2085, respectively), but actually increased between the baseline and the high emission scenarios for both time periods, by 7.2% and 8.3% for 2055 and 2085, respectively (Fig. 3-4). These measures of ideal habitat or a correlate of range size within the study area, closely mirrored the pattern of range size calculated from the number of occupied pixels (of any abundance) across scenarios (not shown).

Bioclimatic velocity revealed rapidly declining habitat suitability (negative bioclimatic velocity) for OSFL in central BC (Fig. 3-5), which is of particular interest because this area corresponded to very high relative predicted abundances from BRT model results (Fig. 3-1A). Negative bioclimatic velocity was also evident throughout much of central Alaska and central

Yukon, and parts of southern Yukon (Fig. 3-5). Areas of positive bioclimatic velocity were evident only in small regions scattered throughout northern BC and in far western Alaska, such as along the Aleutian Peninsula (Fig. 3-5). Patterns were similar, geographically, between high and low emission scenarios, although magnitude of change was noticeably different. Negative bioclimatic velocity was less evident in central Alaska under low emission scenarios, compared to a high. For WEWP, negative bioclimatic velocity was evident in many regions in central BC, northwestern BC and southern Yukon, in an elongated north-south axis region along the west (possibly corresponding to mid-elevation conditions). Positive bioclimatic velocity for WEWP occurred in small isolated regions in interior and south-central BC (see Fig. 3-5). Patterns were geographically different between high and low emission scenarios for WEWP. Negative bioclimatic velocity was much more evident in north-central Alberta and the interior west coast of BC under a high emission scenario, whereas under a low emission scenario, negative bioclimatic velocity was much more evident in a montane region of central interior BC, the Alpine Tundra, Boreal White and Black Spruce, and Montane Spruce biogeoclimatic zones (Meidinger and Pojar 1991, Government of British Columbia). Negative bioclimatic velocity was less evident in central Alaska in a low emission scenario, compared to a high. Although correlated (Kendall correlation of 0.48, $P < 0.001$), the velocity was greater between baseline conditions and the 2085 time period than between baseline conditions and the 2055 time period (OSFL: - 0.05 and -0.08 km/year, WEWP: - 0.01 and – 0.08 km/year). These results suggest that bioclimatic velocity will likely increase in speed between now and the end of the century, especially for WEWP.

Refugia

Projected losses and gains in abundance from climate change between the baseline and the 2055 time period, taking into account the most likely time lag from vegetation change, revealed spatial heterogeneity. For both species, more losses occurred in central terrestrial regions, such as central Alaska and Yukon and more gains occurred in the far west (Aleutian peninsula in Alaska), and parts of the eastern portion of the study area (such as central NWT), as well as scattered and isolated regions throughout (Fig. 3-6A, B). These areas of gain represent potential areas of climate refugia for these species, although the isolation and small sizes are of concern. Climate-only models revealed relatively similar patterns (with losses in inland areas such as central Alaska and Yukon), but with noticeable gains in the Arctic tundra (Fig. 3-6C), an area unlikely to be occupied by either of these species due to lack of appropriate vegetation and landcover, even in future scenarios with vegetation adjustment to climate change (Rehfelt et al. 2012). Population size estimates were also unrealistically large for these analyses, reflecting the large area in the arctic that was assumed to be "gained", despite being unlikely to have appropriate vegetation to support the species (for example, about 9.5 million WEWP males in 2085).

3.5 DISCUSSION

Projected distribution and relative abundance

Both OSFL and WEWP had high predicted relative abundances in the western and interior regions of the study area. These findings agree with the results of national modeling (Haché et al. 2014, Stralberg et al. 2015b), that found higher relative predicted abundances of OSFL in northern and western regions of Canada (as well as far eastern parts of Canada). An area of particularly high predicted abundance occurred in the plateaus of central BC (the Central Interior and Sub-Boreal Interior ecoprovinces, especially pronounced within the Sub-Boreal

Pine–Spruce and the Montane Spruce biogeoclimatic zones of BC, Meidinger and Pojar 1991, Government of British Columbia). A remarkably similar area of very high predicted relative abundance was also found by Weber (2015b), which he linked to the Mountain Pine Beetle (*Dendroctonus ponderosae*) epidemic in the region. The Sub-Boreal Pine-Spruce biogeoclimatic zone is characterized as relatively dry, mid-high elevation, with numerous lakes, lodgepole pine (*Pinus contorta*) forests and wetlands, with the potential for Mountain Pine Beetle outbreaks (Meidinger and Pojar 1991). Epidemic-scale mountain pine beetle outbreaks caused avian community turnover, but did not necessarily impact overall bird species richness in lodgepole pine-dominated forests in the greater Rocky Mountain region of the USA (Janousek et al. 2019). Some forest species increased in abundance in response, such as cavity nesters and some insectivores such as OSFL, whereas others, such as shrub-associated species, decreased in the 10-year period following an outbreak (Janousek et al. 2019). My predictions of distribution and abundance for WEWP were very similar to those of Sólymos et al. (2017); both revealed a comparatively very high predicted abundance of WEWP in south-central BC (Central and Southern Interior) and then again to the west in the lower elevation regions of western Alberta, but a comparatively low predicted abundance in the high elevation regions of the Rocky Mountains (and in coastal regions). High predicted abundance was associated with the Interior Douglas Fir and Sub-Boreal Pine–Spruce and Sub-Boreal Spruce biogeoclimatic zones of BC (Meidinger and Pojar 1991).

Although estimates are not available for the same study area for comparison, the population size estimates here are likely higher (9.39 million OSFL males for the baseline time period) than those of others (e.g. Partners in Flight Science Committee (2013) estimated only 900,000 OSFL individuals occurred in all of Canada). These discrepancies are mostly from methodological differences in utilization of detection distances. Techniques utilized here involve quantitative measures of effective detection distances (for example of 146 ± 25 m in open forest and 154 ± 32 m in non-forest habitats for OSFL, Matsuoka et al. 2012), whereas the techniques used by PIF involve maximum detection distance (400 m) to determine the presence of a bird. These differences in corrective factors for detection can lead to varying estimates of population size. In addition, the dataset utilized here contains an even representation of both on and off-road sampling, whereas many others used only BBS data, which is exclusively on-road survey data.

Sólymos et al. (ABMI and BAM 2018), using similar data to those that I used, estimated that 7.5 million OSFL males occurred within western Canada, with the highest densities in the country found in BC. Stralberg et al. (2015b) utilized similar methods to those used here, and estimated that 4.1 million OSFL males (2.96 – 5.52, 95% CI) occurred in the boreal and southern arctic regions of North America during the baseline period of 1961-1990, and this population size was projected to decline by 3.1% by the period 2011 – 2040. Haché et al. (2014) predicted that 6.4 million OSFL males occurred within Canada during the breeding season, with approximately 45% of the Canadian population found within only Quebec and British Columbia and 30% found only in the "Arctic" region (BCRs 3 and 7 combined) in northern Canada. These results are similar to mine (my study area included a large part of Alaska) although mine represent overestimates because I did not include all absence data available (in order to constrain spatial autocorrelation). In addition, OSFL reveals large tracts of unoccupied areas in seemingly suitable habitat (personal observations). Statistically correcting for tracts of seemingly unoccupied habitat could not be accounted for at the time of writing because the causes were unknown, but likely related to poorly-understood factors in non-breeding areas (see Greenberg et al. 2011 for a similar example in Rusty Blackbird). Future study in which population size is an objective would include all available absences and quantification of this under-use of all available habitat.

For estimates of WEWP population sizes, ABMI and BAM (2018b) estimated that approximately 4.3 million WEWP males occurred in Canada, with the highest relative densities occurring in BC. Stralberg et al (2015a) predicted that 4.3 million WEWP males (3.29 – 5.30, 95% CI) occurred in the boreal and southern arctic region of North America during the baseline period of 1961-1990. These estimates are comparable to mine (5.03 million WEWP males in the northwestern region of North America, including major portions of Alaska), but again represent an overestimate because not all absence data were included in my analyses.

Abundance and distributions patterns were predicted to change between the baseline and future time periods assessed, but with notable differences between species. Large areas of negative differences were predicted to occur in central Alaska, central Yukon, coastal BC and parts of north-central BC for the OSFL. For WEWP, areas of loss were more scattered throughout central Alaska with notable positive differences in central BC and Yukon.

Despite the broad scale of study, areas of riparian and lakeshore habitat revealed potential to support relatively high abundances of future predicted distributions for both of these species. Wet habitats such as these likely support high abundances and diversity of insects, through the provision of environmental heterogeneity from topography and small-scale disturbance regimes from flooding, channel movement, and debris (e.g. Naiman et al. 1993). Lakeshores may provide similarly heterogenous habitat and consequently higher bird abundances than upland boreal forest in Alberta (Macdonald et al. 2006). These findings and those of others (Weber 2015a, Sólymos 2017) highlight the importance of effective landscape-scale conservation and management of areas that contain riparian habitat (Naiman et al. 1993, Whitaker et al. 2000), especially with changing areas of conservation priority with climate change (Carroll et al. 2018). Complex topography also has the potential to create "microrefugia", or small areas of reprieve from climate change; these areas are not always evident in results from the broad-scale analyses of SDM (Ashcroft 2010, Keppel et al. 2015). Broad-scale topographic features, such as mountain passes, also may provide key connectivity for organisms to disperse according to new climate conditions (Carroll et al. 2018).

Uncertainty in predictions from sampling error was generally low for both species, providing relatively high confidence in predictions of distribution and abundance for these species. Areas of relatively high uncertainty occurred in far northern regions, such as far northern NWT, where sampling was very limited. Accuracy of models is reduced when sampling is sparse (Hernandez et al. 2006, Wisz et al. 2008). There were also regions of high uncertainty in the high elevation regions close to the west coast, also likely from very low sample numbers as well as low abundances. Uncertainty decreased between baseline conditions and future time periods for WEWP, and for the high emissions scenario for OSFL probably because areas of higher sampled climate space move northward into areas of sparse sampling (Stralberg et al. 2015b). Cohen's *d* values calculated here were intermediate to large in size between future and baseline scenarios, and similar to those calculated by Stralberg et al. (2015b). These relatively large effect sizes (signal of climate influences) indicate the influence of climate on both species is important in predicting distribution and abundance, despite the relative importance of covariates that may decouple with climate in future scenarios, such as some vegetation layers or forest loss. Despite values of > 1 for all Cohen's *d* values, effect sizes were somewhat lower for WEWP than for OSFL, possibly indicating greater decoupling for that species. Decoupling may result from several processes, but for this species, a likely cause would be time lags from vegetation change with climate.

The inclusion of landcover layers that may become decoupled from climate in future scenarios would likely make predictions of distribution and abundance more conservative (e.g. Matthews et al. 2011). Conceivably, vegetation in areas of predicted range gains will become more appropriate to support these species as climate changes (Matthews et al. 2011, Rehfeldt et al. 2012), albeit with potentially long time lags and disparate trajectories among vegetation types (Serra-Diaz et al. 2014). Projections using climate only produced some areas of unrealistic “gains” to range; for example, in the far northern tundra near the arctic ocean, making these projections and the complete elimination of landcover layers comparatively less realistic.

Choice of GCM can have a large impact on results of SDM exercises (Naujokaitis-Lewis et al. 2013), but ensemble models can combine information across models. In addition, the change in distribution and abundance from climate exceeded that between the two climate scenarios (GCMs) selected, suggesting that the signal from climate change is greater than error arising from model selection. The RCP4.5 scenario would require stabilization of greenhouse gas concentrations from major shifts to electricity use, the use of lower emission and carbon capture techniques and geologic storage of carbon (Thomson et al. 2011, Davies-Barnard et al. 2014), all of which may not be realistic. RCP8.5 does not assume stabilization, but rather a continued use of fossil fuels at similar increasing rates as are used currently (Riahi et al. 2011), but it may overestimate the availability of these fossil fuels to industry. These scenarios were selected because they represent two different scenarios, and the actual concentrations of greenhouse gases may be somewhere in between the two. Despite questions of realism, an incredible amount of work, expertise and thought goes into the development of an RCP model; they take into account such diverse impacts as changing climate policies, changing land uses and land cover, vegetation regeneration, impacts of atmospheric dust, and the chemistry of reactive gases (van Vuuren et al. 2011).

Ideal habitat and bioclimatic velocity

The area of habitat considered ideal climatically was predicted to decline in all comparisons with the baseline time period for the OSFL. This area was predicted to decline for the WEWP as well between the baseline and the low emission scenario for both time periods, but increase between the baseline and the high emission scenario for both time periods (Fig. 3-4). The increases in ideal habitat could indicate that northward expansion in range with predicted climate warming may be possible for WEWP. Increases in temperature, spring temperature in particular, increased productivity (number of fledged young per individual) for some cold-weather adapted long-distance migrants in the boreal zone of Finland (Meller et al. 2018). Despite warming, temperatures remained within the thermal neutral zone for these cold-adapted species. The ideal habitat calculations did not take into account species-specific uses of habitat, such as density within a climatically suitable area or impediments to dispersal. Birds are generally able to disperse, given their high mobility, but other impediments exist, such as site fidelity, territoriality, relatively small body size, and low population density to provide dispersers (Estrada et al. 2018).

The bioclimatic velocity analyses indicated that both species will experience changes to climate suitability that are spatially heterogeneous and specific to species. Despite species-specific patterns, the coastal interior (interior montane regions of BC) revealed relatively high (negative in particular) bioclimatic velocity for both species, indicating that change in temperature (km/per year) that species will encounter is greatest in terrestrial montane and interior habitats. Of particular concern from my results was an area of negative bioclimatic velocity in the montane regions of interior BC (biogeoclimatic zones known as Alpine Tundra, Boreal White and Black Spruce, and Montane Spruce; Meidinger and Pojar 1991), corresponding to areas of very high predicted abundances of both of these species in the baseline and future climate scenarios. Temperatures would likely increase more quickly in these regions of the interior, especially in low density forests of northern regions (Loarie et al. 2009). Some forested areas, such as tropical or sub-tropical forest, have the potential to retain more water in soil and release water via evapotranspiration, assisting with temperature moderation. Similarly, in coastal regions temperature change is ameliorated by the high specific heat of water moderating temperatures near large water bodies (Loarie et al. 2009). High elevation regions had lower values, probably because climate varies more widely in these regions (Ackerly et al. 2010), and climate conditions can even be removed or “pushed off” mountaintops (Carroll et al. 2015), whereas slightly lower elevation (leeward regions of the highest Rocky mountains) and flatter regions had more positive bioclimatic velocities (see Appendix 1, Figure A1 for a topographical map of the region).

Bioclimatic velocity assessments for the WEWP suggest that central interior BC will change rapidly (negatively), but isolated regions could remain climatically suitable. These results call into question the possibility of fragmentation of isolation of future populations for the WEWP. Overall, predicted changes to distribution and abundance for this species suggest that, although population size could increase, the potential for the northwest to provide climate change refugia is questionable, and highlights the importance of conservation and management of areas that currently support high abundances, such as southcentral and interior BC, and western Alberta.

Positive bioclimatic velocity can be interpreted as increased suitability in climate for a species (Serra-Diaz et al. 2014), but does not take into account other aspects of habitat velocity, such as vegetation change or provision of micro-habitat requirements. Serra-Diaz et al. (2014) found increasing suitability from climate velocity at the northern edge of range for eight endemic tree species in California, and decreasing suitability at centres and southern edges of ranges, but with significant and species-specific changes to fragmentation or filling of range overall. A north-south gradient of positive to negative bioclimatic velocity was not obvious in my results. My analyses did not include the southern portion of the very large ranges of these species, which would be needed to calculate potential bioclimatic velocity changes to overall range, such as overall shift and fragmentation. Endemics (simply defined here as species that have geographically isolated, and often, limited range) are generally associated with lower climate velocities (Schwartz et al. 2006), as far back as the last glacial maximum (Sandel et al. 2011). On the other hand, migratory birds breeding in North America have a history of high climate velocity (Sandel et al. 2011). Because of this, combined with their incredible mobility and relatively large ranges, migratory birds may have some ability to track climate change (Chen et al. 2011), assuming vegetation time lags are not prohibitive. However, an ability to track climate change says nothing directly about connectivity of climate (Carroll et al. 2018), which would allow access to refugia, or about the extent to which potential ranges are filled. It also does not imply that other organisms in a community that they rely on, potentially weaker dispersers such as insects, will track climate change concurrently.

Refugia

The spatial distribution of losses and gains in areas that will support relatively high densities can be used as an approximation of macrorefugia (both *ex situ* and *in situ* for these relatively mobile species, Ashcroft 2010). Potential losses of southern portions of habitat within the study area and gains in northern regions were evident for both species. Evidence for species-specific potential range alterations with climate change is mounting (Methorst et al. 2017), but a common pattern is loss of southern regions and gains of some northern regions (Valle et al. 2018).

Much of macrorefugia or areas of gain identified were small and in isolation, with the possible exception, of the Alaskan Peninsula/Bristol Bay lowlands and Chugach-St. Elias Mountains in the west, and central NWT (Fig. 3-6A, B). The high negative bioclimatic velocity for parts of the northwest for OSFL (central Alaska and central BC) suggest that the pace of negative exposure to climate change is high in these regions, and although some of these areas could be occupied in the future, assuming vegetation (and other components of the community) will be appropriate to support them, rapid bioclimatic velocity could impede use of potential macro-refugia. Incomplete range filling is analogous to range fragmentation, a predicted phenomenon with range alterations in response to climate change in other species (Serra-Diaz et al. 2014). Overall, these results suggest that parts of northwestern North America, especially western Alaska (Alaskan Peninsula, Bristol Bay lowlands), central NWT, parts of central Yukon, northern and central interior BC, have the potential to provide some areas of refugia from climate change for these species, but further study is needed on dispersal, vegetation time lags and rapid exposure to climate change (measures of velocity).

Most losses to range for WEWP were predicted to occur in central and interior areas, such as interior central Alaska, central/east Yukon and south-central NWT. Most gains or areas of macrorefugia were predicted to occur in coastal Alaska, an area less likely to be a part of the range of this species because of its more southern distribution and the distance that range would have to change to incorporate this area (e.g. Figs. 3-1, 3-6B). The inherent value of refugia depends on many factors; one important one is access between old and new areas of climatic suitability, as well as size of climate refugia (Keppel et al. 2015).

These results have particular relevance and utility in conservation planning, as they represent the potential areas of range gain (and loss) for each species under future climate change (and under two alternate emission scenarios) assuming there no impediments to dispersal (Carroll et al. 2018), such as tracts of unsuitable land from disturbance, novel climates, or land use. Areas of climate connectivity may differ from areas of strict refugia, and would not necessarily be captured in modeling exercises using refugia-only approaches (Carroll et al. 2018). A key impacted region identified by Carroll et al. (2018) was the Boreal Cordillera, central to the study area selected for this research. This area was identified as having high connectivity between present and future climate envelopes, but with very little protected area (Carroll et al. 2018). Across multiple management objective scenarios, mountainous regions of Yukon and northern BC were also highly selected in area prioritization for songbird conservation in boreal Canada, in part because of high topographical diversity (Stralberg et al. 2018a). These prioritization exercises are particularly important in the region because only approximately 14% of the Alaska and Canadian boreal region is protected (Stralberg et al. 2015a), with only 8.1% of Canada's boreal forest protected; much less than the global percentage of protected land of 12.7% (although criteria for inclusion of protected status vary across countries, Andrew et al. 2014).

Overall, these results suggest that regions that could potentially support each of these species, or the areas that are climatically suitable, could occur in the future time periods and under the two emission scenarios considered (RCP 4.5 and RCP 8.5), but with species-specific patterns in distribution and serious reservations about limitations to dispersal. Isolated areas of refugia could also fragment range. Fragmentation can isolate patches of suitable habitat and exacerbate impacts of climate change, and in particular impact the potential for dispersal between fragments or to new areas (Noss 2001). Populations in relative isolation are vulnerable to many processes that reduce fitness, such as inbreeding or genetic drift (Hanski 2011). Increased future land use in the boreal forest, combined with the low proportion that is protected, may exacerbate these climate change impacts from alterations in range.

Slight differences in conclusions can be drawn depending on which product is utilized (SDM results alone, ideal habitat or range size, total abundance calculations, bioclimatic velocity and macrorefugia or gains), supporting the importance of summarizing results of SDM exercises using multiple methods. There are also multiple methods to calculate “velocity”, resulting in different conclusions (Carroll et al. 2015, Carroll et al. 2017).

Considerations of future work

It is important to note that these models did not include potential changes to land use in future scenarios. Land use rates are increasing in some regions of the boreal forest (Andrew et al. 2014), such as from forest harvest and energy features in boreal Alberta (Schieck et al. 2014). Predictive layers of land use were not yet available for the western boreal forest at the time of analyses, although these are currently under development by members of the BAM research team. Roads may have a disproportionate impact on projections of OSFL in places such as Alberta (ABMI and BAM 2018). Direct habitat loss may have a larger or very different impact on organisms than climate change alone (Junker et al. 2012, Naujokaitis-Lewis et al. 2013, Methorst et al. 2017, Zamora-Gutierrez et al. 2018), and thus must be considered in future analyses. Methorst et al. (2017) found that projected range of the Ortolan Bunting (*Emberiza* *hortulana*) in Europe increased under two emission scenarios (RCP4.5 and RCP8.5), although this increase was much reduced and even decreased when projected future land uses and species-specific dispersal abilities were incorporated into projected range changes. Despite positive influences on abundance from climate change for terrestrial bird species in Denmark, negative influences from land use change, particularly agriculture, have caused overall population declines (Bowler et al. 2018).

The overall area that has been altered from anthropogenic land use is likely comparatively small in the study region utilized here (Ellis et al. 2013, Watson et al. 2013), allowing for only minimal decoupling with climate variables utilised. A 16% total land conversion was estimated for boreal Alberta, mostly from agriculture (Schieck et al. 2014). Most anthropogenic disturbance in the remaining area (YT, northern BC) was from forestry, mining and energy (oil and gas) exploration and development, although overall harvested area for forestry has declined since about 2005 (Brandt et al. 2013). The steepest increase in land use in the western boreal was from the energy sector: oil and gas exploration and development (Brandt et al. 2013, Schieck et al. 2014), and hydroelectric activity (Brandt et al. 2013, Venier et al. 2014). Cumulative impacts of land use were estimated to be only about 3% for boreal and sub-boreal forests of northern BC, mostly from agriculture, oil and gas development and various indirect effects, but with alarming changes to patch and edge characteristics (Shackelford et al. 2018). Despite a comparatively small human population in the northwestern boreal, extensive resource extraction activities have impacted wildlife and biodiversity cumulatively in some areas (Vernier et al. 2014, Shackelford et al. 2018), and thus, predicted land use changes should be incorporated into future analyses.

Similarly, inclusion of predictive layers of vegetation (e.g. Matthews et al. 2011, Rehfeldt et al. 2012) altered predictions of distribution and abundances for these two species. Predictions of abundances were more favorable in future scenarios (T. E. Stehelin, *unpublished data*), because some vegetation types may keep abreast of climate change to some degree. Similarly, White et al. (2011) found that predicted occurrences of three species of birds in the Chihuahuan Desert of USA potentially increased with changing desert vegetation with climate change and various fire management scenarios, although with species-specific spatial patterns. Predictive vegetation layers were not yet available for my study region for all future time periods or scenarios selected.

Climate stability is predicted to be low in areas of high latitude; however, intactness of vegetation must be taken into consideration in future conservation planning of ecosystems because it provides information about potential adaptive capacity. Intactness was found to be relatively high in northern North America, despite high vulnerability to climate change (Watson et al. 2013). When both of these factors were considered simultaneously, regions of highest vulnerability to ecosystems were southeastern North America, central Europe, China, southeast Asia, northeastern South America – a sharp contrast to predictions from other studies that only examine climate change or land use change individually (Watson et al. 2013). Management recommendations for regions that have high vegetation intactness, but low climate stability, include maintaining intactness to allow potential adaptation, identifying regions of potential climate refugia (and that may allow emigration), and monitoring individual species that may be particularly climate-sensitive (Watson et al. 2013). These considerations stress the importance of studies such as this, that focus on two species previously-identified as potentially vulnerable to impacts of climate and land use change (Bemis and Rising 1999, Altman and Sallabanks 2000, Roberton and Hutto 2007), in a region with relatively high levels of intactness.

Taxon-specific vulnerability assessments need to broaden in scope to include not only exposure to climate change, but sensitivity and adaptive capacity of species or groups of species; inclusion of these factors can alter future predicted changes to distribution and abundance (Dawson et al. 2011, Crossman et al. 2012). For example, dispersal ability should be incorporated into future modeling efforts, to predict the ability of these species to adjust range in accordance to climate change, and the inclusion of thermal metabolic optima (as was done for the Ortolan Bunting, *Emberiza hortulana*, Methorst et al. 2017), and connection between conservation lands, such as has been done for Alaska (Magness et al. 2018). Connectivity and dispersal may be particularly relevant for WEWP, because predicted changes to range likely exceed northern limits of dispersal ability, due to distance and low likelihood that vegetation changes (and other community interactions) will keep abreast of climate change. Community dissimilarity in face of changing climates is predicted to be disproportionately high in the boreal forest of North America with approximately 70 species gained from the south and 80 species lost by 2100 (Langham et al. 2015).

Conclusions

Impacts of climate change on distribution and abundances of these two species are likely to be species-specific. Some areas of the northwest have the potential to provide climate refugia, with important caveats from limitations to dispersal and necessary concurrent changes to communities, in particular, to vegetation. Although abundances of WEWP (and resultant overall population size) are predicted to increase with climate change in two future time periods, and range could potentially be gained in some areas of the far northwest and northeast, dispersal to and connection between, areas of refugia are questionable. In addition, a bioclimatic velocity assessment for WEWP suggested that climate conditions may change very rapidly for this species throughout the study area. Abundances were predicted to remain relatively stable or decline for OSFL, but dispersal capacity may be greater for this more northern-breeding species, increasing potential utility of macrorefugia. Furthermore, inter-annual variability analyses suggested that both species fluctuate widely, but overall have declined in abundance over the past 20 years in the northwestern boreal region (see Chapter II), with no sign of slowing down. Declining populations will have fewer individuals and thus capacity to colonize new areas with changing climates.

Informed management and potential protection of areas from land use change are essential for maintaining refugia from climate change, and connectivity between these areas. The importance of some regions cannot be overstated: central and northern interior of BC, central and northern AB (for WEWP in particular), south and central YT, and interior Alaska (for OSFL in particular) may support the highest densities of these species in North America in future time periods (Stralberg et al. 2015a), but currently only about 8% of the region is protected in Canada. Maintenance of intactness may also be an under-stated but essential piece for conservation of boreal-breeding birds (Watson et al. 2013). More detailed climate data, such as inclusion of micro-climate, and modelling climate change using more precise time scales (monthly data), could help establish specific links between climate change and local population change (Cahill et al. 2013). More detailed vegetation data, such as predictive layers of important tree species, will help generate more reliable representations of future distributions of birds under climate change scenarios (Matthews et al. 2011).

Studies of regionally-specific habitat associations, and predicted future distribution and abundance and areas of refugia, can help us understand impacts of climate change, and make detailed and informed management recommendations for planners. These modeling projects are especially important for the OSFL, because over half of its breeding range is in Canada, with potentially half of the Canadian breeding population in only two regions; British Columbia and Québec (Haché et al. 2014). Survey data are comparatively limited in northwestern North America, a gap that could be filled through future sampling efforts.

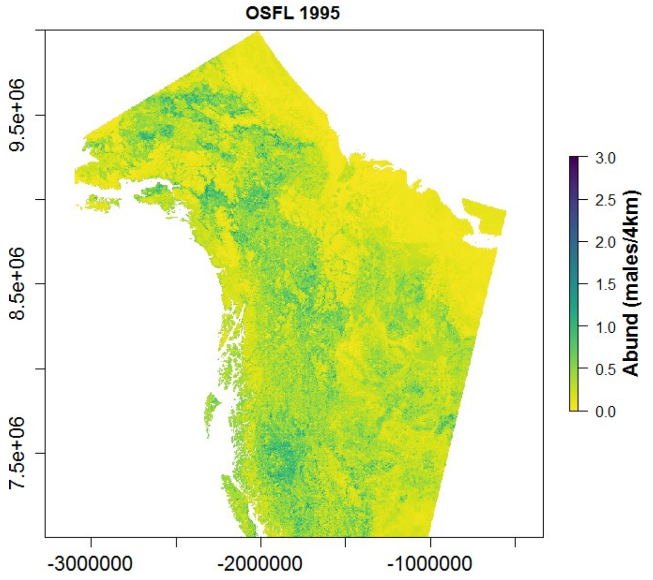
3.6 Tables

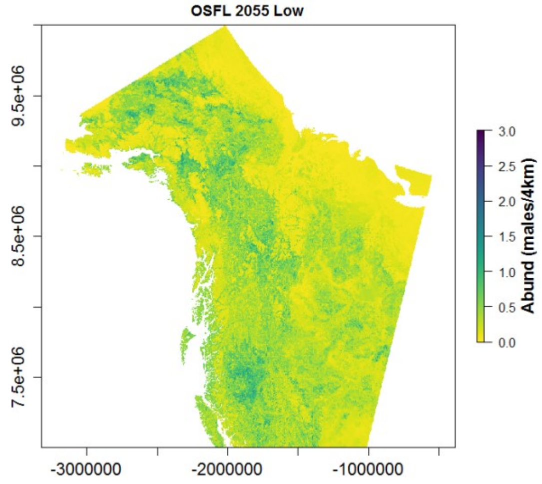
Table 3-1. Summaries of boosted regression tree model results. BRTs were run for the Olive-sided flycatcher (OSFL) and the Western Wood-Pewee (WEWP) in North America using current landcover and current climate conditions (baseline of 1981 - 2010) and predicted climate conditions in two time periods (median years of 2055 and 2085) and under two emission scenarios (RCP4.5 and RCP8.5). Statistics shown are means across multiple runs (25 runs per scenario).

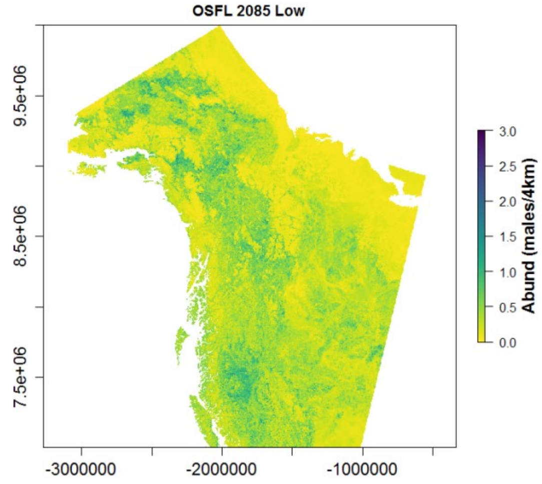
Species and scenario	n	ntrees	Correlation	deviance	Abundance (males/4 km^2) x 10^{-3}	Projected n x 10^6	Cohen's D (mean$_2$ – mean$_1$/ sd$_{pooled}$)
OSFL							
baseline	3379	8185	0.689	0.441	10.2	9.39	-
2055L	3361	8090	0.689	0.444	9.34	8.91	6.58
2085L	2908	8168	0.689	0.437	9.04	8.04	5.91
2055H	2876	5975	0.678	0.462	9.23	8.27	6.48
2085H	2241	6350	0.661	0.515	7.17	6.93	6.50
WEWP							
baseline	2637	8577	0.690	0.408	1.04	1.39	-
2055L		8730	0.698	0.414	8.32	7.46	1.56
2085L		8872	0.687	0.410	8.24	7.47	0.99
2055H	3671	7766	0.632	0.426	8.86	7.90	1.03
2085H	3236	8950	0.673	0.430	9.50	8.54	1.58

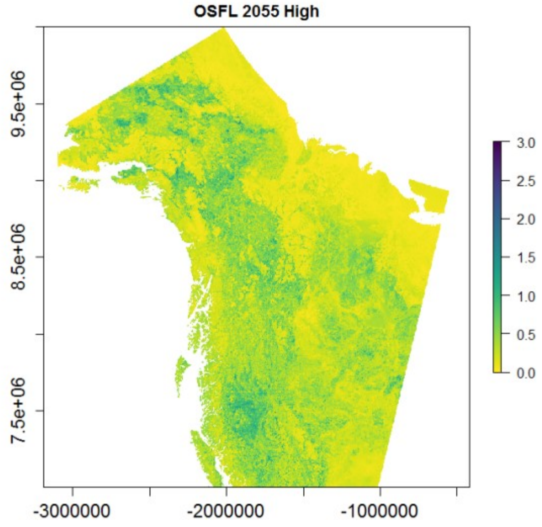
3.7 Figures

Figure 3-1A. Projected distribution and abundance from boosted regression tree models using seven climate covariates, five landcover, one disturbance and one topographical layer for prediction at 4 km resolution for the Olive-sided Flycatcher under five scenarios each. Scenarios are shown above each grid: baseline climatic conditions 1981 – 2010 (median of 1995), two future time periods: 2041-2070 (median 2055) and 2071-2100 (median 2085) with high (RCP8.5, Representative Concentration Pathways) and low (RCP4.5) greenhouse gas emission concentrations.




OSFL 2055 Low


OSFL 2085 Low


OSFL 2055 High

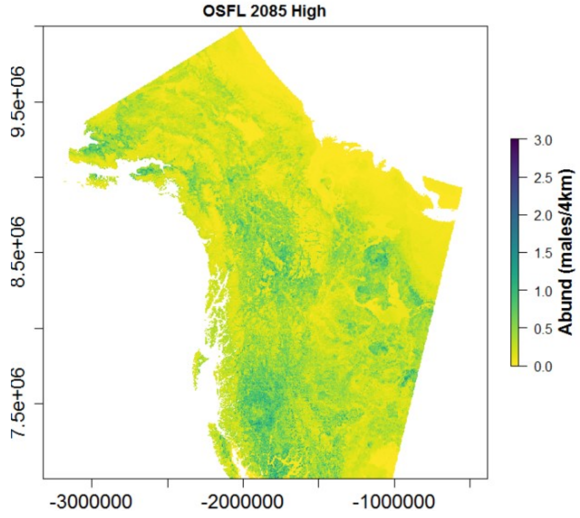
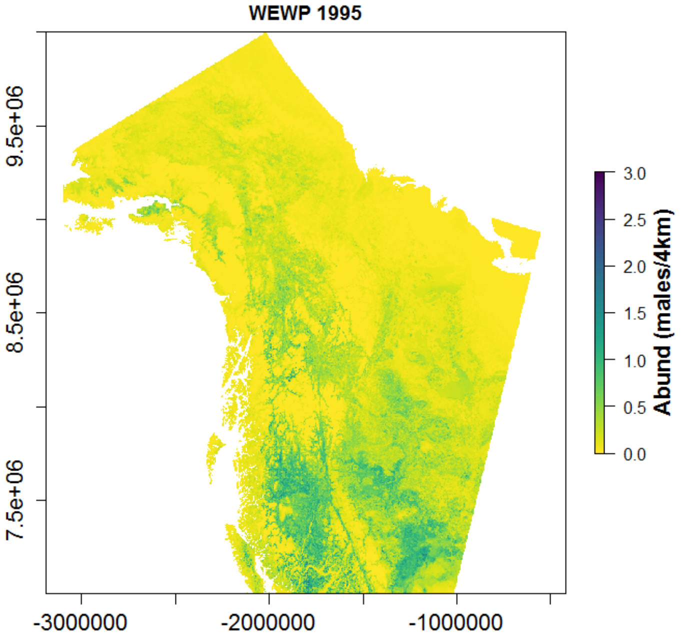
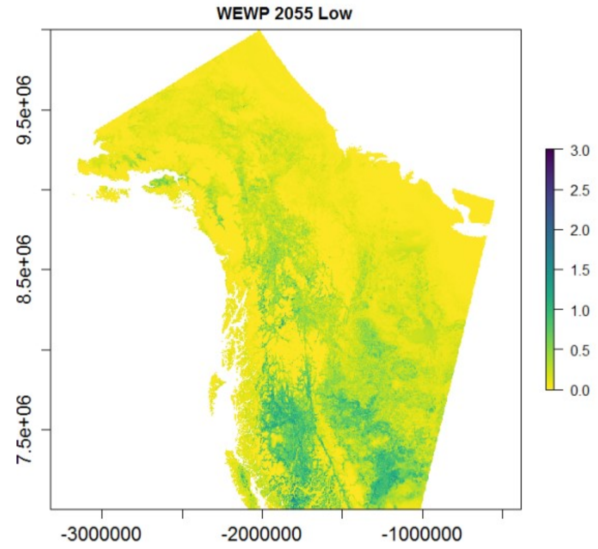
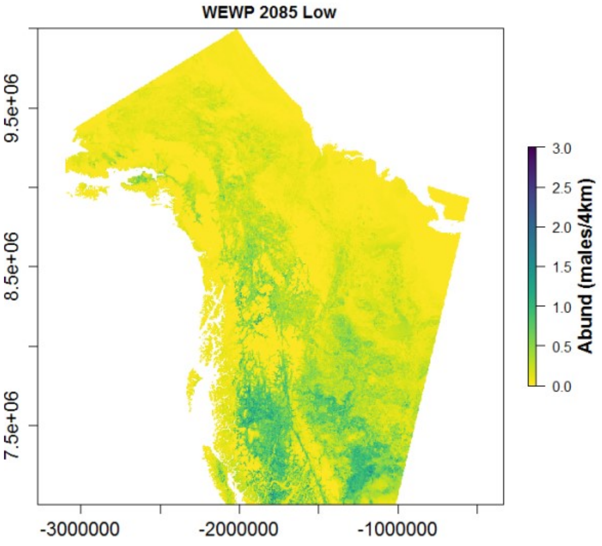
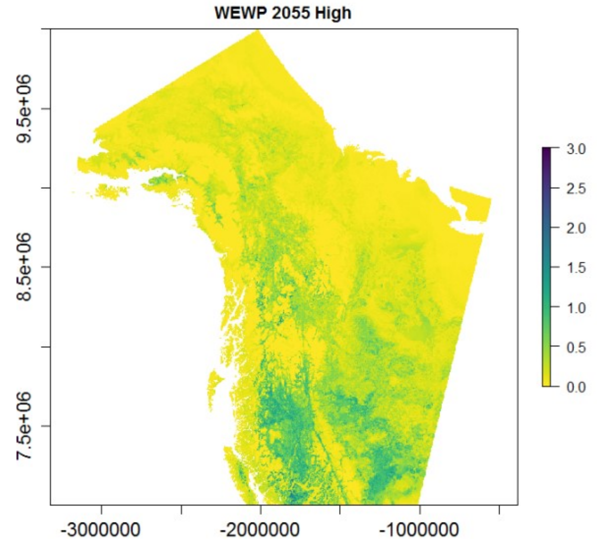

OSFL 2085 High

Figure 3-1B. Projected distribution and abundance from boosted regression tree models using seven climate covariates, five landcover, one disturbance and one topographical layer for prediction at 4 km resolution for the Western Wood-Pewee for five scenarios each. Scenarios are shown above each grid: baseline climatic conditions 1981 – 2010 (median of 1995), two future time periods: 2041-2070 (median 2055) and 2071-2100 (median 2085) with high (RCP8.5, Representative Concentration Pathways) and low (RCP4.5) greenhouse gas emission concentrations.




WEWP 2055 Low
9.5e+06
8.5e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0


WEWP 2085 Low
9.5e+06
8.5e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Abund (males/4km)


WEWP 2055 High
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8.5e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0

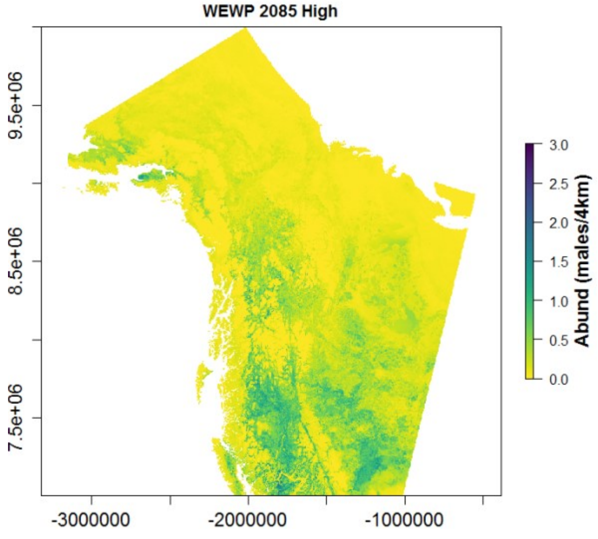
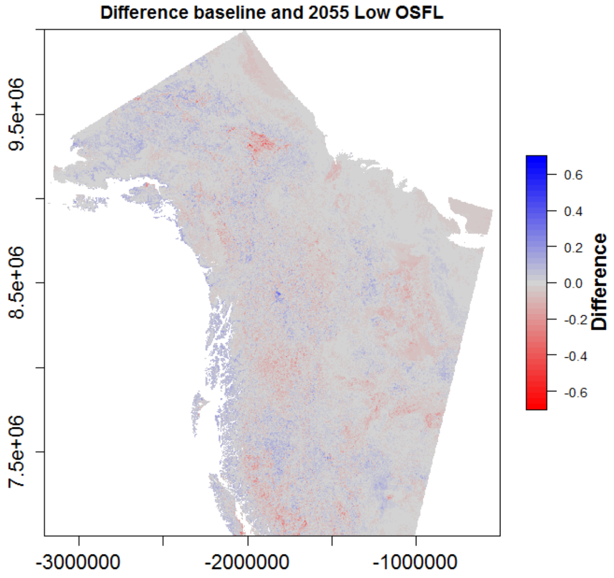
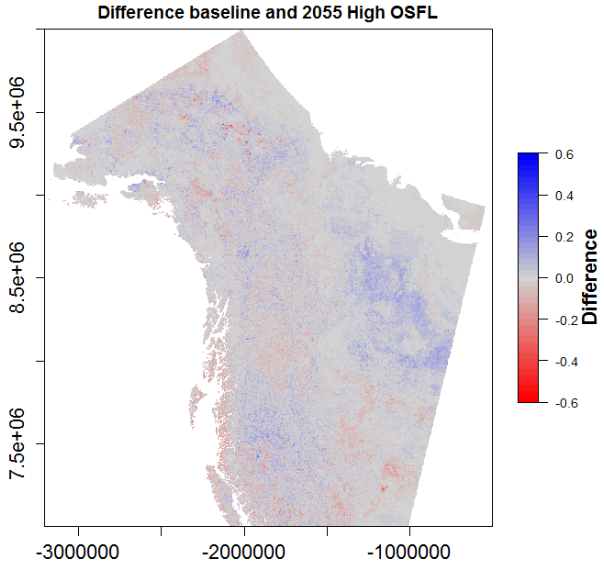
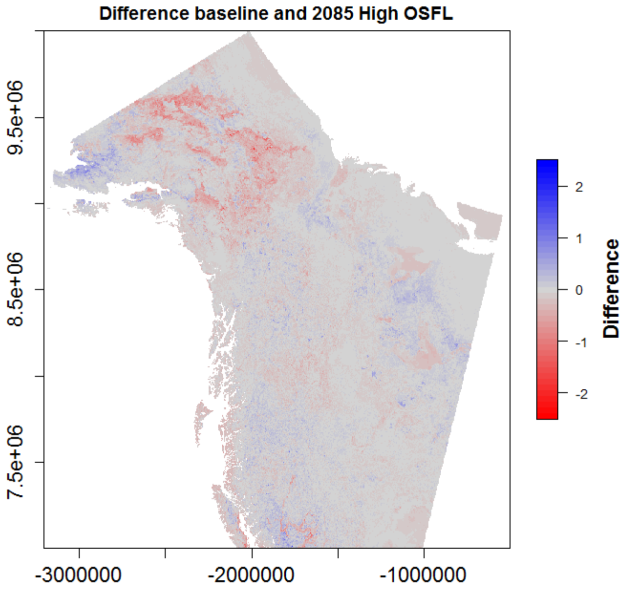
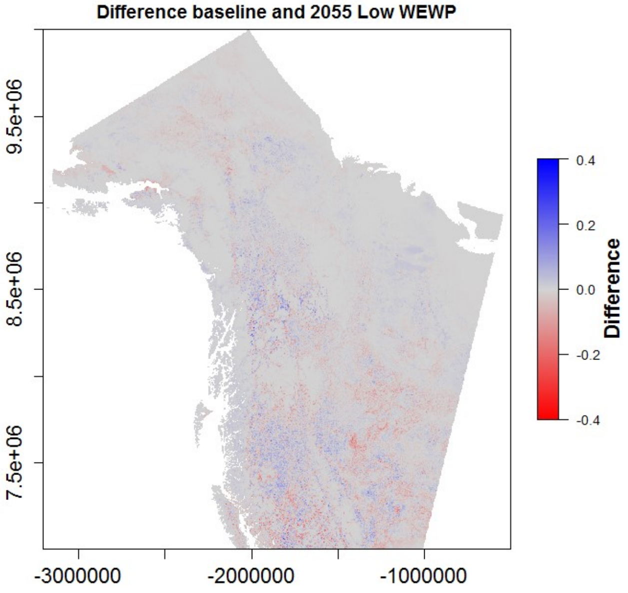

WEWP 2085 High
9.5e+06
8.5e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Abund (males/4km)

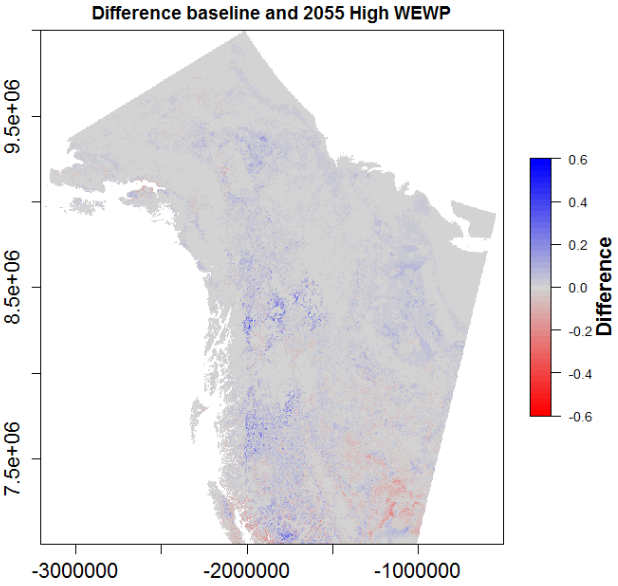
Figure 3-1C. Differences between projected distributions from boosted regression tree models between baseline projections and selected future scenarios. Species and scenario are shown above each grid: baseline climatic conditions 1981 – 2010 (median of 1995), two future time periods: 2041-2070 (median 2055) and 2071-2100 (median 2085) with high (RCP8.5, Representative Concentration Pathways) and low (RCP4.5) greenhouse gas emission concentrations.

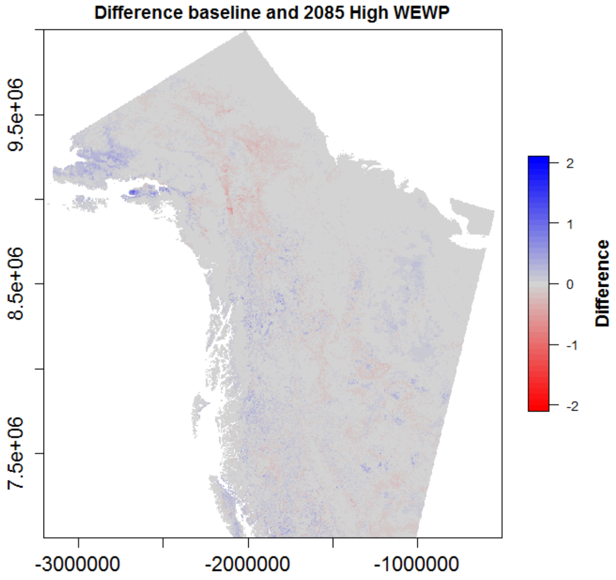





Difference baseline and 2085 High OSFL


Difference baseline and 2055 Low WEWP


Difference baseline and 2055 High WEWP


Difference baseline and 2085 High WEWP

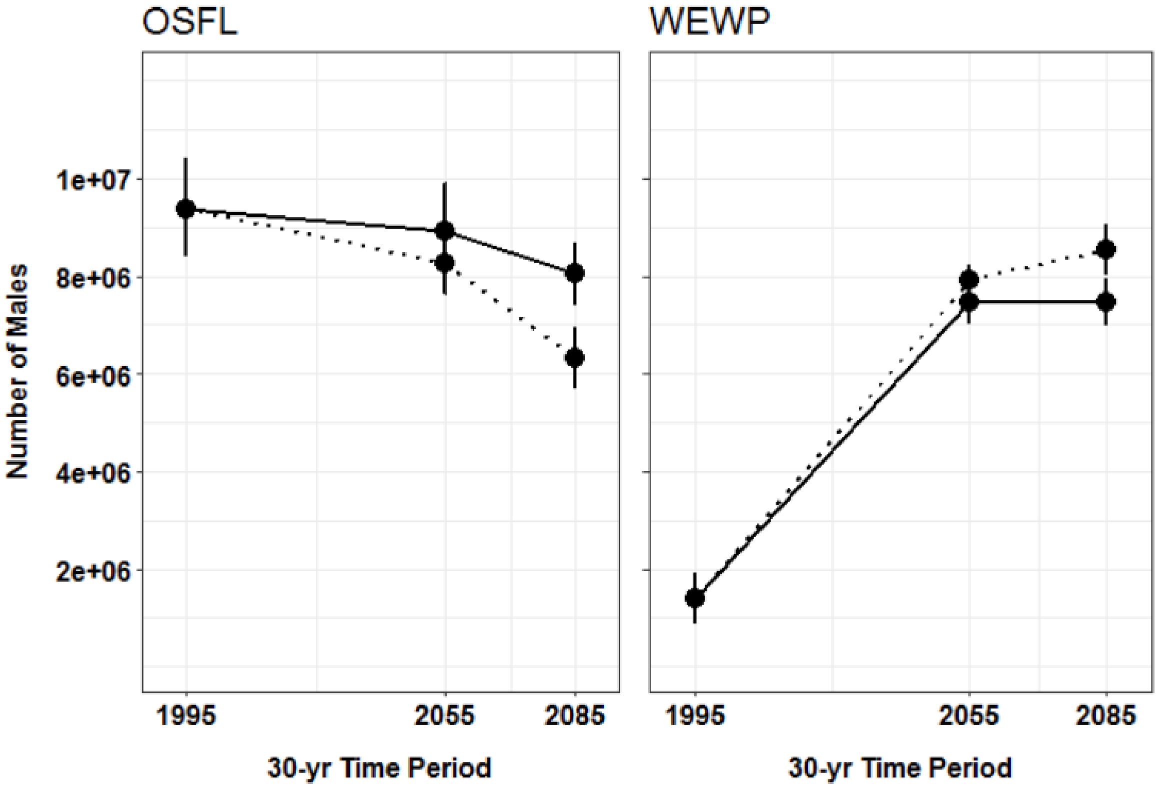
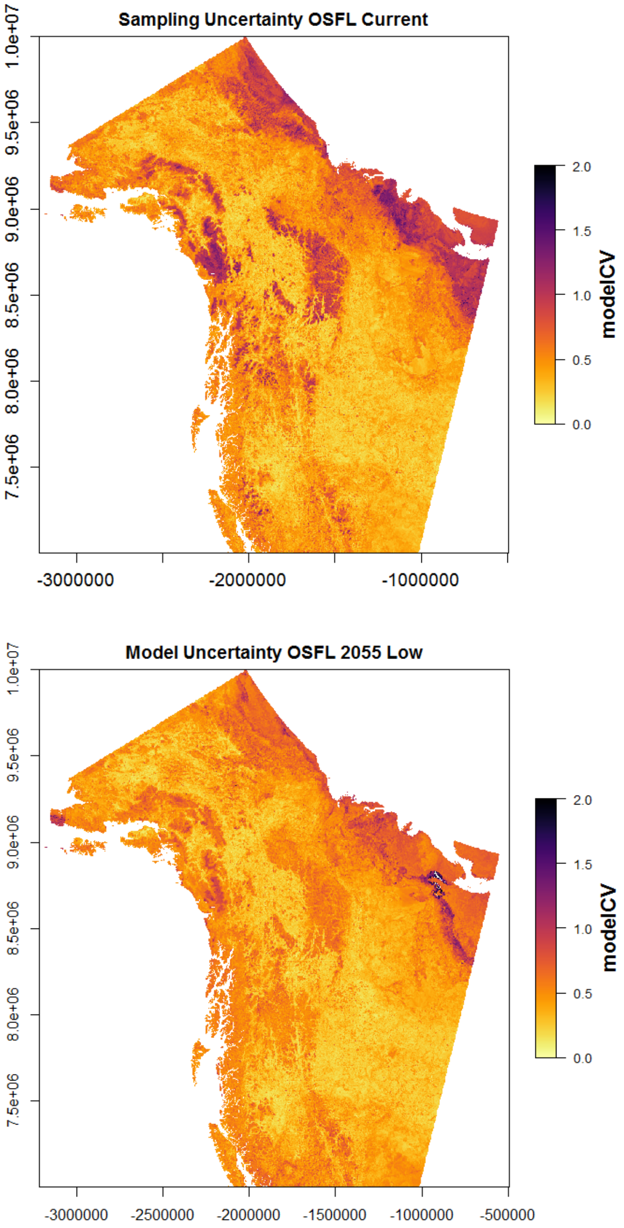
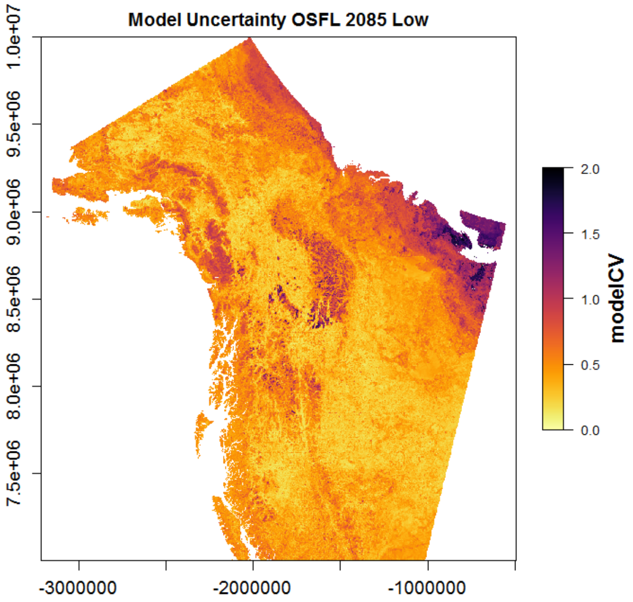
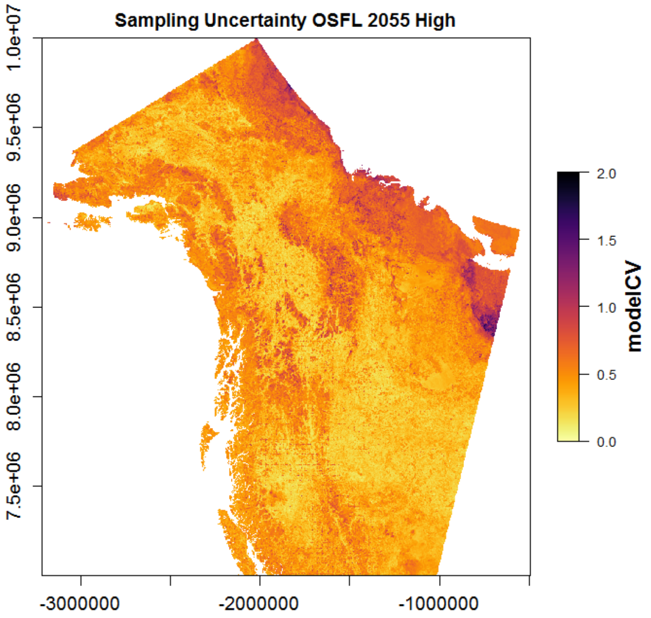


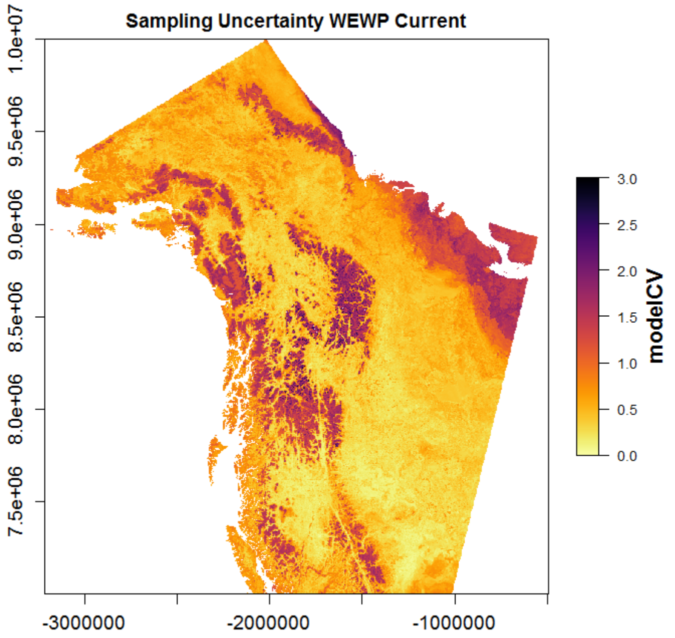
Figure 3-2. Total predicted abundances of the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP) for various scenarios. Scenarios included a baseline time period (median year of 1995) and two future 30-year time periods under a low concentration of greenhouse gas emission pathway (RCP4.5, solid lines) and a high one (RCP8.5, dashed lines) in northwestern North America. Horizontal lines are ± 95% Confidence Intervals around the mean.

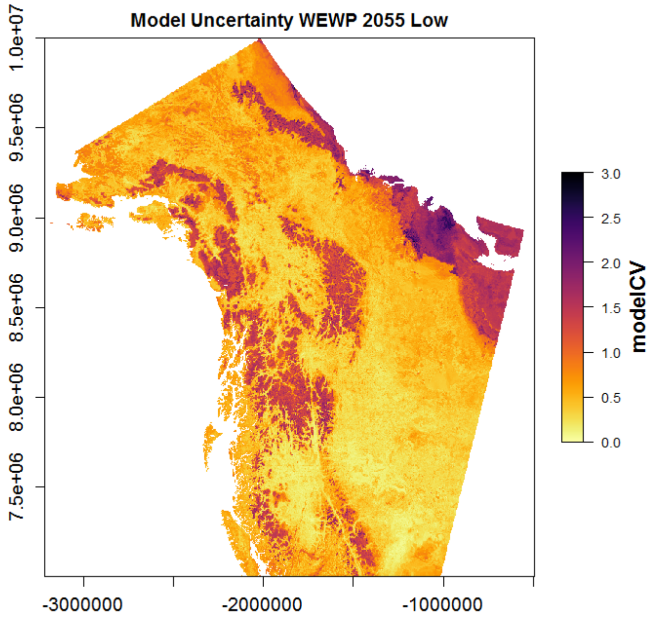
Figure 3-3. Projected uncertainty from sampling (sd/mean) from 25 bootstrap iterations of boosted regression tree models used for prediction at 4 km resolution for the Olive-sided Flycatcher (OSFL) and Western Wood-Pewee (WEWP) under various scenarios. Scenarios are shown above each grid: baseline climatic conditions 1981 – 2010 (median of 1995), two future time periods: 2041-2070 (median 2055) and 2071-2100 (median 2085) with high (RCP8.5, Representative Concentration Pathways) and low (RCP4.5) greenhouse gas emission concentrations.

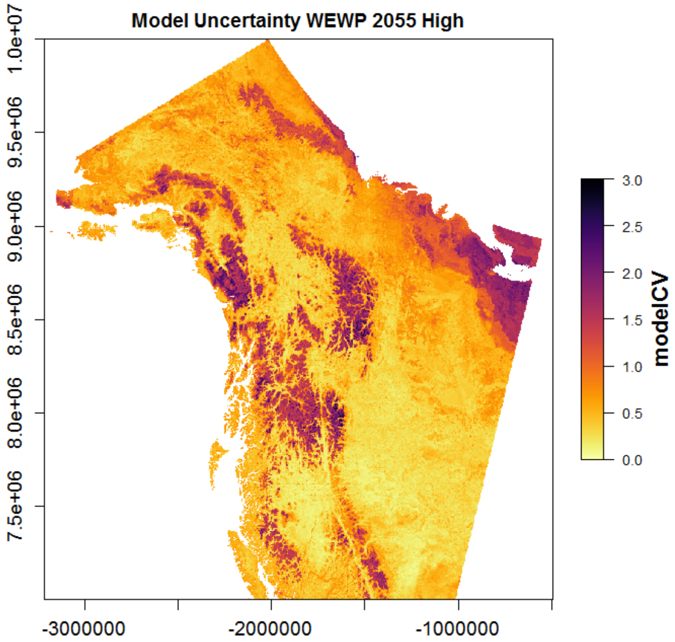


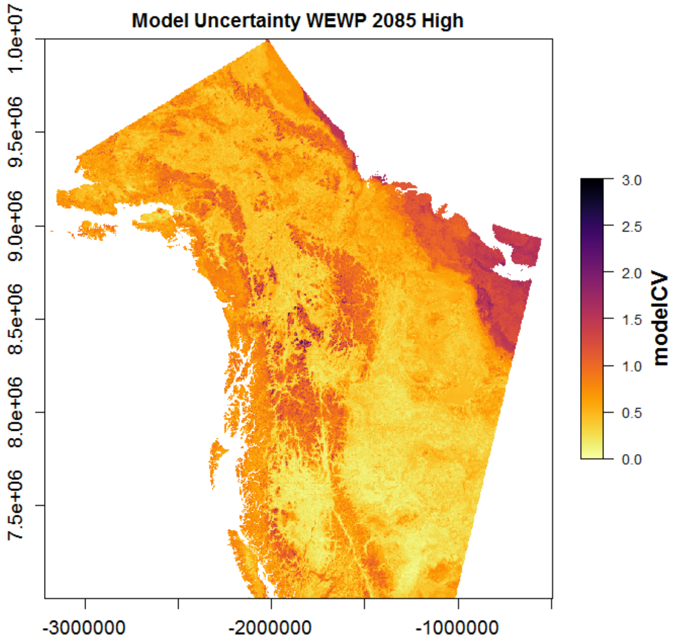

Model Uncertainty OSFL 2085 Low
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
-3000000
-2000000
-1000000
2.0
1.5
1.0
0.5
0.0
modelCV


Sampling Uncertainty OSFL 2055 High
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
-3000000
-2000000
-1000000
2.0
1.5
1.0
0.5
0.0
modelCV


Sampling Uncertainty WEWP Current


Model Uncertainty WEWP 2055 Low


Model Uncertainty WEWP 2055 High
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0
modelCV


Model Uncertainty WEWP 2085 High
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
-3000000
-2000000
-1000000
3.0
2.5
2.0
1.5
1.0
0.5
0.0
modelCV

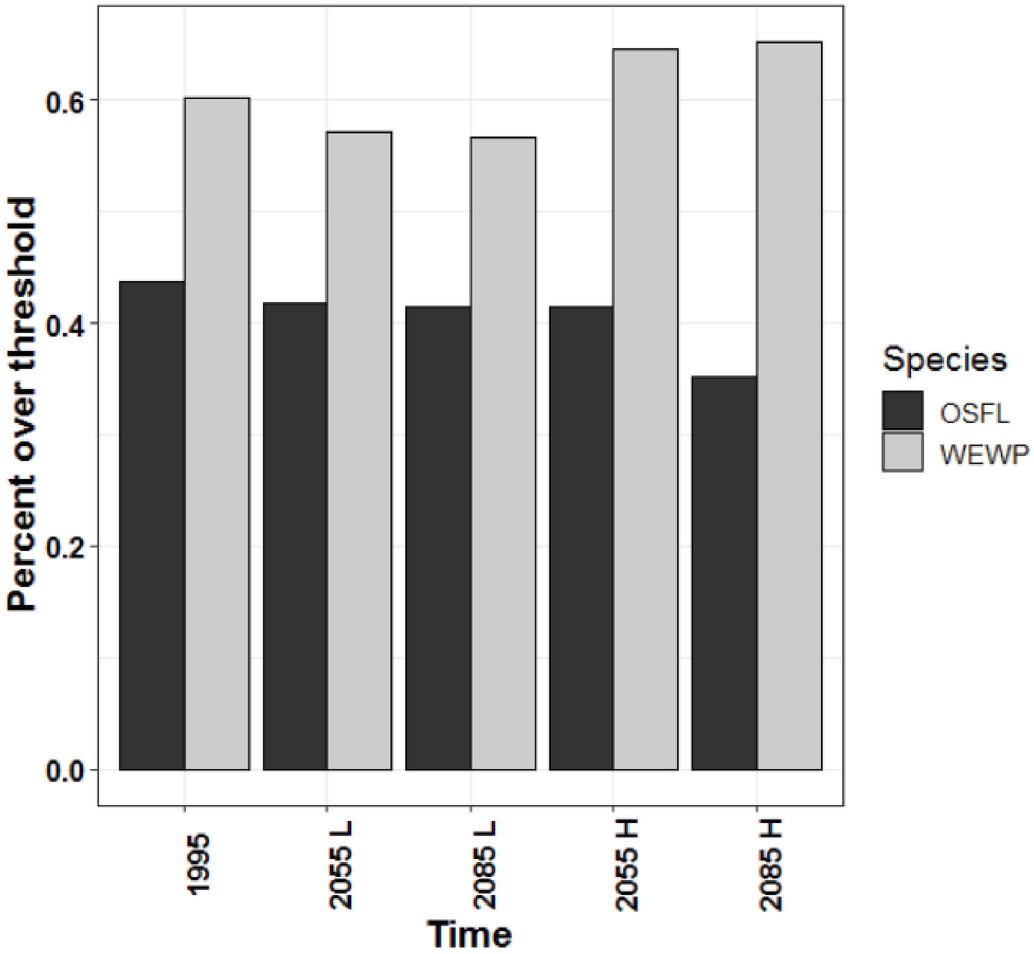
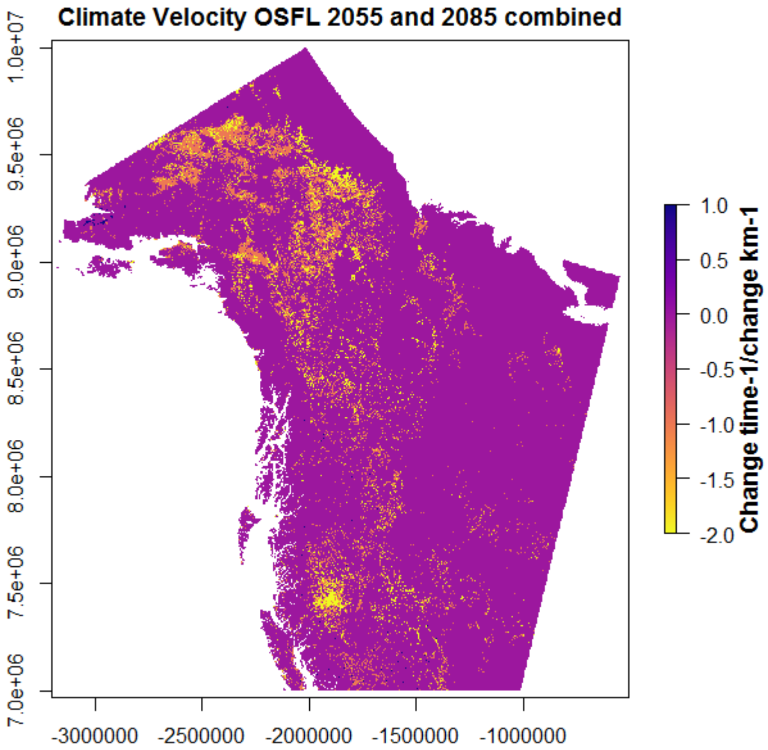
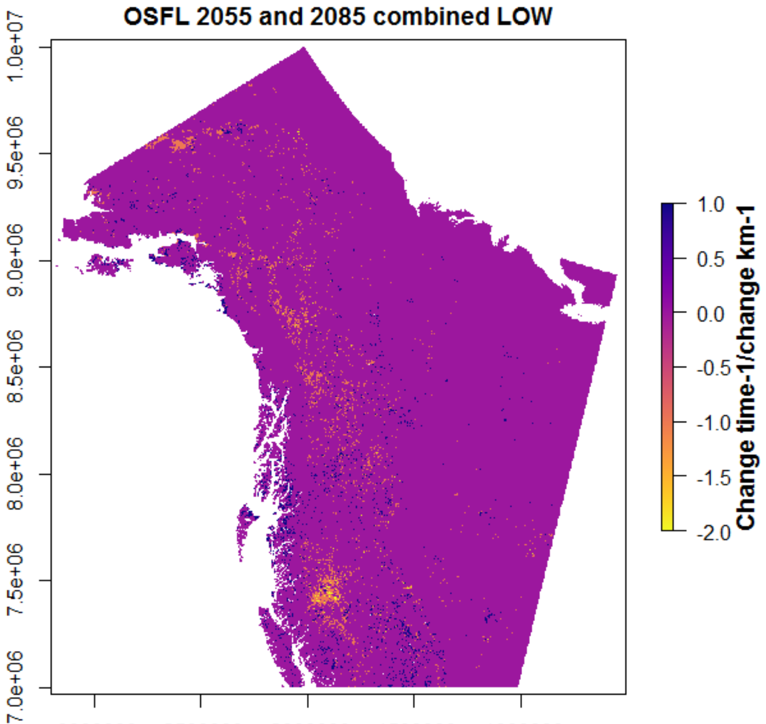
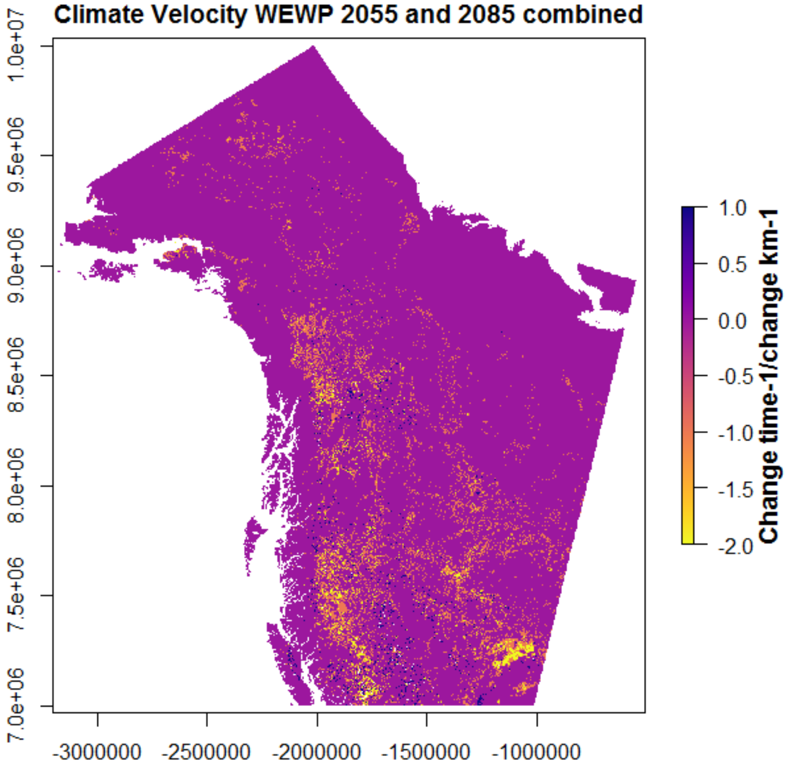


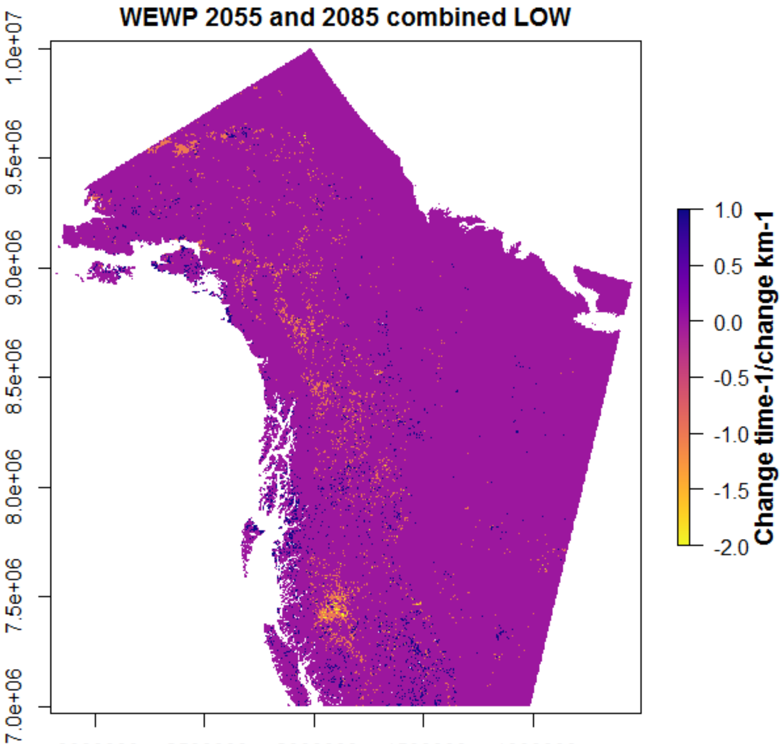
Figure 3-4. Percent of area predicted to support abundances over a threshold density (ideal habitat). The threshold was defined as percent of pixels that were over the mean abundance during the baseline period of 1981 – 2010 (median of 1995) for the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP). Scenarios were two future time periods of 2041-2070 (median 2055) and 2071-2100 (median 2085) two green gas emission concentrations: high (RCP8.5, Representative Concentration Pathways) and low (RCP4.5).

Figure 3-5. Bioclimatic velocity calculated from the change in projected distribution and abundance from boosted regression tree models per unit of time (60- and 90-year periods were combined) divided by the spatial gradient in abundance (per km) at 4-km resolution for the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP). Species and scenario are indicated above each plot between baseline climatic conditions 1981 – 2010 (median of 1995) and two future time periods: 2041-2070 (median 2055) and 2071 – 2110 (2085) assuming low-moderate (RCP4.5) and high (RCP8.5) greenhouse gas emission scenarios.




OSFL 2055 and 2085 combined LOW


Climate Velocity WEWP 2055 and 2085 combined


WEWP 2055 and 2085 combined LOW
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
7.0e+06
-3000000
-2500000
-2000000
-1500000
-1000000
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Change time-1/change km-1

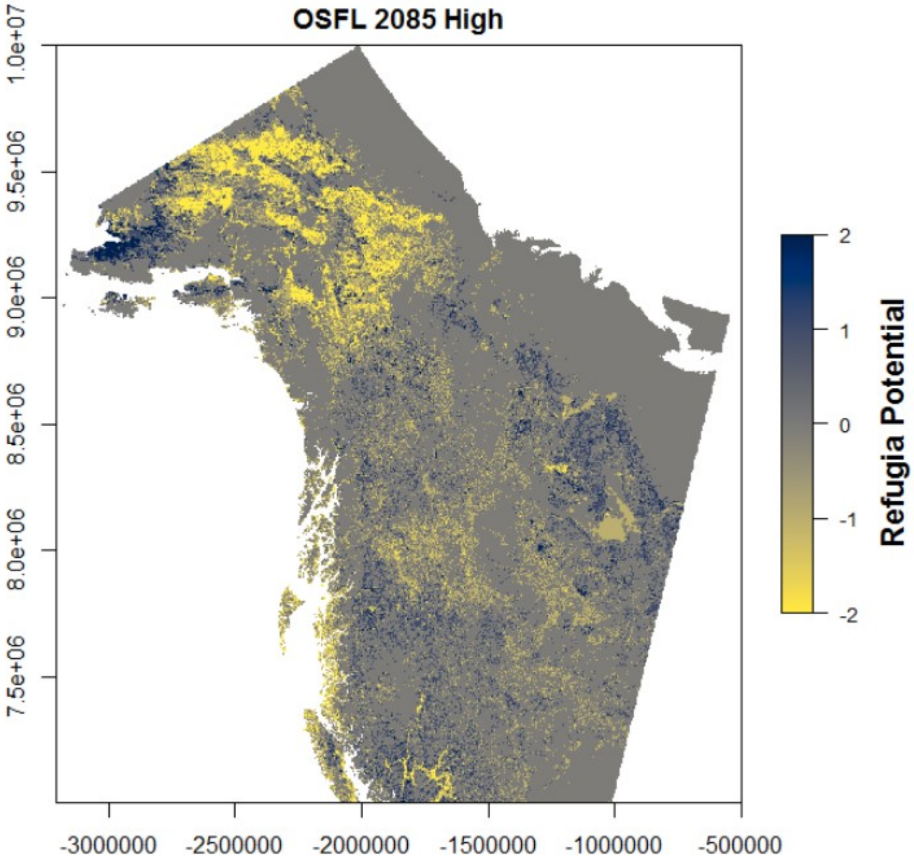


Figure 3-6A. Projected losses and gains in predicted abundance from boosted regression tree models for prediction at 4-km resolution for the Olive-sided Flycatcher. Losses and gains were calculated between the baseline climatic conditions 1981 – 2010 (median of 1995) and one future time period 2071-2100 (median 2085) assuming a high (RCP8.5) greenhouse gas emission trajectory.

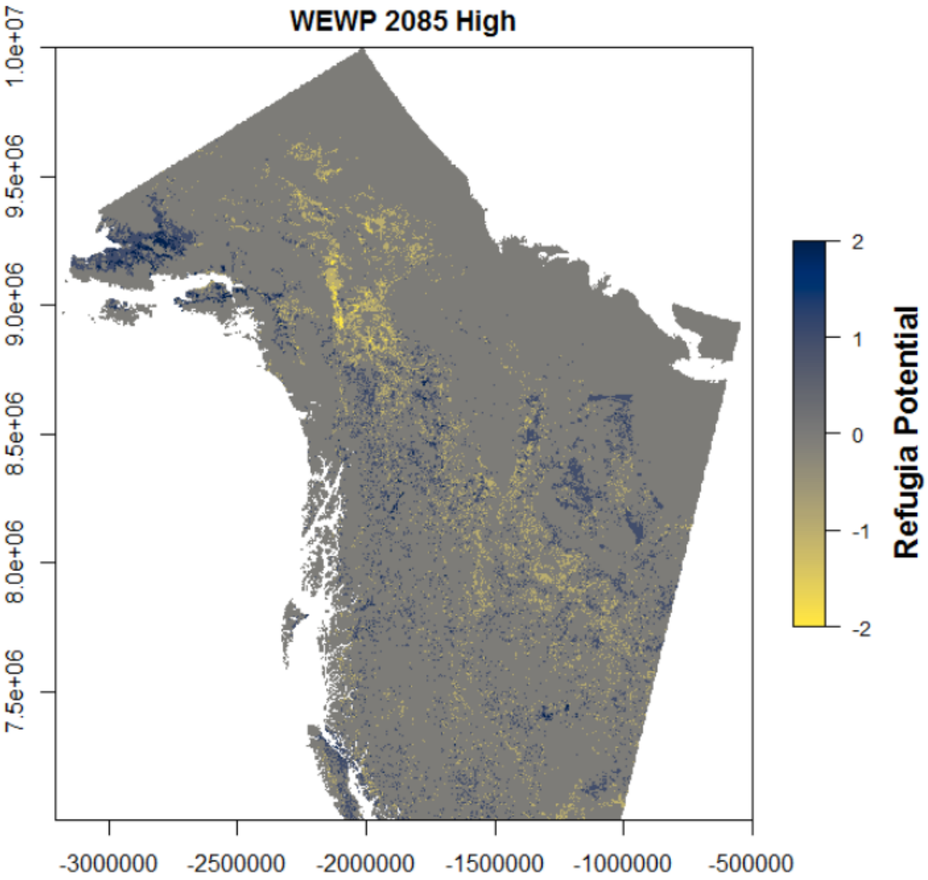
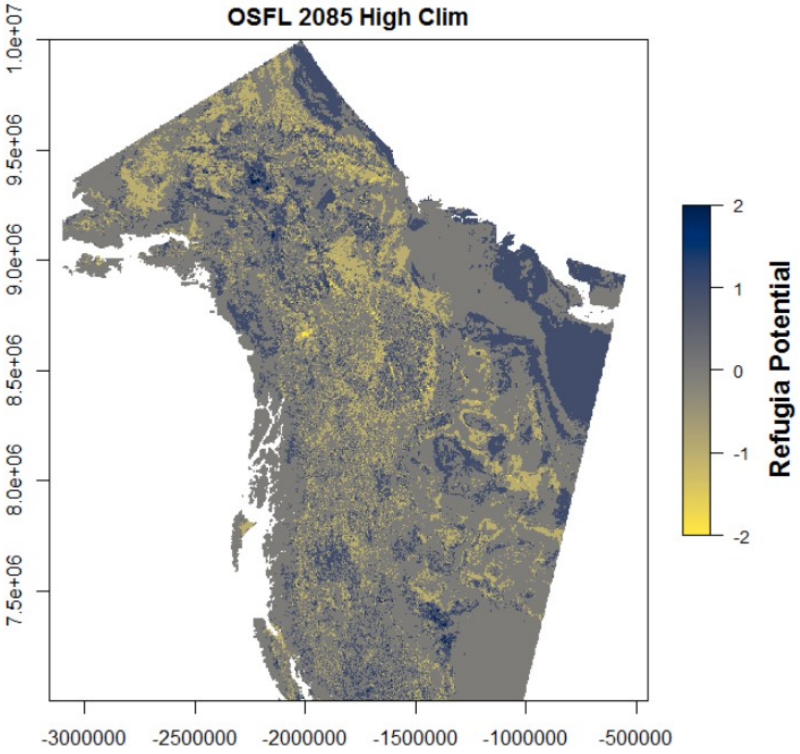
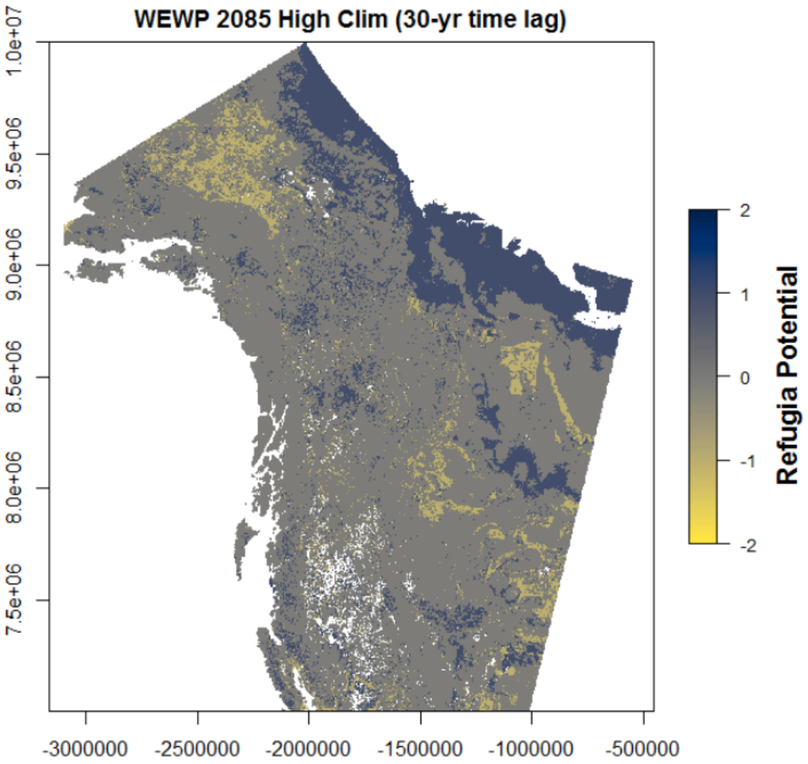


Figure 3-6B. Projected losses and gains in predicted abundance from boosted regression tree climate models for prediction at 4-km resolution for the Western Wood-Pewee. Losses and gains were calculated between the baseline climatic conditions 1981 – 2010 (median of 1995) and one future time period 2071-2100 (median of 2085) assuming a high (RCP8.5) greenhouse gas emission trajectory.

Figure 3-6C. Projected losses and gains in predicted abundance from boosted regression tree climate models using climate and topography only (no vegetation layers) for prediction at 4-km resolution. Species and scenarios are shown above each gird. For the Olive-sided Flycatcher, no time lag was assumed from vegetation change and for the Western Wood-Pewee a 30 - 60 year time lag was assumed between the baseline climatic conditions 1981 – 2010 (median of 1995) and one future time period 2071-2100 (median of 2085) (under a high RCP8.5, greenhouse gas emission trajectory). White represents areas "lost" due to vegetation time lag.




WEWP 2085 High Clim (30-yr time lag)
1.0e+07
9.5e+06
9.0e+06
8.5e+06
8.0e+06
7.5e+06
-3000000
-2500000
-2000000
-1500000
-1000000
-500000
Refugia Potential
2
1
0
-1
-2

CHAPTER IV: PHENOLOGY OF TWO AERIAL INSECTIVOROUS BIRDS (OLIVE-SIDED FLYCATCHER AND WESTERN WOOD-PEWEE) AND THEIR POTENTIAL INSECT PREY IN SOUTHERN YUKON.

4.1 SUMMARY

Our understanding of phenological shifts that will accompany climate change is in its infancy in North America. Community-based data are required to investigate potential impacts of climate change on timing of life history events of interacting members of northern ecosystems. In this chapter I investigate potential phenological patterns and breeding success of two species of aerial insectivorous birds and their potential prey by examining patterns of insect activity on breeding territories of birds in southern Yukon between 2013 and 2017. Dates of arrival of migrants to breeding territories did not change with year, but onset of incubation became progressively earlier each year in both species of birds. Nesting success of both species varied greatly with year, and between nesting attempts within the same year. A daily insect biomass index, calculated from insects captured in hanging malaise traps, varied between years, possibly declining with year. An annual time of peak insect activity was not easily discernible or predictable between years. A population level bird breeding score was calculated for each day, where each breeding pair received a score based on breeding stage progression (the highest score was achieved during the brooding stage between 5 days old until fledging). The insect abundance index was significant in predicting daily bird breeding scores for OSFL and was marginally significant for WEWP (although overall model fits were not high). There was a significant effect of days of offset from insect peaks predicting breeding success for OSFL, but not for WEWP pairs. Thus, I provide some evidence of phenological adjustment to climate change and some influence of timing of insect activity on phenology and breeding success in these two bird species, and a concerning pattern of possibly declining insect abundance with year.

4.2 INTRODUCTION

Climate change is a major factor in population declines, range alterations, and extinctions across many taxa, and our planet may be experiencing a 6th mass extinction event given the speed of global warming and consequent impacts (Parmesan and Yohe 2003, Devictor et al. 2008, Mayhew et al. 2008, Cahill et al. 2013). Reviews on impacts of climate change describe changes in distribution such as poleward shifts (Walther et al. 2002, Araújo and Rahbek 2006, Matthews et al. 2011), reduced abundance and diversity (Peterson et al. 2002, Araújo and Rahbek 2006, Distler et al. 2015), and altered timing of annual cycle events (Walther et al. 2002, Parmesan and Yohe 2003, Yang and Rudolf 2010, Donnelly et al. 2012, Hassall 2015).

Spring events such as first emergence of plants and fungi, and first breeding events of animals such as insects and birds are occurring earlier than observed historically in many species of the temperate zone (Bradley et al. 1999, Walther et al. 2002, Butler 2003, Parmesan and Yohe 2003, Root et al. 2003, Lappalainen et al. 2008). Temperature is correlated with first spring emergence of trees (first flowering or leafing date), frogs (spawning), butterflies (first appearance) (Stefanescu et al. 2003, Donnelly et al. 2012, Ovaskainen et al. 2013), and arrival or clutch initiation in breeding birds (Hussell 2003, Torti and Dunn 2005). With warmer springs these events take place earlier. Birds are generally mobile organisms and may be able to track climate change by altering ranges and timing of annual events, although not all are likely to track climate change fast enough (e.g. Devictor et al. 2008), and time lags from vegetation change may delay adjustments (Stralberg et al. 2015a). Migratory birds are arriving earlier to many temperate breeding areas. and some initiate breeding earlier (Visser et al. 1998, Hussell 2003, Both et al. 2004, Miller-Rushing et al. 2008). Such species include Cliff Swallows (*Petrochelidon pyrrhonota*, Brown and Brown 2000) and Tree Swallows (*Tachycineta bicolor*), both aerial insectivores (Hussell 2003). Not adjusting to climate change using earlier migration explained declines in European species of birds between 1990 and 2000 (Móller et al. 2008). Earlier breeding can have positive impacts on individual fitness (Barba et al. 1995, Potti 1998, Dunn 2004) by leading to higher recruitment or higher probability of females surviving. Earlier breeding does not always translate into detectable population-level changes (Reed et al. 2013) because of the potential for altered interspecific interactions (Wilson and Arcese 2003).

Changes in phenology and distribution can result in altered community dynamics, such as lower availability of prey species, changes to the predator community, and changes to timing of abundance peaks between predator and prey (Both et al. 2006a, Ludwig et al. 2006, Reed et al. 2013), such as between herbivores such as caribou and essential plants (Post and Forchhammer 2008). In addition, the vegetation community may be altered in such a way to reduce habitat for prey populations or sites for foraging and nesting. Both the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP) may depend on complex forest structure with multi-aged and/or multi-species trees, open areas, edge, riparian habitat and snags for foraging, a matrix influenced by vegetation time lags and altered disturbance regimes from climate change (See *Chapter II*).

Changes to phenology often occur via phenotypic plasticity, or the range of behaviors possible with a given genotype (Gienapp et al. 2008). Pairs of species may adjust phenology to climate change, but not necessarily to the same degree or even direction (Bradley et al. 1999, Buse et al. 1999, Peñuelas et al. 2002, Sanz et al. 2003, Both et al. 2006a, Ovaskainen et al. 2013). In a boreal-forested region of Russia, birds adjusted spring phenological events, but to varying degree depending on migratory strategy, and not as rapidly as plants or insects over a 40-year period (Ovaskainen et al. 2013). In Wisconsin, some birds arrived earlier and some plants revealed earlier flowering in spring between 1976 and 1998, but many others did not (Bradley et al. 1999). Invertebrates revealed greater phenology and range alteration from climate change than other taxonomic groups, such as amphibians, fish and plants, in the UK (Hassall 2015). Phenological advance has been well documented for insects of the order Odonata, and given their high detectability, dragonflies and their relatives have been suggested as a barometer for climate change impacts (Hassall 2015).

Differential shifts across species can occur from varying cues for phenological events between species; birds and insects may be primarily triggered by short-term climatic cues (such as temperature and snow cover), whereas plants and fungi may be affected by long-term climatic averages (Ovaskainen et al. 2013). Many of these shifts result from phenotypic plasticity, but a genetic shift in response to global warming occurred in some insects in as little as five years (Bradshaw and Holzapfel 2001). Predators such as aerial insectivores have smaller population sizes and longer generation times relative to their prey, making synchronous genetic change via natural selection less likely than some other groups in the short term. Genetic variation can also be lost as populations decline from impacts of climate change, limiting potential for adaptive evolution (Pulido and Berthold 2004).

Adding to the complexity of disparate responses to climate change across species and geographical regions, even populations of the same species do not change timing uniformly (Visser et al. 1998, Sanz 2003, Ahola et al. 2004), or equally across years (Reed et al. 2013). Changes to population sizes, such as declines that have been reported in several bird and insect populations (Warren et al. 2001, Benton et al. 2002, Shortall et al. 2009, Nocera et al. 2012), also make it challenging to track adjustment in phenology to climate change (Miller-Rushing et al. 2008). Declines in insects have been linked to agricultural intensification (in Scotland, Benton et al. 2002), including specifically from loss or alteration of riparian habitat (Maser and Schowalter 2013a), and insect declines have been correlated to declines of birds in the UK (Shortall et al. 2009).

A seasonal pulse or peak of abundance with comparatively little predation occurs in many temperate insect groups (Shortall et al. 2009, Maser and Schowalter 2013a, Cutting et al. 2016), and this pulse may be particularly condensed into a short time period in northern climates or high elevations. Although often triggered by photoperiod, precipitation and temperature also both influence timing of these pulses (Hodkinson 2005).

Timing of breeding in many birds is thought to coincide with a contracted peak of insect abundance, so that high food availability occurs during the time of peak energetic demands of nestling feeding (Perrins 1991, Visser et al. 1998, Both et al. 2006a, Visser et al. 2006). For many passerine birds peak energetic demands occur from the mid-nestling period to fledging (Martin 1987, Vatka et al. 2011). Because the peak of food availability occurs after nesting is initiated, other proxies may be used as cues to time breeding onset, such as photoperiod, temperature, precipitation (Eeva et al. 2000, Dunn 2004, Both et al. 2006b), food availability (Dunn et al. 2011), as well as individual body condition or predator activity (Husek et al. 2012, Lany et al. 2016). Early spring temperature is a commonly used cue (Visser et al. 2006), fine-tuned in conjunction with many of the others (mentioned above). A limited range of prey types (e.g., some birds specialize on caterpillars to feed young), or a highly contracted seasonal pulse of insects in northern and high elevation environments (Maser and Schowalter 2013a), provide potential for asynchrony between predator and prey. However, it may also result in greater specialization by co-existing insectivorous birds, and less overlap in diet (e.g. Cutting et al.

2016). Reduced overlap resulted in increased energetic condition in two species of sparrows in a sagebrush ecosystem in Montana (Cutting et al. 2016).

Changes in timing of breeding events in migratory birds could result in asynchrony between breeding birds and their insect prey, needed in abundance to feed young. This has been termed “match/mismatch” or “mismatch” by Cushing (1969) in aquatic systems of fish larvae and zooplankton (Cushing 1969, Visser et al. 1998), or “mistiming” (Both et al. 2006a), and also broadened to include synchrony/asynchrony terms because they make less stringent assumptions about what the optimal timing may be for predators and fitness (Johansson et al. 2015). These include “phenological trophic asynchrony” (Visser and Both 2005, Franks et al. 2018) or “phenology mismatch hypothesis” (Jones and Cresswell 2010, Reed et al. 2013), as well as “trophic mismatch” (Lany et al. 2015). I use the term phenological asynchrony, or simply ***asynchrony*** for brevity.

There is evidence for asynchrony between several European bird populations and their insect prey (Both et al. 2006a, Visser et al. 2006, Jones and Cresswell 2010, Reed et al. 2013). Many of these studies were conducted on Great Tits (*Parus major*) that utilize mostly caterpillars of the winter moth (*Operophtera brumata*) to feed relatively large clutches (Perrins 1991). Between 1973 and 1995, egg-laying dates did not advance to the same degree as caterpillar biomass peaks in one population of Great Tits in the Netherlands, although hatch dates did advance by lessening the gap between egg-laying and hatch dates (Visser et al. 1998). Laying dates since 1970 did advance for another population of Great Tits in the UK (McCleery and Perrins 1998). Great Tits fledge more chicks and chicks with greater mass when laying is synchronized with caterpillar peaks (Visser et al. 2006). In Europe, migratory bird species that have advanced their laying dates show more positive population trends than those that have not

(Móller et al. 2008, Saino et al. 2011). However, in some cases, phenological shifts of breeding events have improved synchrony with food availability (Vatka et al. 2011), with possible benefits to productivity, defined as annual number of offspring per adult in the population (Meller et al. 2018, Alves et al. 2019).

In European broad-leaf forests, essential prey such as calorie-rich caterpillars may develop too early or too rapidly during warm springs for effective use by bird parents feeding chicks (Perrins 1991, Buse et al. 1999, Reed et al. 2013). Reed et al. (2013) found that Great Tit females that arrived earliest to the Netherlands enjoyed several fitness benefits resulting from better synchrony with caterpillar emergence, although population-wide effects on fitness were not evident. Population-level consequences for phenological disjunction may be difficult to detect because of year-to-year climate fluctuations, density dependent factors, and changes to the predator community (Reed et al. 2013). Arrival date to breeding grounds may be under strong selective pressure because of the influence of arrival date on reproductive success (Barba et al. 1995, Aebischer et al. 1996). For example, earlier arriving males and females enjoyed greater reproductive success in the Savi's Warbler (*Locustella luscinioides*, Aebischer et al. 1996) and the American Redstart (*Setophaga ruticilla*, Smith and Moore 2005). However, breeding events may shift differentially, such that early arrival may not necessarily result in early breeding (Ahola et al. 2004), or may result in breeding that is much too early relative to spring weather conditions (Ludwig et al. 2006).

The potential for asynchrony may depend on many factors specific to species and geographic locations, such as inter-annual variation in warming, and the pattern of seasonality and diversity in local prey, such as the shape and size of insect peaks and inter-species variation in phenology (Dunn et al. 2011). Differences in flexibility in breeding onset between species

(Drever et al. 2012), conspecific density and competition, differences in specific cues to time breeding, migration patterns, or even on the prevalence of double brooding (Visser and Both 2005, Visser et al. 2006, Johansson et al. 2015, Franks et al. 2018), and/or patterns of predation on the birds themselves (Husek et al. 2012) may influence outcomes.

Most studies of phenology of breeding and synchrony with food peaks have been conducted in broad-leaved forests of Europe (Buse et al. 1999, Both et al. 2004, Visser and Both 2005, Visser et al. 2006, Franks et al. 2018). The few exceptions include Dunn et al. (2011) Tree Swallows in North America and Lany et al. (2015); Black-throated Blue Warblers in New Hampshire, USA. Many studies also involved small oscine Parids utilizing caterpillars to feed young (Visser et al. 1998, Visser et al. 2006). However, many bird species of the boreal forest, such has aerial insectivores, feed their young adult insects. More investigation into northern and/or boreal species in North America would help determine the generality of findings.

Our understanding of interactions and potential shifts with climate change is incomplete, especially in northern North America. Community-based data are required to investigate potential impacts of climate change on timing of life history events between interacting members of northern ecosystems. Quantifying some of these impacts to climate change can inform potential conservation or management actions (Guisan et al. 2013).

My objective for this chapter was to investigate community-level interactions between two obligate aerial insectivorous birds (including their breeding phenology and breeding success) and their prey, including emergence times, and abundance and diversity of insects across the breeding season. In the absence of long-term data on insect abundance or breeding phenology, my aim over a five-year period was to examine feeding habits of birds, describe insect and bird phenology and the potential for asynchrony across the breeding season, and to compare insect abundance among years. My general hypothesis was that pattern of energetic requirements for breeding birds to feed their young would be influenced by the timing of insect abundance across the breeding season, with selection working to synchronize breeding demands and insect abundance. I also expected that year to year variation would be a factor influencing these relationships in a montane, high latitude environment in southern Yukon.

4.3 METHODS

Study Area

The area I selected for this regional study was a topographically heterogenous area in southern Yukon with overlapping OSFL and WEWP territories. Because OSFL territories are often remote, large in size, and spaced apart by long distances (Wright 1997), accessibility was a factor in selecting areas for study. I utilized an area from approximately 60° 53, 135° 23' in the north to 60° 36' N, 134° 44' W at the southern, an area of approximately 450 km^2 with over 30 small lakes and ponds (elevation range of 650 - 1140 m asl). Not every bird territory was included in the study, due to access constraints, and because there were many more WEWP than OSFL territories. The study area encompassed some areas considered to be within the city of Whitehorse (with various small vegetation disturbances such as roads and trails used for recreation), but I did not collect data on birds located closer than 300 m to urban or industrial development because of potential impacts on behavior. The dominant vegetation in most areas was white spruce (*Picea glauca*), with some black spruce (*P. mariana*), and small amounts of lodgepole pine, and at higher elevations subalpine fir (*Abies l*as*iocarpa*), mixed with site-specific amounts of deciduous trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). Shrub layers were dominated by willow (*Salix* spp.) and dwarf birch (*Betula* *glandulosa*), and many areas were wet from muskeg, damp moss layers, small ponds, flooded creeks, or swamp.

Phenology

In order to track local phenological events, breeding pairs were checked for stage and breeding success in a cyclical pattern so that each pair was checked at least once every 4 - 6 days (minimum of 10 pairs of each species in each year between 2013 and 2017). Because of the long distances between territories, and travel required in both vehicle and on foot in difficult terrain, each pair could not be checked every day, but nesting stage could be determined daily using either video capture or retroactive calculation. Nests that were particularly challenging to access or monitor without disturbing nesting birds (such as in habitat with vegetation of low overall canopy height, or very sparse trees such as in muskeg or subalpine) were monitored with a Bushnell Trophy motion-triggered camera with both photo and video capability placed in a tree 8 – 12 m away. Nest contents were checked visually using binoculars, spotting scopes, or if nests were not visible, using an aluminum pole and Nikon Coolpix waterproof camera set on a timer, or by climbing nearby trees. If nests were still too high, nest contents were inferred from sounds and behavior of adult birds. All points on the territory important in breeding, such as those on the outermost perimeter of the territory, the nest site, perch sites, or feeding sites were marked using portable Garmin 76CSx GPS units.

In order to examine timing of insect peaks in abundance and biomass, I conducted insect sampling on four OSFL territories that overlapped with at least one WEWP territory. Insect sampling locations were also chosen based on elevation, with one placed at relatively high elevation, one medium and two at low. Aerial arthropod sampling was conducted using modified Malaise Sante (santetraps.com) traps hoisted to 3 m from the top of the canopy, from a spruce or pine tree located within 50 m of an OSFL nest (Meehan and George 2003) and overlapping at least one WEWP territory. Insect catch was removed every 4 - 8 days to allow calculation of a "daily" insect biomass and progressive change in taxonomic groups with date. Arthropods were stored in 70% ethyl alcohol and water solution at 4 °C until they could be sorted and identified to order using Zeiss Discovery V8 stereomicroscopes. Arthropods with body length of $\geq$ 3mm (Meehan and George 2003) were measured to the nearest millimeter using transparent rulers and stereomicroscopes. Following identification and body measurements, insect samples were placed in a drying oven at 70˚C for 24 hours and then weighed. For corroboration, weight was also calculated using previously-determined length-weight relationships for each insect order (Rogers et al. 1976, Sabo et al. 2002). W (weight in mg) = aL^b, where a and b are constants specific to the order of invertebrate (e.g. calculated dry weight for order Diptera = $0.04*(\text{body length})^{2.26}$).

Because dragonflies and damselflies (members of order Odonata) were not captured in Malaise traps in 2013 and 2014, and dragonflies were observed being fed to young by adults, 50 m transect sampling of large insects was conducted weekly during the summers of 2015 - 2017 to augment aerial arthropod sampling on OSFL and WEWP territories. Transects were located in areas that overlapped an OSFL territory and a WEWP territory, and were 50 m or less from the waterfront of a pond. All large insects (dragonflies, large bees and wasps, flying ants, and large flies) encountered or flushed from within 1.5 m on either side of the transect were recorded. Relative sizes were also recorded, such has large, medium or small. If identification to order could not be completed visually, large insects were captured with a sweep net for closer examination.

In order to examine preferred prey and feeding habits, feeding observations were conducted from a location 10 – 25 m from nest sites or perches using spotting scopes or binoculars. Observation bouts were 10 minutes in duration and consisted of counting all insect forays by adult birds and recording prey type (if visible). Feeding observations at nest sites were conducted every 3 - 5 days during the brooding period at known nest sites (not all nests were found and some were not visible). Often prey type could not be identified; relative size was recorded in these cases, e.g. large, medium or small insect.

Data Analyses

I calculated a daily bird breeding score to quantify population-wide energetics utilized for breeding, with 1 representing an unpaired male, 2 a paired male, 3 a pair that was nest-building or egg-laying, 4 representing incubation or nestlings up to 5 days old, and 5 representing the nestling stage from day 5 until fledging, and 3 representing fledged chicks. Scores were summed across individuals for each day to give an estimate of population-wide energy demands. Scores were then converted to a proportion of maximum to account for an unequal total of breeding birds present on each day and then arc-sin transformed to improve normality prior to analyses.

I calculated an index of daily insect abundance using the calculated insect weight (W), times the number of insects captured in a sample, divided by number of days the trap was open. Nest success was calculated using the Mayfield method (Mayfield 1975) that takes into account the lower likelihood of finding nests that do not make it to the end of the nesting cycle compared to those that are “successful”. Re-nesting attempts after a failure are considered common for the OSFL (COSEWIC 2018), so re-nesting attempts were carefully tracked whenever possible (Thompson et al. 2001). For comparison, I also calculated nest success as simply the proportion of nests that fledged at least one young, because Mayfield estimates may not be as reliable with sample sizes of < 20 (Heath et al. 2010), and sample sizes for OSFL nests were < 20 (14 for most years).

In order to examine the influence of insect abundance and temperature on bird breeding scores I used generalized additive mixed models (GAMMs) using the *mgcv*/*gamm4* packages (Wood 2016) in R (R Foundation for Statistical Computing, Vienna, AT). GAMMs are appropriate for phenological data because they are flexible enough to allow inference of non-linear functions of covariates (through smoothing), can capture periodicity, and do not require prior knowledge of these response patterns (Polansky and Robbins 2013). They also allow inclusion of random effects without overly protracting computational time. Random effects are a useful addition to models when multiple samples are taken from the same pairs of birds on sequential days, creating an obvious potential for pseudoreplication and overdispersion. Overdispersion can occur with response variables of higher variance than expected given the parameters, for example from a large number of zeros or small values. Overdispersion was quantified using the sum of squared Pearson residuals divided by sample size minus the number of parameters (Hilbe 2017), and compared across models. I used a Gaussian distribution and log-link function.

Two dimensional smoothers were included for the insect biomass index and temperature (measured in °C the day before sampling). Julian date was included as a random factor because phenological stages are sequential, causing an unavoidable dependence between Julian date and bird breeding score. Year was included as a factor given the high anticipated annual variation. Location of trap was originally included in models, but later removed because it was not a significant factor in any model and was not a factor of interest. Pearson residuals were examined for potential sources of overdispersion. Final models (of three considered) were selected based on the unbiased risk estimator/likelihood ratio test (scaled) compared between a candidate model and the null model, maximizing the deviance explained, and r^2 values (Table 4-1).

Although difficult to calculate with a high level of precision, because insect abundance was quite variable among days, a population-level "offset" - or difference between date of peak insect biomass and (first) peak breeding scores (in days) - was calculated using the day of insect peaks as zero. The insect biomass peak or "ideal" for maximum insect abundance was estimated using the date of the maximum value of biomass. Offset was calculated as the difference, in number of days, from the peak of total insect abundance for each year to the day that pairs were feeding 9-day old nestlings for WEWP and 10-day old nestlings for OSFL (perfect synchrony would be zero). If nesting was initiated (egg-laying or later) but failed, then the approximate date that pairs would be feeding 9-day old/10 day-old nestlings was used. The influence of offsets between peak energetic demands of breeding bird pairs and the peak of insect abundance (from Malaise traps) on breeding success was investigated using GAMMs, with individual breeding success (clutch size of fledged young, 0, 3, or 4) as the dependent variable, and offset (in days) as a predictor for each species. I included individual bird identity and year as random factors, and utilized a Poisson distribution.

4.4 RESULTS

An average of 14 OSFL pairs and 19 WEWP pairs were assessed for breeding phenology and nesting success in each of five breeding seasons (2013 – 2017). Breeding success rates were calculated for 9 OSFL nests in 2014 and 14 OSFL nests annually between 2015 and 2017, and 9 WEWP nests in 2014 and 19 – 21 WEWP nests annually between 2015 and 2017. Data from 2013 were excluded due to low confidence in successful determination of nesting fate. Mayfield estimates of nest success for OSFL over the season, including second attempt if first failed, averaged 67.7%, and ranged from 60.5% in 2016 to a maximum of 73.2% in 2015. The percent of OSFL nests that fledged at least one young (71.4%), as well as the pattern across years, were both similar to the Mayfield estimates. When restricted to only first nesting attempts, Mayfield estimates for nest success in OSFL were much lower in some years, e.g. 19.8% and 27.5% in 2016 and 2017 respectively (Fig. 4-1). Only three of 14 OSFL nests from first attempts were successful in fledging at least one young in 2016, and only two fledged at least one young in 2017 (Fig. 4-1). Thus, in some years, population-wide nesting success was achieved almost exclusively from second nesting attempts.

Nesting success (Mayfield estimate) was 75.1% in WEWP (and ranged from 65.3% in 2014 to 84.2% in 2015) overall. The percent of WEWP nests with at least one fledged young was quite similar (77.4%). The Mayfield estimate for the first nesting attempt by WEWP in 2017 was very low (11.5%), but ranged to a maximum of 78.3% in 2015 (Fig. 4-1).

Start dates of incubation were estimated using first nesting attempts, and it is possible that second nesting attempts were misidentified as first nesting attempts in some cases, especially in 2013 when observers were not familiar with signs of nesting stages. However, confirmed second nesting attempts were initiated much later than first attempts (approximately 15 days later), and this would create a larger margin of error than observed if misidentification of first attempts had occurred.

Territory size averaged 11.4 ha (mean ± SE 1.19, n = 16 territories) for OSFL and 0.85 ha (0.24, n = 12) for WEWP. Only one data point was used per territory for this summary statistic because territory size and characteristics, such as shape, at each location did not differ much from year to year. Elevation of territories averaged 787.8 m asl (34.1, n = 16) for OSFL and 672.1 m asl (7.37, n = 20) for WEWP. Territory size in both species was negatively correlated with elevation (OSFL: $r = -0.42$, $P = 0.07$, $n = 16$, WEWP: $r = -0.42$, $P = 0.08$, $n = 12$). Shapes of

OSFL territories were often long and narrow (rather than round), whereas territory shape of WEWP territories were closer to circular in shape (data not shown). Many OSFL territories had overlapping WEWP territories (from zero to five). Direct interspecific territorial interactions were never observed.

OSFL territories were located in open spruce forest, or open mixed forest of spruce and pine, or mixed forest with spruce and subalpine fir. Most were located in muskeg or marsh areas, and almost all were close to one or more small water bodies (see below). Many had a well-developed shrub layer of willow and aspen, and a ground cover of diverse herbaceous plants, mosses, and lichens (data not shown). Standing dead trees comprised 15.9% of tree structure around nest sites (n = 20 nests). Many were located on slopes (16 ± 10% slope, n = 22), with singing perches located overlooking these slopes.

WEWP territories were located in aspen forest, usually open aspen or partially closed aspen and mixed forest, with ground cover of diverse herbaceous shrubs and grasses. Each territory was located near a small water body (usually a pond) and also very close to forest-non-forest edge (see nest site characteristics below). Standing dead trees comprised 19.5% of tree structure around nest sites (n = 21 nests).

OSFL males first began to sing on territories (first day of territory defense) from May 14 (2016) until as late as June 9 (2017). Mean arrival dates of OSFL males onto territories ranged from May 21 - 27 (Julian Date 147.8 ± 2.0, n = 22 in 2014 to 142.6 ± 1.8, n =14 in 2016, Fig. 4-2A). Mean arrival date did not vary significantly by year ($F = 0.90$, df = 4, 62, $P = 0.47$). WEWP males began to sing on territories as early as May 12 (in 2016) to as late as June 16 (2016). Mean arrival dates of WEWP males onto territories ranged from May 22 – 28 (142.2 ± 0.55, n = 12, Julian date 142 = May 22 in 2015 at the earliest to Julian Date 148.3 ± 1.00, n = 8 in 2014 at the latest, Fig. 4-2B). Mean arrival date did not vary significantly by year for WEWP (*F* = 0.84, df = 4, 37, *P* = 0.50).

Although females were likely in the area (Hagelin et al. 2014), OSFL males were unpaired for an average of 8 days before becoming paired. A male was considered "paired" if a female stayed on the territory for at least 24 hours. WEWP males were unpaired for an average of 11 days before becoming paired.

Incubation period of OSFL averaged 15.1 days (range 14 – 17 days, n = 10 per year?), and brooding averaged 15.7 days (range 14 – 18 days, n = 10). Incubation (first attempt) was initiated on average at Julian Date 164.7 (day 164 = June 13, 156 – 182 ± 1.01, n = 38). Mean start of incubation varied significantly with year (*F* = 15.9, df = 4,42, P < 0.001). Incubation for first nesting attempts was initiated progressively earlier from 2013 to 2017 (Fig. 4-3A), from an average of 176.6 in 2013 to 160.0 in 2017, although sample sizes were small for some years (n = 5 in 2013). Many OSFL first nesting attempts were not successful and second nesting attempts were initiated (see Fig. 4-1A). In these cases, the incubation and brooding stage lengths were calculated using the second, successful nesting attempt. Incubation initiation reported here was calculated using the first nesting attempt. The average date of nest loss was day 13.8 (range 4 – 30) in the nesting cycle (start of incubation was day 1). Only females were observed incubating.

OSFL adults defended nests vigorously from potential predators, with loud pipping and other calls, and direct attacks (dive bombing). Predation by Canada Jay was one probably cause of failed nests, supported by direct observations of jays mobbing and eating contents of nests on at least two occasions. Canada Jay could be heard or seen on almost every OSFL territory at least once, and were often heard regularly. Jays followed observers on territories on several occasions. We did not visit nests when this occurred to avoid attracting a nest predator. Red Squirrel (*Tamiasciurus hudsonicus*) was also a likely nest predator, and a direct encounter between a red squirrel and an OSFL nest was observed directly at least once. Other mammals (e.g., Mustelids) likely predated nests, but were not observed directly. Several territories had breeding Red-tailed Hawk (*Buteo jamaicensis*) in the area, although it was unclear if they predated OSFL. One adult female OSFL was observed being preyed on by a Sharp-shinned Hawk (*Accipiter striatus*). OSFL fledglings were observed on territories with adult birds as long as 17 days after fledging from the nest.

Incubation stage of WEWP averaged 14.4 days (range 10 – 15 days, n = 20) and brooding averaged 15.8 days (range 14 – 17 days, n = 14) in length (for successful incubation and brooding attempts). Average incubation initiation of first nesting attempts in WEWP was on Julian Date 166.3 (day 166 = June 15; June 14 in 2016, range 156 - 180). Mean start of incubation varied with year ($F = 6.26$, df = 3,28, $P = 0.002$), and tended to get progressively earlier between 2014 and 2017 (Fig. 4-3B). The average date of nest loss was day 21.2 (range 11 – 27) in the nesting cycle (start of incubation was day 1). WEWP nest failures were assumed to be mostly from predation. Predatory events were never observed directly, but adult WEWPs were most agitated and defensive when corvids were in the area (Common Raven, *Corvus corax* and Black-billed Magpie, *Pica hudsonia*).

Observations of OSFL adults feeding hatchlings at nests overwhelmingly included large insects, such as large dragonflies (Odonata, such as blue darners, *Aeshna interrupta*), large flies (Diptera), and bees or wasps (Hymenoptera). Many other feeding observations were of unknown insect material, but often at least portions of these insects were visible to indicate at least a large or medium-sized insect was present. Very large insects, such as dragonflies, and beetles (Coleoptera) were “bashed” against a tree trunk prior to being fed to hatchlings. Average feeding rate was 1.6 feeding events/min (± 0.33, n = 10 territories). Interestingly, feeding rate of adults to nestlings did not seem to change with age of nestlings, although sample sizes were too small for quantitate assessment. Females were observed feeding young more often than males, but often only one at a time (the male or female). Fledglings were also fed by both male and female adults after leaving the nest. Birds near nests were sexed by behavior and appearance. Female OSFL were visibly “unkempt” (not preened) during incubation and brooding stages. Adult OSFL were observed expelling a black and surprisingly large pellet after eating (not feeding young necessarily, but after foraging), presumably made of exoskeleton material from insects.

Observations of WEWP adults feeding hatchlings at nests, when insect material could be clearly seen and identifiable, included flies and mosquitos (Diptera), with an average feeding rate of 1.3 feeding events/min (± 0.43, n = 10 territories). Similar to OSFL, feeding rate of adults to nestlings did not seem to change with age of nestlings. Fecal sacs were removed from one nestling at a time, immediately after it had eaten and produced the fecal sac. Males and females both fed nestlings but they seemed to feed at different times (rarely were both adults seen feeding during an observation period). Fledglings were fed by adults after leaving the nest, up to ten days after fledging.

OSFL nests were placed near the top (nest height/tree height: 7.91 m/10.91 m or 0.79, n = 21 nests) of white spruce trees (17/21), the remainder were placed in subalpine fir, 11.5 (± 4.34) cm from tree trunks. All nests were located near small water bodies (average 192 m from a pond, lake or marsh) or other types of edge (average 148 m from a trail, road, powerline, or cliff).

WEWP nests were placed 0.64 (4.69 m/7.70 m) from the top of mostly aspen (21/22) and one was placed in white spruce, 16.9 (± 8.20) cm from tree trunks. All nests were located near small water bodies (average of 155 m from a pond, lake or marsh) or other types of forest-disturbance edge, such as a trail, powerline, road or cliff (average of 45 m).

Insects caught in Malaise traps were predominantly of order Diptera (84.3%) followed by Hymenoptera (4.74%), Lepidoptera (3.52%) and Coleoptera (1.50%, n = 147,000 insects were captured in total. The remainder were spread amongst 11 orders of insects in small numbers (< 5%). An average of 186.2 insects were caught per day and per trap (± 21.2, n = 75 days, but ranged from 6 to 912). Most large insects identified on transects were Odonata (70%), followed by Lepidoptera (27%), Hymenoptera (2.5%) and Diptera (< 0.5%). A peak of overall abundance indices (with data from all years combined) possibly occurred between approximately days 175 - 200 (June 24 – 29, Fig. 4-4), but was difficult to discern, because of variation in insect abundance between days and years (see below).

Count data from insect transects indicated that large insects, mostly Odonata, peaked in the early part of the season (from Julian date 154 - 194, June 3 to July 13) with the largest peak possibly occurring between June 27 – 29 (Julian dates 178 – 180, Fig. 4-5), and dropping noticeably after this.

The insect biomass peaks (from Malaise traps) appeared smaller in 2015, 2016 and 2017 than in the previous two years (Fig. 4-6). Median insect abundance from Malaise traps differed significantly across years (Kruskal-Wallis test, $x^2 = 17.5$, df = 4,70, $P = 0.002$). Results from large insect transects revealed a different pattern across years of slightly increasing abundance with year, but sample sizes were too small for a quantitative comparison between years (Fig. 4-

6). Average temperature in May be related to these marked differences between years (plotted on Figure 4-6 for comparison).

Breeding scores of both species of birds seemed to peak later than insect abundance peaks in 2015, 2016 and 2017, but peaked earlier in 2013 and 2014 (Fig. 4-7A). However, in some years the peak energetic needs of birds seem to last for an extended period of time (2013 and 2017), allowing for potential synchrony in 2013, because the first peak of energetic demands of birds preceded the most likely insect peak. Synchrony was particularly improbable in 2016 and 2017, because insect peaks preceded breeding score peaks by a large margin, especially for WEWP in 2017 (Fig. 4-7A). Data from large insects transects also indicated that bird breeding scores may have occurred late in 2016, but seemed to be synchronous in 2015 and 2017 (for WEWP, but OSFL peak of breeding score was early relative to the insect peak in 2017, Fig. 4-7B).

It is important to note that estimated offsets were used only as an operational definition of offset, as I did not know if fitness was highest for pairs of birds that had an offset of 0. These offsets ranged from a maximum of 14 days (earlier than the insect peak) for both species in 2014, to -28 days in 2016 (same value for each species, Table 4-2). Offsets were essentially the same between species in most years, except in 2017, where it was -7 days for OSFL, but -28 days for WEWP (mean offsets were -6 for OSFL and -10.2 for WEWP). There was a second, smaller insect peak in 2017 (one early and one very late, Fig. 4-7A). When the second peak was used, the offset for OSFL changed from -7 to 55. The pattern of variation across years was similar using data from transects, although offsets were often of smaller magnitude. Synchrony was high in 2015 (values of 1 for both species) and in 2017 for WEWP (a value of 0 or “perfect” synchrony), but the peak of OSFL breeding was early in 2017 relative to the peak abundance of large insects counted on transects (21, Fig. 4-7B, Table 4-2). The breeding peak was much later than the peak of large insects in 2016 (-28 for both species), and insect counts were generally low across this entire season (Fig. 4-7B). Data from transects were too sparse for further quantitative analyses (such as a comparison across years), and it was difficult to discern an exact "peak" day, so results should be interpreted with caution.

The highest overdispersion value across for final GAMMs was 0.44 and was thus not considered a potential problem for models (Table 4-1). Results from GAMMs indicated that bird breeding scores generally increased and then stabilized as insect abundance increased, although uncertainty in model predictions increased as the insect abundance index increased (Fig. 4-8). The influence of insect biomass was significant on bird breeding score for OSFL (GAMM: $F = 9.39$, df = 9.39, $P = 0.006$), but temperature was not ($F = 1.38$, df = 2.40, $P = 0.23$). The parametric coefficients for the factor year were significant for 2014, 2016 and 2017 (overall $F = 40.2$, df = 4, $P < 0.001$). The smoothing function for insect biomass indicated a non-linear but generally increasing and then decreasing pattern across the dataset (Fig. 4-9). The final model had an adjusted r^2 value of 0.23.

The influence of insect biomass was significant on bird breeding score for WEWP ($F = 3.14$, df = 2.0, $P = 0.045$). The smoothing function for temperature was significant ($F = 17.9$, df = 1, $P < 0.001$). The parametric coefficient for the factor year approached significance (overall $F = 2.47$, df = 4, $P = 0.053$, and was significant for 2017, $P = 0.04$). The final model had an adjusted r^2 value of 0.22. The smoothing function for biomass indicated a non-linear but generally increasing and then decreasing pattern across the dataset (Fig. 4-9). The smoothing function for temperature showed an increase in values across the dataset (not shown).

Offset from insect peaks did not seem to have an influence on breeding success of individual pairs (clutch size that fledged). There was a significant effect of offset predicting breeding success for OSFL pairs (x^2 = 8.13, n = 45, P = 0.022, Fig. 4-10), but no influence for WEWP (x^2 = 2.78, n = 45, P = 0.095).

4.5 DISCUSSION

I investigated trophic interactions and potential asynchrony between breeding birds and their insect prey to explore the hypothesis that energetic needs of two bird species and nesting success is synchronized with abundance of insect prey. The overall pattern of insect abundance across years, and offsets from insect activity peaks, generally corresponded to the pattern of overall nesting success (Figs. 4-6 and 4-7 compared with Fig. 4-1). Years of higher insect abundance (from Malaise traps) and with positive offsets, such as 2013 and 2014, seemed to have higher nesting success (at least for first nesting attempts) than the years 2015 - 2017, although WEWP had relatively high nest success in 2016. A daily insect biomass index was significant in predicting bird breeding scores for OSFL and WEWP (although overall model fits were not high). The effect of year was also significant on bird breeding scores, especially for OSFL, probably because of large inter-annual fluctuations in insect abundance. Temperature influenced the bird breeding scores for WEWP but not OSFL, possibly because this species is closer to its northern edge of range in southern Yukon (see Chapter III for predicted distributions).

The overall year-to-year pattern of offsets matched that of breeding success and offsets (between timing of peak breeding events and insect abundance) predicted nesting success for individual pairs of OSFL (although not for WEWP). However, these data were limited by small sample sizes per year and year-to-year variation was large (see Fig. 4-1 as well as results of

GAMMS), and only included breeding attempts that occurred beyond egg-laying, because the peak of energetic demand could only be calculated for pairs that were beyond this stage. These data would therefore disproportionately include second-nesting attempts. The r^2 (adjusted) value for model fit was only 0.15 for OSFL and 0.05 for WEWP, suggesting that many other factors influenced breeding success, such as predation and individual quality of pairs.

It was difficult to estimate the dates of insect biomass peaks because of variation among days. It is possible that peaks occurred at other times and locations that were not detected by insect sampling, or showed no obvious peak. Insect peaks were variable in Finland because of geographic and inter-annual variability (Eeva et al. 2000). Birds are only able to predict insect abundance peaks very generally, because once breeding has begun, the rate of growth and development cannot be changed significantly, unlike insects that are predominately regulated by temperature, where rate of development can change, even within developmental stages (Eeva et al. 2000). Laying date of Tree Swallows in North America has advanced by about 9 days since the 1950s (Dunn and Winkler 1999), but insect activity peaks were not obviously timed with feeding of nestlings over a 24 year period (37 site-years, Dunn et al. 2011). Factors that influence earlier laying occur during laying, not during the nestling stages (Dunn et al. 2011). Insect activity did not show obvious peaks and, instead, showed a steady increase with date of season in most years (Dunn et al. 2011). Similar results were found for food availability to Black-throated Blue Warblers in New Hampshire; insect abundance (caterpillars and flying insects) showed no predictable seasonal peak over a 25-year period, probably because of the high diversity of insects found there (Lany et al. 2016). Also similar to my results, phenology (insect abundance peaks or leaf-out timing) did not influence annual reproductive success in Black-throated Blue Warblers (Lany et al. 2016). Nestling survival and mass were also not related to insect abundance in three species of swallows in New Brunswick (Imlay et al. 2017). Thus, insect activity on breeding territories of some birds in North America may be more protracted across the summer season, with less-pronounced or possibly less predictable peaks, compared to some of the broad-leaved forests of Europe. Onset of insect abundance in southern Yukon may occur earlier than previously, with no obvious sharp peak, because temperatures (mean monthly for May and June) have been increasing since about 1970 (see Appendix 3, Figure A3).

Declines in populations of both predators and prey, resulting from a multitude of factors (Warren et al. 2001, Maser and Schowalter 2013a, Bowler et al. 2018), make quantifying predator prey interactions challenging. Trends or causal links are almost impossible to determine when numbers of both cohorts, predator and prey, show evidence of decline, although specialized predators tied closely to prey have shown obvious responses to changes in populations of prey (Schmidt et al. 2012). It is possible that aerial insectivores in North America can switch prey in response to abundance changes (Eeva et al. 2000), and broad peaks of insect activity across the season here (almost 50 days of relatively high levels) suggest that birds can switch across types and sizes of prey (Lany et al. 2016), even after the largest abundance peak. Chimney Swift (*Chaetura pelagica*) switched from Coleoptera to other prey sources such as Hemiptera because of differential susceptibility to DDT poisoning of insect groups between 1944 and 1992 (Nocera et al. 2012), although population of swifts continue to decline rapidly (Nebel et al. 2010).

Adding to uncertainty is that insects in general are comparatively little-studied, in terms of identification of species, assessing impacts of climate change, and risk of extinction (Andrew et al. 2013). This is a surprising fact given that they are Earth’s most abundant taxonomic group, in diversity, abundance and biomass, and play crucial roles in all ecosystems, especially terrestrial ones, as well as providing a plethora of human ecosystem services (Maser and Schowalter 2013a).

The variable and possibly increasing offset between insect abundance and energetic demands of breeding birds across the years of the study may be resulting from climate change, although five years is a short time period to assess year-to-year patterns. In 2014, and to a lesser extent 2013, the peak of energetic demands of breeding birds occurred before the insect peak. In all other years, the energetic demands (bird breeding scores) peaked after insect peaks, by as much as 28 days in 2016. Longer term study is needed to examine consequences to fitness from these delays. Results differed between data from Malaise traps and data from transects, highlighting the need from more than one insect capture or counting technique. Data from transects were limited but revealed better synchrony with peak energetic demands than data from Malaise traps. Data from Malaise traps may overestimate potential asynchrony for species that feed on large active insects, such as dragonflies.

The influence of warming and potential asynchrony on demography or fitness is mixed among species. Spring warming influenced the productivity (number of offspring per adult bird) of boreal birds (20 species) positively in Finland, regardless of migratory strategy, but consistent changes in population size were not detected between 1987 and 2013 (Meller et al. 2018). In one boreal-breeding species of Finland, the Willow Tit (*Poecile montanus*), synchrony actually improved between caterpillar availability and feeding of young between 1996 and 2009 (Vatka et al. 2011), with a positive influence on breeding success (Vatka et al. 2014). In fact, synchrony exists (has been maintained) or has increased in three species in Finland, with associated improved quality and number of offspring (Vatka et al. 2014). Franks et al. (2018) found little evidence that greater asynchrony resulted in reduced productivity of twenty bird species in

Britain. More asynchronous species did show greater population declines, but productivity was only marginally reduced, and was not related to migratory strategy (Franks et al. 2018). For species breeding at high latitudes or elevations, warmer spring conditions can increase insect availability and reduce energy expenditure in early spring when weather can be inclement, as well as prolong the breeding season (Dunn 2004). A longer breeding season can be beneficial for species with multiple broods or high frequency of failed first nesting attempts (Lany et al. 2015, Dunn 2004, Dunn et al. 2011, Tomotani et al. 2018). However, there is an obvious limit to how early eggs can be laid in migratory species breeding in the temperate zone from lack of time and energetic reserves when females arrive, especially if arrival time does not advance. My results suggest that warmer spring temperatures coincided with lower insect abundance, earlier laying, but lower annual reproductive success. However, further study is needed to establish causal links.

Instead of adjustment, *plasticity* in response may be a more important determinant of fitness consequences of phenological change and potential asynchrony. Black-throated Blue Warblers showed greater annual reproductive success with plasticity in adjustments of breeding time. Seasonal peaks in food availability were not predictable and reproductive outcomes were more attributable to predation than to insect abundance peaks (Lany et al. 2016).

I found evidence of a high prevalence of failed first nests and relatively high success of second nesting attempts for OSFL, particularly in some years (e.g.: Mayfield estimates of 27.5% success for first nests and 66.0% for overall attempts in 2016). This pattern is similar to what Wright (1997) found in Alaska for OSFL (Mayfield estimates of first nests 26.6% and second nests 72.1%). Although the second nesting success estimate was based on only four nests by Wright (1997), the estimates I found were strikingly similar in some years. Mayfield estimates of nest success were highest in postfire habitat (62%) in central Oregon, compared to other forest categories (such as harvested forests with <20% retained trees, Altman and Sallabanks 2012). The Mayfield estimates of nest success I found vary widely across the years of study, with a marked decrease in success of first nesting attempts in 2016 and 2017 compared to 2014 and 2015, likely because of inter-annual differences in onset of incubation (possibly too early) and year-to-year variation in insect abundance. Insect abundance (using indices of abundance from Malaise traps) seemed to decrease with year. These results and the results of others (e.g. Wright 1997) underscore the importance of second nesting attempts for this species, at least in some years. Because these second nesting attempts occur later in the breeding season, asynchrony between insect abundance and energetic demands of breeding birds (or other community interactions) may be of even greater relevance; and offsets did influence nesting success in OSFL.

The nesting success for WEWP that I found (Mayfield estimate of 75.1%) is higher than what has been reported elsewhere (43% in New Mexico, Bemis and Rising 1999, 66% in Colorado, Chace et al. 1997. Although it varied from 45 – 73% depending on the year in Colorado (Ortega and Ortega 2016). I also found that nesting success varied greatly from year to year (65.3 – 84.2%), especially for first attempts (only 12% to 78%) and seemed to decline across the years 2015 - 2017. The statistical model with the most support of nesting success in WEWP was one that included the ratio of nest height to substrate height and year in Colorado (Ortega and Ortega 2016). Variation in nesting success from year to year could be from climate, insect availability, or changes in the predator community. In my study, insect biomass appeared lower in the years 2015 – 2017 than in 2013 and 2014. The largest offset between insect biomass peak and breeding score (reflecting energy demands of birds feeding young) was in 2016 (for both species). Thus, I would predict a lower nesting success for this year, which was the case for OSFL, whereas for WEWP the lowest nesting success was for first attempts in 2017. Nesting success is undoubtedly influenced by many factors not considered in this analysis, such as changes in the predator community (Husek et al. 2012), in addition to individual male quality or territory quality. Predators may find it easier to detect breeding birds early in the season, and breeding may be timed for to allow for a second clutch if the first one is predated. Canada Jay are present allofeeding young (as groups of adults) until early June (Strickland and Ouellet 2018), making spring a particularly risky time for exposure to potential nest predators.

The incubation stage of WEWP found here (14.4 days) was very similar to that found by Bemis and Rising (1999, 14.8 days) and by Ortega and Ortega (2016, 14.7 days), however, because I did not check nests every day, these measures of incubation duration should be interpreted with caution. Nests of WEWP in other locations were also placed in poplar or aspen (*Populus* spp.) in British Columbia or other deciduous trees, although in New Mexico piñon pine represented 100% of nest sites (Bemis and Rising 1999) and in Colorado most were in ponderosa pine (*Pinus spp.*) (Chace et al. 1997).

The sizes of OSFL territories (11.4 ha) were smaller here than what has been reported elsewhere (18.4 ha, range 10.5 – 26.4 in Alaska), and territory size was negatively influenced by elevation. Higher elevation territories were smaller, possibly corresponding to higher insect abundance or greater insect diversity at mid-high elevations. Territory size found here in WEWP (0.85 ha) was smaller than what was reported in a willow-scrub floodplain of Colorado, 1.7 ha (Eckhardt 1979), but larger than those reported in a ponderosa pine forest in Arizona (0.22 - 0.35 ha) (Szaro and Balda 1979, Bemis and Rising 1999). Variation in territory size could be attributable to density of trees used for foraging (more open habitat may have fewer appropriate foraging trees) as well as insect abundance.

Abundance of insects varied greatly between years, although this was a short time series of study to examine a long term trend. Variation between years may represent variability of specific local weather patterns and impacts of climate change. Temperature means are increasing with year locally (see Appendix 3, Figure A3). Insect declines reported elsewhere may be attributed to anthropogenic land use factors, such as agriculture intensification, that are of potentially less relevance for this study area. In Germany, a 27-year study of flying insects captured about < 1 m from the ground in protected nature areas (63 sites) revealed a dramatic overall decline of 76%, and even a higher decline of 82% in midsummer (Hallmann et al. 2017). The authors attributed these wide-spread and alarming declines to agricultural intensification (changes to pesticide use, year round tillage and use of fertilizers) more so than climate change or land use change (Hallmann et al. 2017). Anthropogenic land use has put many North American insect populations at risk, often from pesticide application and loss of refuges in riparian habitat (Maser and Schowalter 2013a), causes highly relevant in central and southern Canada.

Arrival dates of males onto territories (the first date that males were defending territories by singing) did not change across years for either species. However, mean start of incubation changed across years for both species, becoming progressively earlier. There may be fitness consequences for a shortened time interval between arrival and breeding, such as impacts on sexual selection (females may not have time or opportunity to choose mates, see Tomotani et al. 2018) and females may not have time to improve body condition prior to egg-laying. Also, too early breeding events could coincide with inclement spring weather events that have disastrous consequences on survival (Brown and Brown 2000). It is interesting to note that in this study, one year with some of the lowest nesting success (2017), especially for first attempts, coincided with the year that incubation was initiated earliest for both species. Failures were not likely because of inclement weather events (it was warm that spring with minimal rain or wind) but were more likely from body condition or predator phenology, although these factors were not examined directly. In addition, there are likely limitations to phenological advance and reproductive investment itself imposed from conditions in non-breeding areas. The period of 2014 – 2016 was associated with one of the strongest ENSO events on record, with very dry conditions reported in northern South America in winter of 2015 (Marengo et al. 2018), possibly impacting body condition of migrants for the breeding season of 2016 and even 2017. ENSO indices correlate with fitness of birds, however direction of correlation depends on overwintering locations. Higher, and thus wetter, ENSO years correlated with higher reproductive success in several species overwintering in the Caribbean (Sillett et al. 2000), parts of Mexico and southern USA, whereas high ENSO levels are correlated with drier conditions in Central and South America, lowering reproductive success (Nott et al. 2002, Mazerolle et al. 2005).

Long-distance migrants may not adjust schedules of migration to the same degree as those with other migratory strategies (e.g. Butler 2003), but some species are breeding earlier while others are not (Torti and Dunn 2005). Earlier breeding has been reported in Mexican Jays (Brown et al. 1999), Tree Swallows (Dunn et al. 2011), and Black-throated Blue Warblers (Lany et al. 2016), but adjustment is species and even population specific (Dunn 2004, Torti and Dunn 2005), and not necessarily similar across phenological events (e.g., moult may change timing more rapidly than migration; (Tomotani et al. 2018). Tomotani et al. (2018) also found that arrival dates and start of breeding changed in disparate ways in the Pied Flycatcher in Europe over a time period of 55 years: arrival did not change but start of breeding became progressively earlier. Fitness consequences in clutch size or adult survival for earlier initiation of incubation were not detected, except that earlier breeding birds recruited more young, possibly because it allowed more time for development of fledglings (Tomotani et al. 2018). However, the interval between arrival and breeding can only get so short. Montane breeding species may benefit from climate change up to a limit, with increasing spring temperatures and earlier peaks of insects, provided they have the plasticity to respond (Saracco et al. 2019). Very high elevation species are subject to the harsh limitation of having nowhere of higher elevation to track temperature change (Sekercioglu et al. 2008), although precipitation changes could cause some limited down-slope elevation shifts (Tingley et al. 2012). OSFL territories here were documented as high as 1156 m asl, which was at tree line.

Results from feeding observations suggest that a wide variety of insects are used to feed young. Although larger insect sizes and possibly Odonata are preferred by OSFL, there were multiple species of Odonata available in the area during the breeding season. Breeding birds may be able to utilize a wide variety of prey to feed young in northern boreal regions where insect diversity and abundance are often high. In addition, insects in a boreal-forested region in Russia adjusted phenology by responding to similar cues (e.g. short term temperature change) and to a comparable degree to some groups of birds (medium-distance migrants), suggesting that phenological asynchrony could be smaller than previously thought for some regions and pairs of taxonomic groups (Ovaskainen et al. 2013).

Although offset from insect peaks predicted nesting success in one species (OSFL), model fit was not high. Nesting outcomes may be dependent on other factors not quantified or included in models directly, such as predator abundance, diversity and phenology (Husek et al.

2012), and quality and age of individual birds (Imlay et al. 2017), which could be related to conditions on non-breeding areas and direct impacts of severe weather associated with cycles of ENSO, more than offset from insect abundance peaks or an index of daily insect abundance. A simpler and more revealing dataset may be annual (or monthly) mean insect abundance and nesting success measured over a long time series. In addition, nest failures, mostly attributed to predation, and re-nesting attempts, were extremely common in both species, especially in some years. The ability to "re-nest" may provide flexibility to adjust to changing spring conditions (Drever et al. 2012). The only measure of individual fitness used here was nesting success (clutch size) and a next step would include recruits, female survival or other longer-term assessment of success, as well as an individual measure of plasticity (or ability to respond; Lany et al. 2015), as an alternative predictor to offset or timing *per se*.

My results suggest that insect abundance is related to population-wide breeding events and energetic demands, and that potential asynchrony may be increasing with year, although a longer time series is needed. However, asynchrony may only explain a relatively small portion of the variation in individual breeding success. Many of the published studies on asynchrony between pairs of species in bird communities, or offsets, have used data on European species (Visser et al. 1998, Visser and Both 2005, Vatka et al. 2011, Franks et al. 2018), and many of these rely strictly on caterpillars of a limited number of species of Lepidoptera to feed young, although there are notable exceptions of similar studies conducted in North America (Dunn et al. 2011, Lany et al. 2016). European breeding members of Paridae, such as the Great Tit, feed relatively large clutches (Gosler and Clement 2007), possibly making timing with food abundance more germane to differential reproductive success between individual pairs. My results suggest that in two populations of flycatchers insect abundance was related to general timing and magnitude of breeding and asynchrony between insect activity peaks, although difficult to measure, was related to individual nesting success in OSFL (but not WEWP). However, many other factors probably influenced nesting timing, such as weather events (e.g. spring storms), or other constraints on breeding times from individual differences in body condition or territory (for example, from non-breeding conditions), and relatedly, the ability of individual birds to adjust timing, as well as the timing of predation on birds (Husek et al. 2012). In addition, feeding young a general diet of several insect types during nestling stages has the potential to buffer birds from some impacts of potential asynchrony (Lany et al. 2016). More study is needed to determine if findings surrounding phenology and climate change can be generalized to other North American birds breeding in the temperate zone.

My results for OSFL and WEWP in the southern YT are concerning for several reasons. Insect prey abundance may be declining for these two obligate aerial insectivores, and offsets between insect abundance and peak breeding demands may also be increasing with year, despite laying occurring earlier via a shortening of the gap between arrival and laying. Breeding success also varied greatly with year, with the two most recent years of the study having the lowest nesting successes, possibly because earlier laying exposed birds to novel predator and climate regimes. General body condition may also have been influenced by conditions in non-breeding areas.

Range-wide populations of many birds are declining, as are populations of some insects, due to a multitude of factors. Community dynamics are a little understood piece of this picture. Birds breeding in northern Canada are and will continue to be subject to a rapidly changing climate. Of particular concern is the average mean rate of temperature change, of three times the global mean average from 1948 to 2016 (2.3 ºC, likely range 1.7 ºC–3.0ºC), although more warming occurred in winter months than in summer (Zhang et al. 2019). My results suggest that this rapidly changing climate has the potential to impact phenology, food availability, and breeding success with significant implications for populations of these two species.

4.6 Tables

Table 4-1. Candidate generalized additive mixed models and diagnostics for bird breeding scores (sequential score with breeding stage) for Olive-sided Flycatcher (OSFL) and Western Wood-Pewee (WEWP).

Rank	Model	r^2	REML[1]	Overdispersion
1 OSFL	s(Insect Biomass) + s(Temp) + Year + random(JDate)	0.27	3.6	0.15
1 WEWP	s(Insect Biomass) + s(Temp) + Year + random(JDate)	0.20	4.8	0.14
2 OSFL	s(Insect Biomass) + s(Temp) + Year + s(Insect Diversity) + random(Jdate)	0.27	4.5	0.44
2 WEWP	s(Insect Biomass) + s(Temp) + Year + s(Insect Diversity) + random(Jdate)	0.19	53	0.15
3 OSFL	s(Insect Biomass)	0.09	23	0.14
3 WEWP	s(Insect Biomass)	0.04	55	0.20

[1] Restricted Maximum Likelihood estimator

Table 4-2. Julian dates and offsets between peak insect abundance and peak energetic demands of breeding Olive-sided Flycatcher (OSFL) and Western Wood-Pewee (WEWP) in southern Yukon.

Year	Insect peak (Malaise traps)	Large insect peak (transects)	OSFL peak	WEWP peak	Offset OSFL (Malaise, transect)	Offset WEWP (Malaise, transect)
2013	185		182	182	3	3
2014	204		190	190	14	14
2015	174	188	187	187	-13, 1	-13, 1
2016	154	153	181	181	-27, -28	-27, -28
2017	150	178	157	178	-7, 21	-28, 0

4.7 Figures

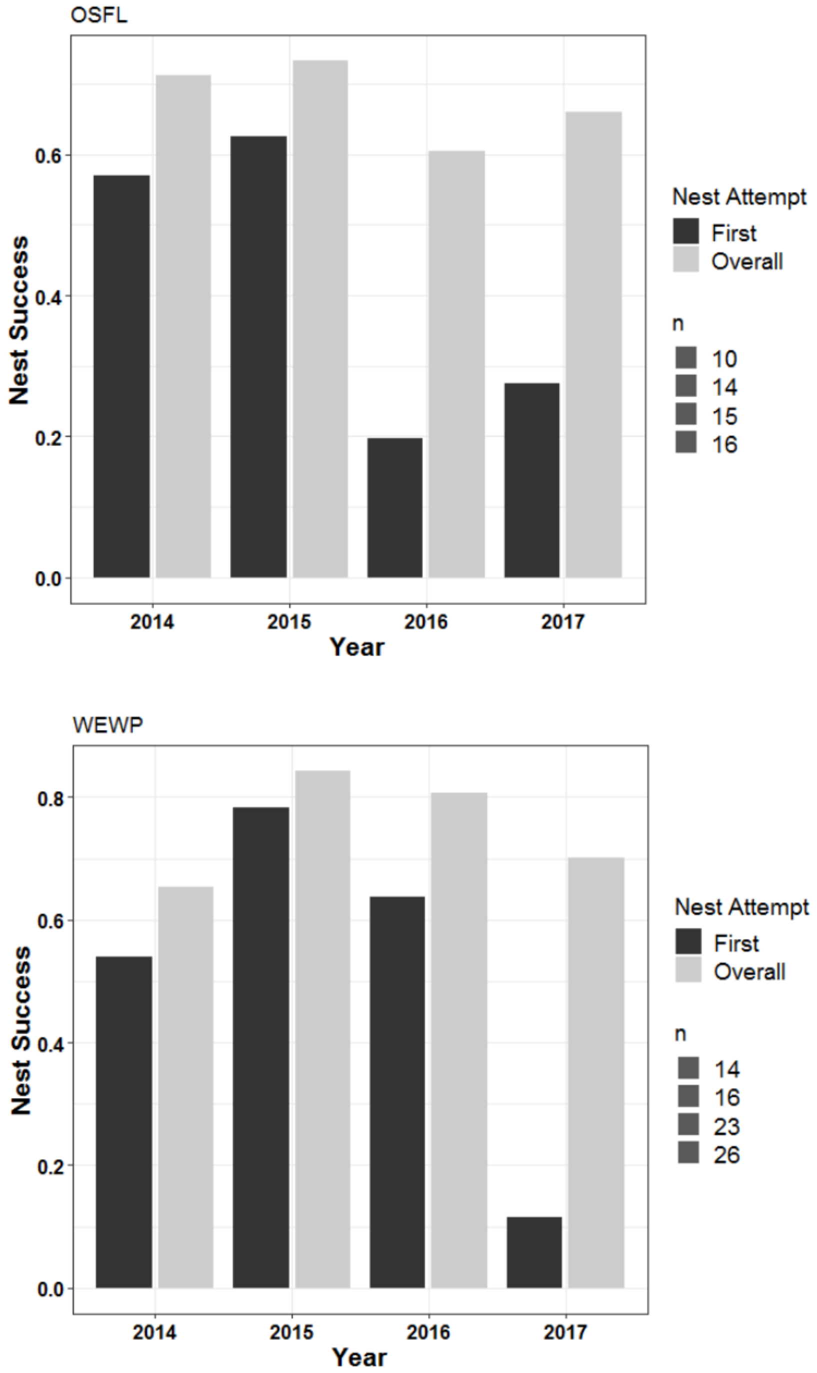


Figure 4-1. Mayfield nest success (overall nest survival probability) for Olive-sided Flycatcher (OSFL, top panel) and Western Wood-Pewee (WEWP, lower panel). Overall nesting success from all nesting attempts are shown in gray, nesting success from first nesting attempts only are shown in black.

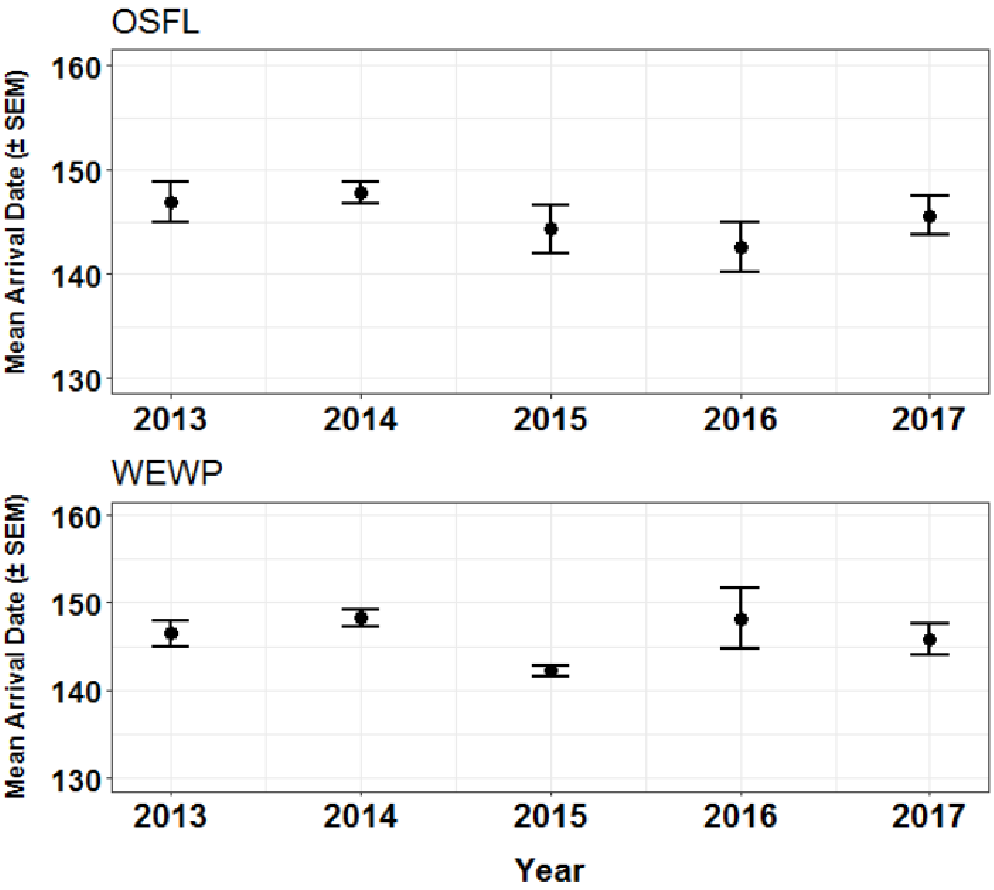


Figure 4-2. First date that males were actively singing on territories in southern Yukon for 24 Olive-sided Flycatchers (OSFL) and 30 Western Wood-Pewees (WEWP) between 2013 and 2017. Julian Date 140 = May 20 (May 19 in 2016). Mean date ± SEM are plotted.

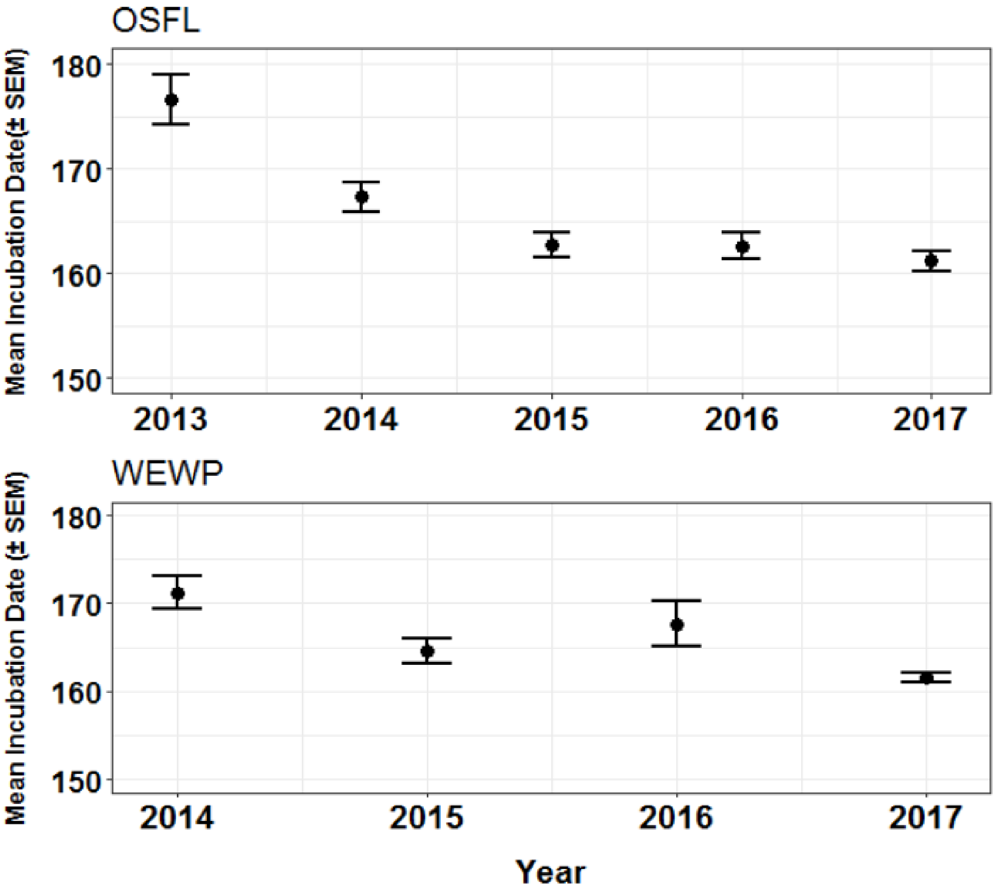


Figure 4-3. Mean start date (± SEM) of incubation in Olive-sided Flycatcher (OSFL) and Western Wood-Pewee (WEWP) between 2013 and 2017. Julian Date 170 = June 19 (June 18 in 2016).

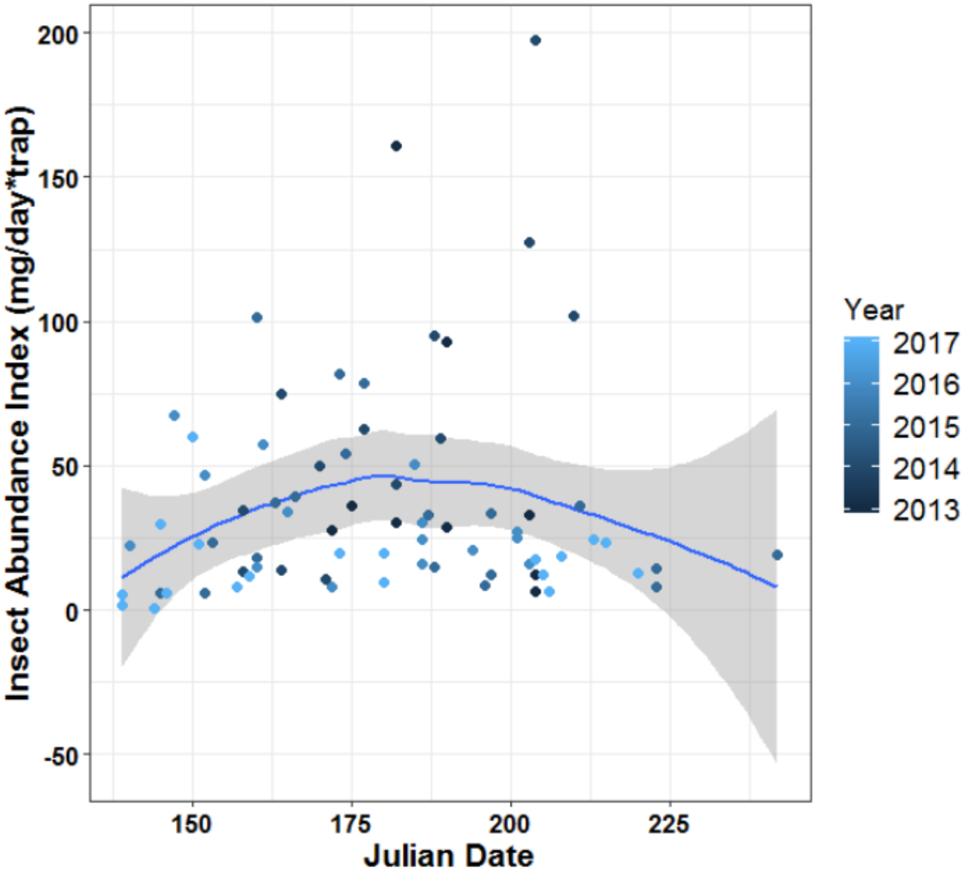


Figure 4-4. Insect abundance index (mg/day*trap) calculated from insects captured in Malaise traps across the breeding season (data combined for 2013 – 2017, Julian Date 150 = May 30). Non-linear relationship is a non-parametric locally weighted least squares regression line (Loess and 95% confidence interval lines) shown for illustrative purposes only.

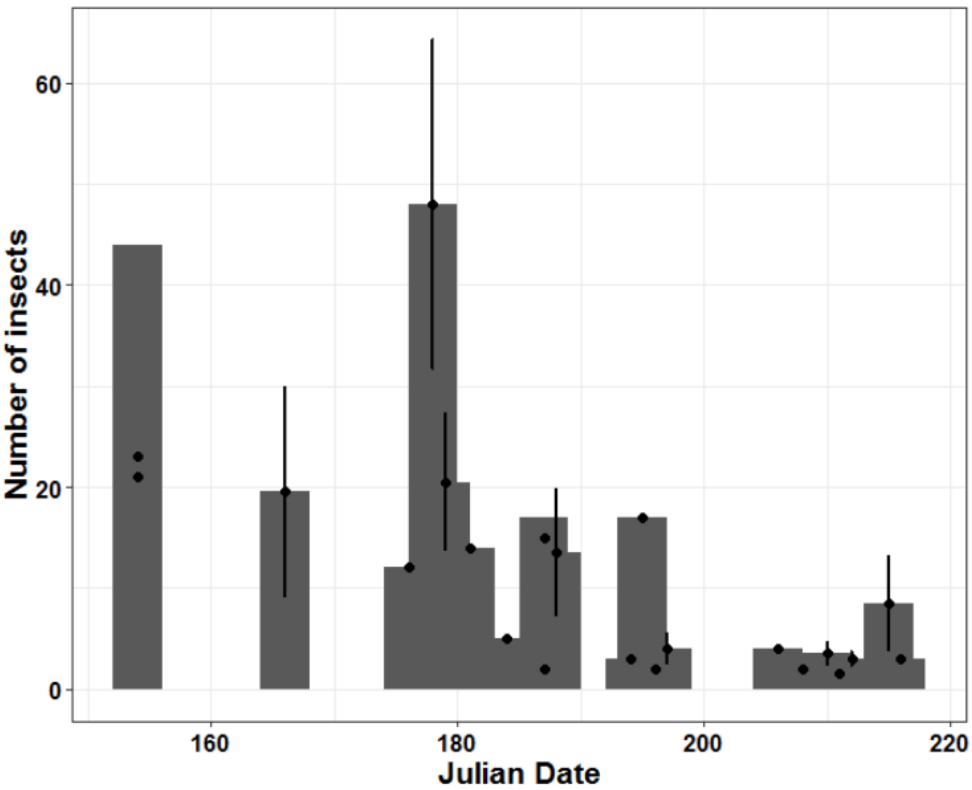


Figure 4-5. Large insects counted on transects. Multiple transects conducted on the same day and same year were averaged with standard error shown with vertical bars (n = 32, Julian date 154 = June 3).

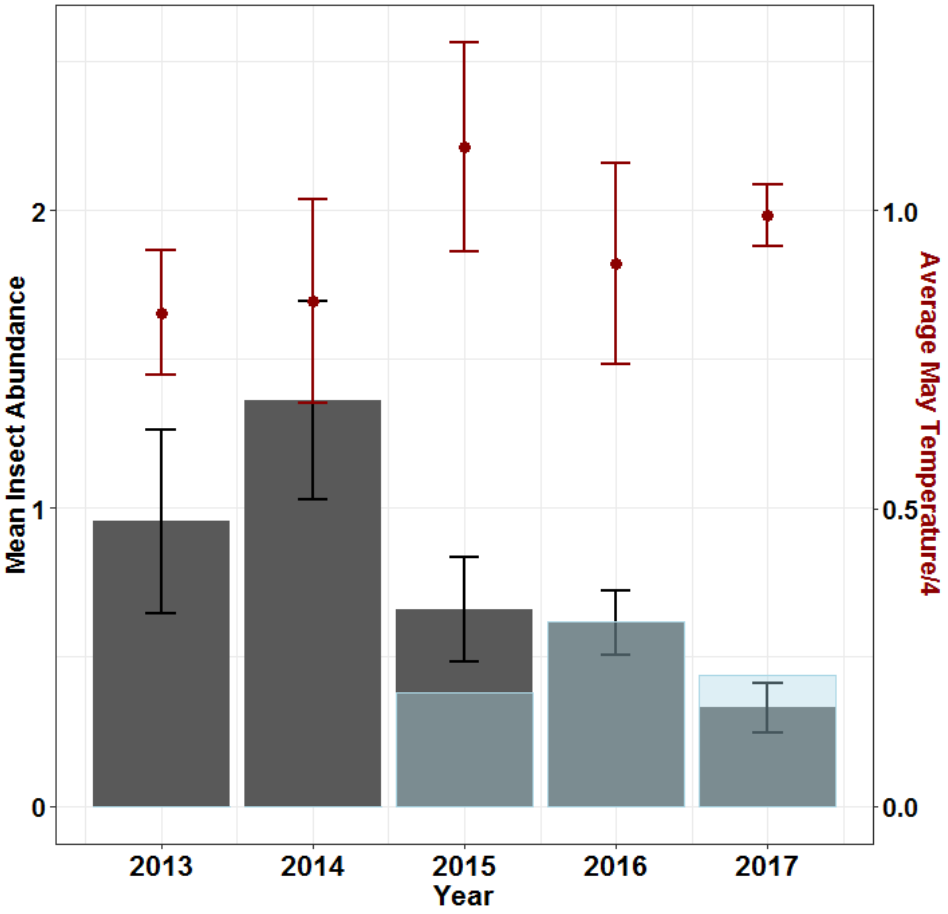


Figure 4-6. Average insect abundance index (mg/day*trap) across years with 95% confidence intervals show with vertical bars. Data from Malaise traps are shown in grey bars and scaled count data from transects are shown in light blue bars. Average May temperature (/4) data are shown in red on right axis with 95% confidence intervals.

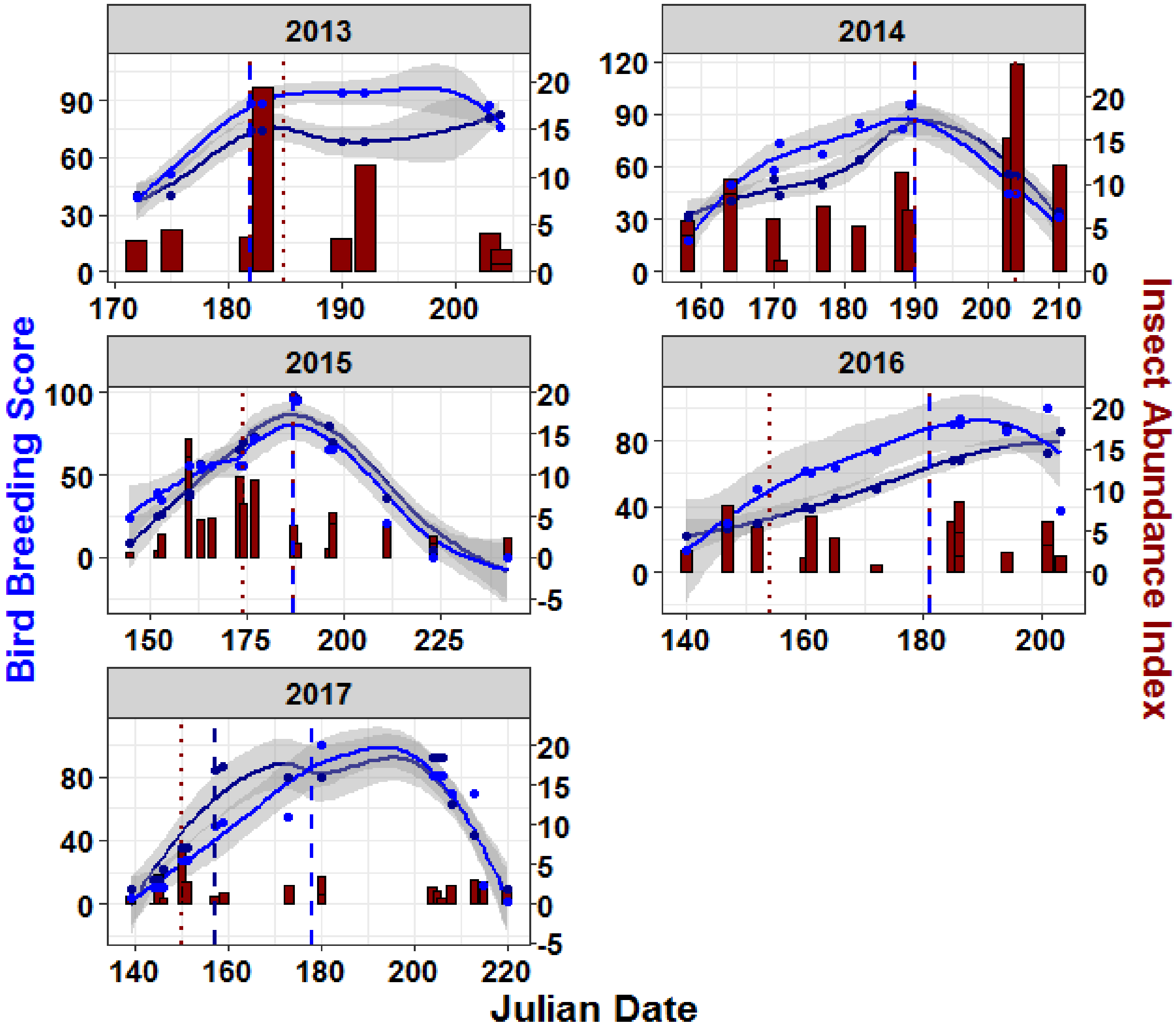


Figure 4-7A. Breeding scores (relative proportion of birds in each breeding stage, where each breeding stage receives a progressively higher score and parents feeding young on day 5 - fledging is the maximum score) for each species (OSFL: dark blue lines, WEWP: blue lines) and an index of daily insect biomass (grey bars). Space between vertical lines indicates approximate "offset" between peak insect abundance (red dotted) and first peak of bird breeding scores (dark blue dashed lines for OSFL, blue dashed lines for WEWP, Julian Date 140 = May 20 in all years except 2016, Julian Date 140 = May 19 in 2016).

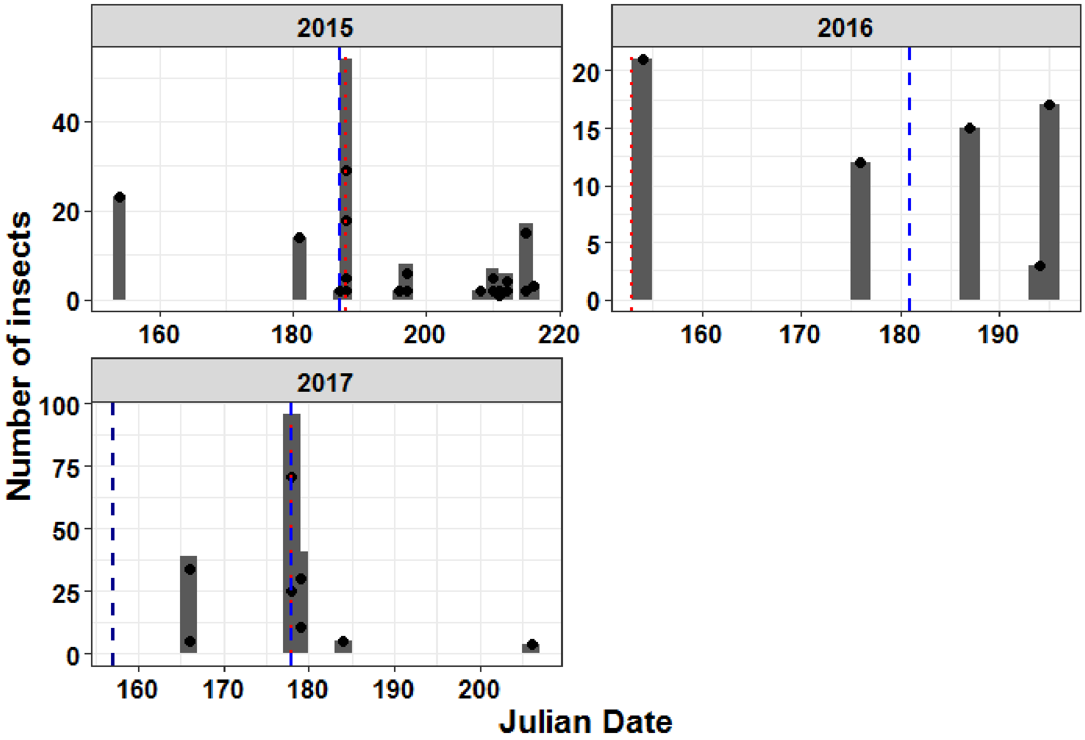


Figure 4-7B. Abundance of large insects counted on transects (mean counts) with approximate "offset" indicated by the space between vertical lines. Peak insect abundance is indicated by red dotted vertical line and first peak of bird breeding scores is indicated by dark blue dashed lines for OSFL and blue dashed lines for WEWP (Julian Date 140 = May 20 in all years except 2016, Julian Date 140 = May 19 in 2016).

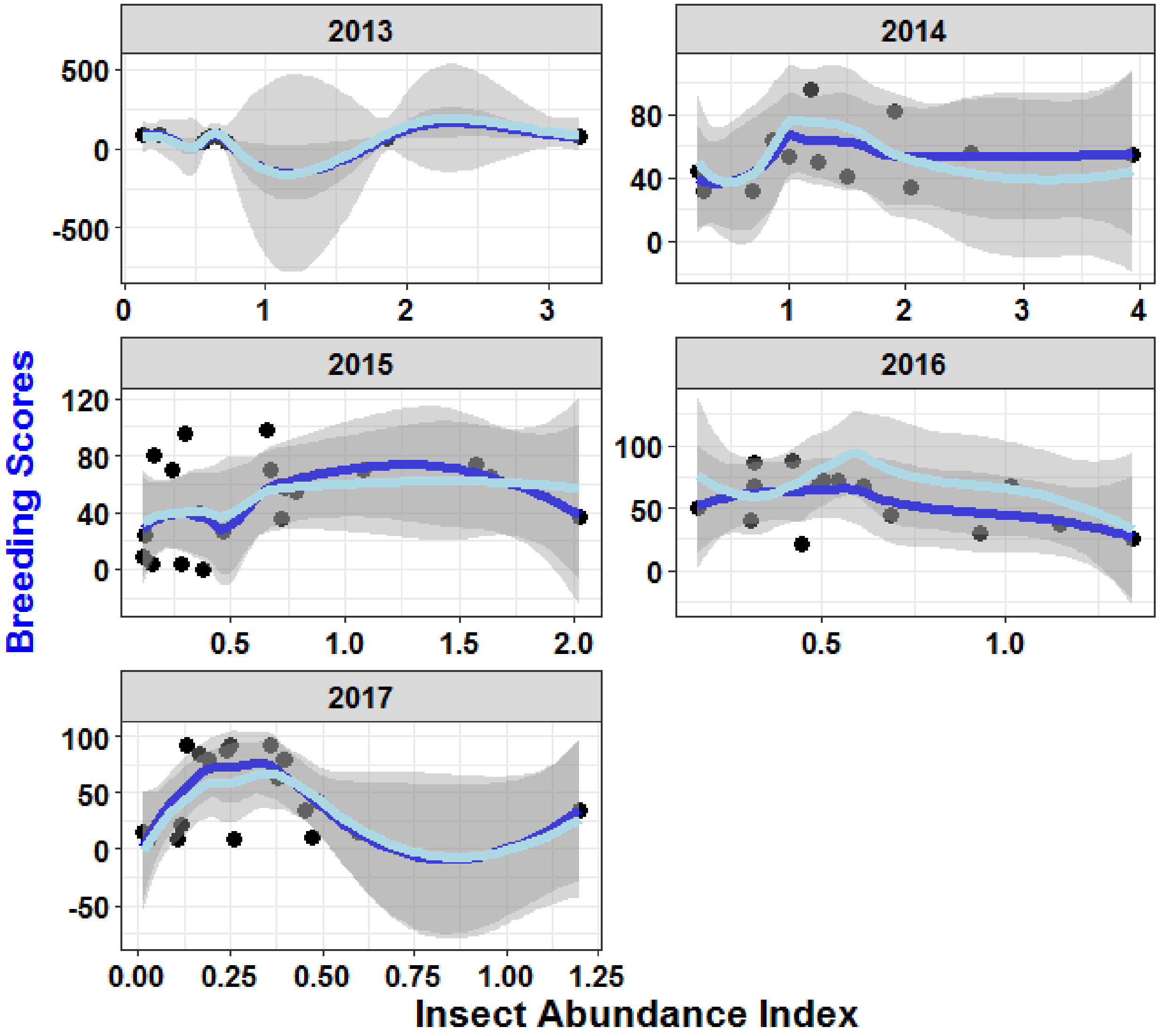


Figure 4-8. Breeding scores (relative proportion of birds in each breeding stage, where each breeding stage receives a progressively higher score and parents feeding young on day 5 - fledging is the maximum score) for OSFL (dark blue) WEWP (light blue) and an index of daily insect biomass (g/day*trap) shown with dots. Shaded areas are 95% confidence intervals.

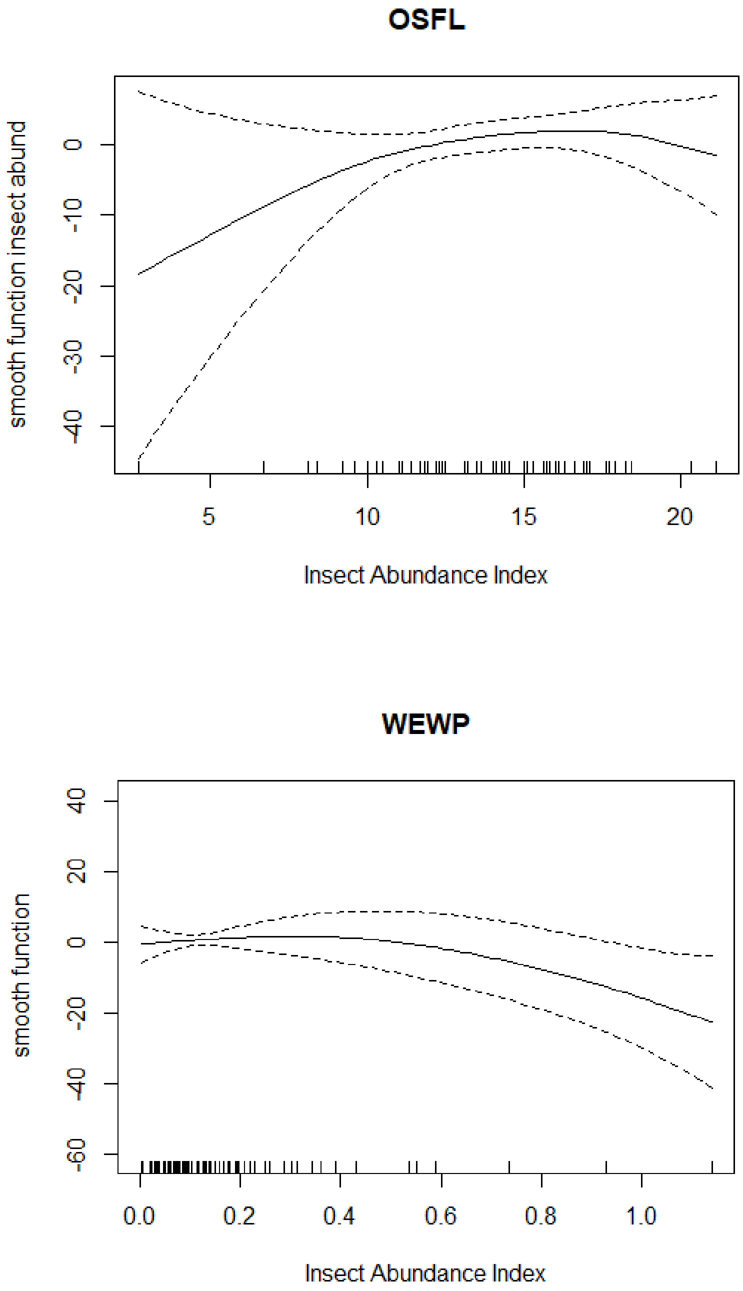


Figure 4-9. Smoothing functions for GAMMs describing bird breeding scores and an index of insect abundance for Olive-sided Flycatcher (OSFL) and Western Wood-Pewee (WEWP).

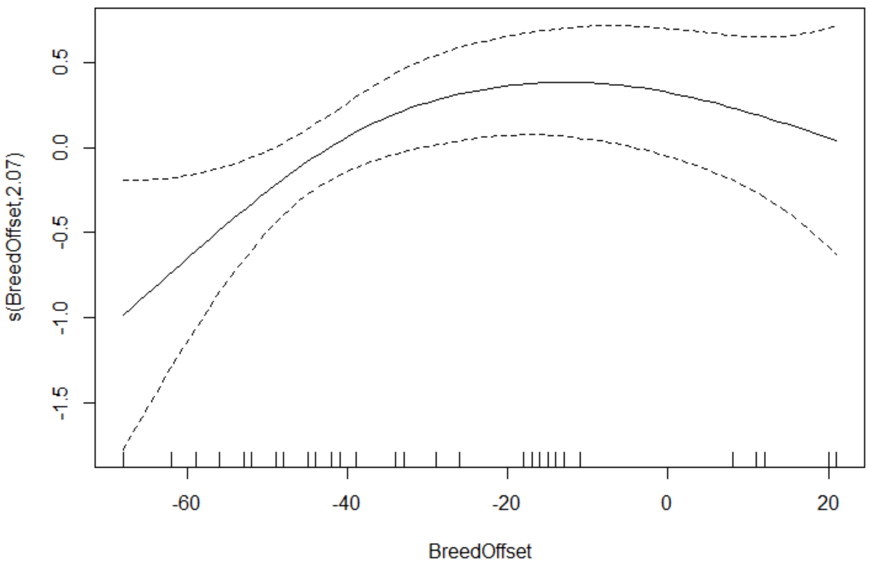


Figure 4-10. Smoothing functions for GAMMs describing breeding success of OSFL using breeding offset from insect "peaks" (year was a factor and individual territories was a random factor).

CHAPTER V: SYNTHESIS AND FUTURE DIRECTIONS

Many migratory landbirds are declining, reflecting action of a multitude of factors operating at many points in their life cycles. Such factors include loss or alteration of habitat resulting from intensification of human land uses such as agriculture, forestry, and urbanization, as well as impacts from climate change. These changes alter disturbance and hydrological regimes and give rise to concomitant changes to species range, distribution, and community interactions. Aerial insectivores in North America are suffering particularly steep declines (Spiller and Dettmers 2019), as are long distance migrants (Böhning-Gaese et al. 1993, Askins 1995, Nebel et al. 2010). OSFL and WEWP exemplify both of these risk factors, overwintering in northern and western South America, with relatively unknown migratory schedules and patterns. Despite the likely population impacts in non-breeding areas by habitat change, impacts on breeding grounds, such as climate change, should not be ignored. Some regions in northwestern North America, with relatively intact vegetation and space for range advancement further north, have potential to provide such macrorefugia from climate change, providing that community dynamics are appropriate to support these species, and that dispersal is not impeded. However, climate is changing rapidly in the region, limiting the potential for macrorefugia provision. Also of concern is the relatively low percentage of area that is protected within the region - only ~8% within Canada (Andrew et al. 2014).

My results from SDMs (using BRTs) indicated that parts of the northwestern region of North America potentially support relatively high densities during the breeding season. This highlights the importance of examination of drivers to distribution and abundance, at more than one scale, to ultimately inform conservation and management planning in the region. Relatively simple vegetation categories were particularly powerful in describing relative abundances and distribution of both species at this regional, but still expansive scale, despite the importance of climate variables describing distributions at broad scales (Cumming et al. 2014, Haché et al. 2014, Stralberg et al. 2015,a,b). OSFL was predicted to be disproportionately associated with open coniferous forest and tundra, wetlands, lichen-spruce bogs and old burns (greater than 10 years old). Medium density evergreen and mixed open forests had high predicted abundances, but not relative to availability of that type of habitat. Haché et al. (2014) also predicted a high density of OSFL in western Canada (with a strong East-West divide), with 45% of the Canadian population of this species predicted to be found in only two political regions: Quebec and British Columbia. From this national modeling exercise, predicted density was highest in conifer stands with taller trees, recent burns, shrubby areas and small water bodies, tempered by a negative roadside bias (Haché et al. 2014). Similar to my results, slope and wetness were ranked highly as predictors of abundance (Haché et al. 2014). BAM (2019) also found that WEWP had high habitat suitability in central BC and AB, in a very similar pattern to what I found. Distribution and abundance patterns in BC were similar to those found by Weber et al. (2015b) for this species, with high predicted abundances in the Central Interior, Sub-Boreal Pine-Spruce and Ponderosa Pine biogeoclimatic zones.

WEWP was associated with a wide variety of habitat types, such as cropland, mixed closed forest and evergreen forest of medium density, and open deciduous forest, but when habitat availability was taken into account, riparian habitat, mixed open forests, tundra, wetlands and burns (both old and new) were predicted to have the highest densities of this species. Not all of these results were expected; mature deciduous forest has been cited as a common habitat association of WEWP in BC and Alberta (Bemis and Rising 1999, Stehelin et al. 2020) but this could be related to the wide availability of this habitat type, not necessarily reflecting a positive association (Sólymos et al. 2014). Godfrey (1986) described WEWP habitat succinctly as “open woodland”. The potential impact of loss of riparian habitat on this species has been noted for some time (Bemis and Rising 1999, The Federation of Alberta Naturalists 2007). Results of national modelling of habitat association were not available for comparison, but within Alberta, high predicted abundances of this species were found within the youngest seral stages of mixedwood, pine and white spruce forests, and young and old deciduous forest (ABMI and BAM 2019). Over 45% of WEWP population in Alberta has been lost since about 1970, with a projected 30% further loss over the next 10 years, much of this attributable to land use change from agriculture and urbanization (Stehelin et al. 2020), and oil and gas sector activities in parts of the province (Sólymos et al. 2014). Impacts of agriculture particularly relevant to this species involve loss of riparian habitat and changes to vegetation, such as losses to diversity from monocultures and the reduced use of hedgerows.

Despite predicted declines in overall abundance for one species (OSFL), marked changes in predicted distribution, and decreases in area considered to be ideal habitat between the baseline and two future time periods, my results indicated that the northwest has the potential to provide some areas of macrorefugia from climate change for these two species, and likely for other aerial insectivores. It is concerning that areas of potentially gained habitat were in scattered and isolated locations, and that one large, mostly contiguous area considered “lost” in future scenarios because of rapid predicted climate change, was in central Alaska and central-northern Yukon; an area of high predicted abundance for OSFL under the baseline scenario. The area considered ideal habitat increased between a baseline time period and future time periods under a high emission scenario for WEWP. However, many areas of potential gain in habitat, and probably the largest contiguous areas, were in the far reaches of the study area, such as northwestern and northeastern edges (in coastal Alaska and northcentral NWT), calling into question whether this more southern-distributed species can disperse successfully into these areas. Also concerning is an area with a high level of negative bioclimatic velocity was found in a central interior region of BC including the Sub-Boreal Pine-Spruce Biogeoclimatic zone; an area overlapping with a high predicted abundances of both species in all scenarios.

I found that bioclimatic velocity was unexpectedly high (and negative) in western, mid-elevation, montane regions (such as central interior BC) in general, highlighting the importance of further study to better inform conservation and management of areas with mid-high elevation and complex topography. In contrast, results of both forward and backward climate velocity analog analyses (although at a much larger scale of the western hemisphere) revealed relatively low overall climate velocities in western North America (Carroll et al. 2015), an unexpected result considering the rapid pace of climate change in the region. Equatorial zones (including most of Central America and north-central South America) revealed high velocities of all types measured, with high potential threats to associated species and local populations (Carroll et al. 2015); areas that overlap with non-breeding areas for both of these species. Despite this, connectivity between current and future climate analogs was found to have high potential for short distance travel in north-south tracts across northwestern North America (Carroll et al. 2018), facilitated in part by north-south valleys or mountain passes. Carroll et al. (2018) found that areas of high climate connectivity did not necessarily overlap with areas of potential refugia, and a key, very large area of high vulnerability from lack of protected land, and high potential for connectivity between current and future climates, made up the majority of Yukon. I also found that some projected gains to range (akin to refugia) opposed areas of high climate velocity, suggesting that more than one method of examining SDM results may be essential in conservation applications. Negative bioclimatic velocity overlapped with areas predicted to be lost from range in some areas (e.g. Alaska), but not in others (e.g. central BC). Velocity analyses stand out in ranking areas of potential refugia, based on connectivity (access), impediments to dispersal, and species diversity (Stralberg et al. 2018b).

Lack of overlap between current protected areas and predicted areas of climate refugia for these species (Fig. 5-1A) is problematic. A more species- and physically-diverse dataset is needed to prioritize areas of conservation to maximize refugia under future climates (Carroll et al. 2017), but based on my results, it appears that current protected areas are not generally congruent with areas of refugia for OSFL and WEWP. There are a few possible exceptions: the Kenai Peninsula, the Alaskan Peninsula/Bristol Bay lowlands in Alaska, and Wood Buffalo National Park in northern AB and NWT, the largest national park in Canada (Fig. 5-1B). Thus, results of my study and others suggest that increasing the area of land that is protected should be among of the highest priorities for conservation in the face of climate change. Such areas would be particularly valuable in YT, central NWT and in northern and central BC, especially in topographically diverse regions (Carroll et al. 2017). In the USA, protecting areas of coastal Alaska that include more of the Seward and Alaska Peninsulas would allow dispersal and continued occupation of climatically suitable habitat within potentially reduced areas of occupation overall.

Despite wide inter-annual variation in abundance and use of a relatively short time series, I found some evidence of declines for both species. Population declines decrease the likelihood of colonization of new areas, especially those at great distances. Available data suggest that declines were most evident in western regions (BCRs 4 and 10) and in Alberta (BCR 6 in part), although other studies revealed declines of OSFL in eastern North America (e.g. New

Brunswick) (COSEWIC 2018, Stehelin et al. 2020). In northwestern North America, mountainous areas have been identified as having high potential for refugia (Carroll et al. 2017, Stralberg et al. 2018b) and high connectivity among areas of climate refugia, although low proportions of the area are protected (Carroll et al. 2018). Accordingly, these areas are ranked highly in conservation prioritization for songbirds (Stralberg et al. 2018a).

My results confirmed the expected importance of riparian and other wet habitats to support high abundances of these species. However, environmental heterogeneity, promoted by complex topography also emerged as important in supporting high abundances of these species, which was somewhat unexpected. Complex topography probably contributes to moisture pooling, and thus also supports microhabitats with relatively high insect abundances. Moisture pooling could also dampen impacts of temperature extremes, given the high specific heat of water. Topography (elevation in particular) is also of importance in exercises identifying areas of refugia and connectivity between areas of potential refugia from climate change (Dobrowski and Parks 2016, Carroll et al. 2018, Stralberg et al. 2018b).

Management recommendations for areas of low climate stability, but with relatively high vegetation intactness, such as northern North America, include maintaining vegetation intactness (including dispersal pathways), identifying areas of potential climate refugia, and monitoring of species that may be particularly vulnerable to climate change (Watson et al. 2013). This thesis provides data relevant to the latter two recommendations for flycatcher species that appear to be sensitive to impacts of climate change. In a weighting exercise to prioritize areas for conservation of songbird diversity and abundance across the Canadian boreal region, climate change was one of the biggest influencers, and some of the highest ranking areas for conservation were northwestern mountainous regions (BC and Yukon in particular) (Stralberg et al. 2018a). Future work should investigate dispersal pathways and connectivity among areas of refugia in relation to future climate change as well as among areas that overlap with existing protected areas (Graham et al. 2019).

Predictions of future distribution and abundance were likely rendered more conservative by including only current landcover layers in my analyses. Including potential vegetation layers (e.g. Rehfeldt et al. 2012) made predictions of distribution and abundance less conservative, or more favorable, in future scenarios (T. E. Stehelin, *unpublished data*). Use of predicted vegetation layers, and potential time lags from vegetation change, will be required to accurately address this significant concern. Also of concern is the omission of future land use information, which was not available at the time of analyses. Relevant predictive models of land use change are currently being developed for other parts of Canada (BAM and ABMI, *unpublished data*) and when available, will contribute significant to the depth of this analysis.

Results from an intensive behavioral investigation into phenology of birds and insect prey in southern Yukon suggest that laying date (onset of incubation) advanced with year for both species, but arrival date (day of first territorial defense) did not. Thus, despite their long-distance migratory strategy, phenological adjustments to increasingly warm spring temperature seem to be occurring in these populations. However, this behavioral adjustment to warmer spring conditions can have fitness consequences and has an obvious limitation over the long term because arrival dates did not change. In addition, the years of lowest reproductive success coincided with the years of earliest laying and the greatest asynchrony with insect abundance, suggesting that earlier laying impacted reproductive success negatively not positively, as one might expect. In a review of British birds, migratory distance did not influence asynchrony with spring phenology, and asynchrony only reduced productivity marginally (Franks et al. 2018).

However, warmer springs were associated with greater asynchrony (Franks et al. 2018), just as my limited time series also suggested is occurring in southern YT. Warmer springs may be drier, producing lower insect abundances at crucial times, such as in early spring. In addition, the warmest springs in this study, and the years with the lowest reproductive success, coincided with peak years of ENSO levels, which are associated with drier than average conditions in overwintering areas of northern South America (Marengo et al. 2018).

Migration is the riskiest period of the full annual cycle (Sillett and Holmes 2002), and severe weather events are a principal cause of mortality – unusually strong fluctuations of the ENSO system produce regionally-specific severe precipitation and wind events such as monsoons, typhoon like conditions, or drought (Carvalho 2019). Links between phenological adjustment, fitness consequences, and migratory strategy may be more precisely investigated using overwintering locations, rather than migratory distances.

In this study, daily insect abundance influenced bird breeding phenology, although model fit was generally low, suggesting that other factors were also important. Insect abundance may be declining with year in the region, and offsets between peak insect activity and energetic demands of breeding birds may also be increasing with year. A more precise measure of asynchrony would include individual measures of plasticity to respond to changing spring conditions before clutch initiation, rather than timing or asynchrony per se, termed “adaptive asynchrony” by Lany et al. (2015). Drier winter and warmer spring conditions may expose birds to overall lower insect abundance for the full annual cycle, resulting in lower reproductive success with only indirect or weak links to asynchrony. Snowmelt and precipitation in spring may influence insect abundances positively in northern, high elevation ecosystems (Cutting et al. 2016), and with warmer spring temperatures, snowmelt may be too early and rainfall reduced, contributing to the variable and possibly decreasing insect abundances with year. Future work will determine if climate patterns such as the ENSO phenomena in distant overwintering areas impact fitness of breeding birds upon arrival to breeding areas.

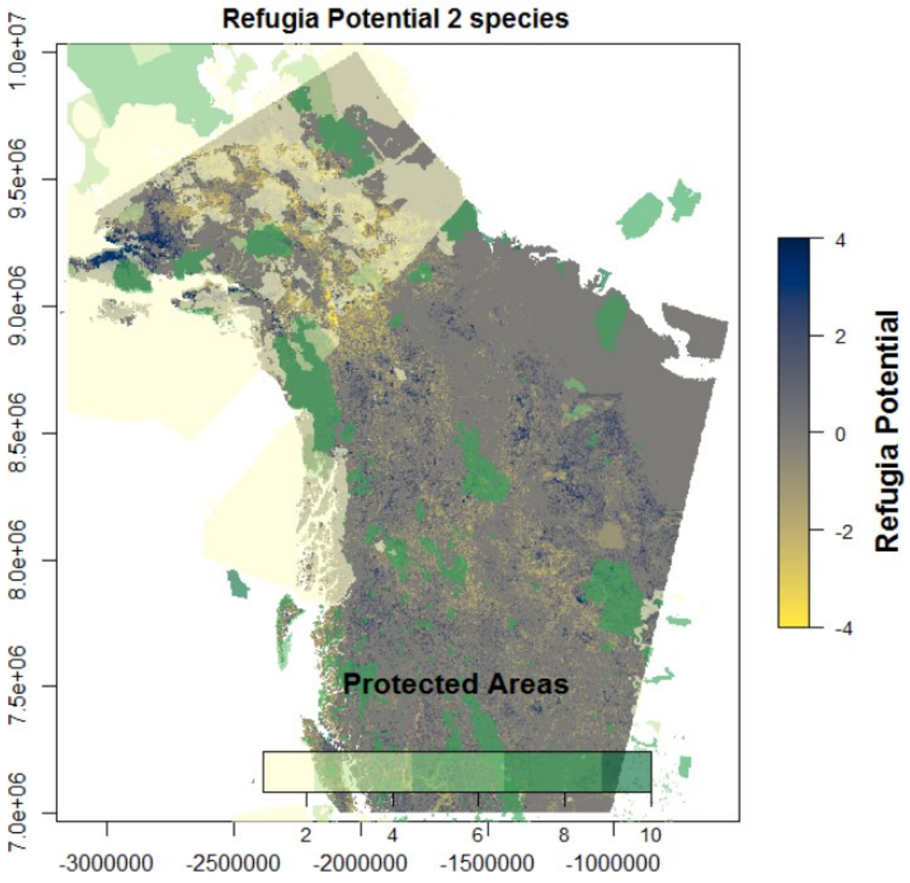
High threats to species and sites in areas of comparatively high biotic and climate velocities in northern South America (Carroll et al. 2015) underscore the importance of further study of overwintering areas for long distance migrants. Western Wood-Pewees overwinter in northern and north-western South America (Bemis and Rising 1999), including many areas of symmpatry with OSFL, but also some areas of allopatry, such as southern Central America, that may implicate overwintering habitat quality in differential declines. Full annual cycle analyses, including habitat and food quality in breeding and non-breeding areas, combined with data on migratory pathways and connectivity, will be essential to completing, the thus far, incomplete picture of drivers of declines in these species. Full annual cycle data will build on the pivotal information for OSFL migration and connectivity provided by Hagelin et al. (2014, 2015, 2019).

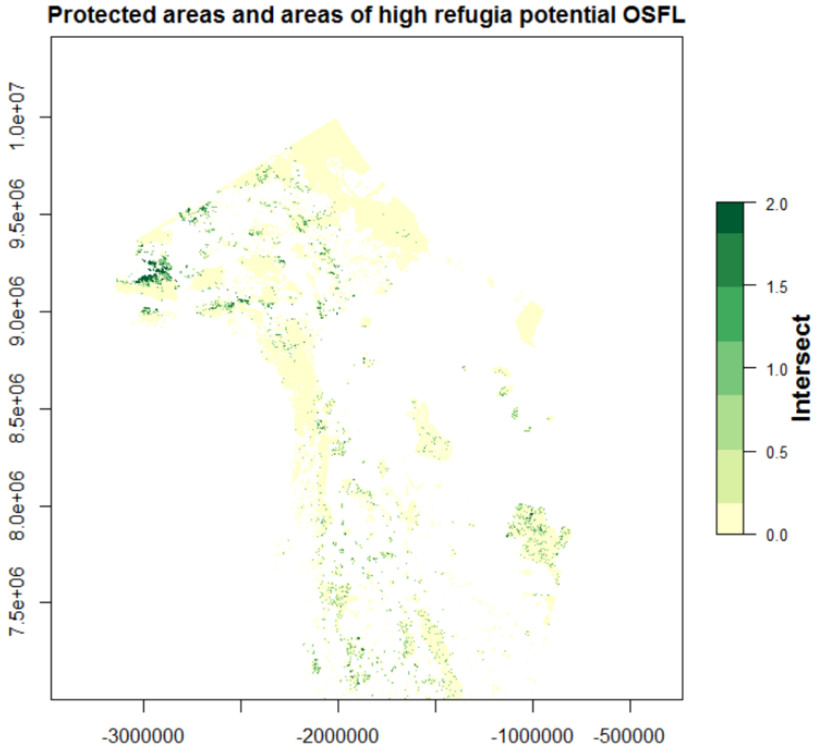
The timing and geographical patterns of forest losses in non-breeding areas, especially areas thought to be overwintering locations in South America, suggest that broad-scale climate patterns, and other factors such as land use change in non-breeding areas, may be long-term and ongoing contributors to declines. In addition, impacts of climate change on species in tropical regions are possibly greater than previously thought, because of the high endemism and low thermal tolerances of species in relatively stable climates of the tropics, minimizing the potential for climate refugia (Carroll et al. 2015). The agriculture intensification of the Green Revolution of the 1950s and 60s, in central and southern North America has and continues to be, a large factor in declines for birds breeding, or stopping, in those regions (Wilcove et al. 1998, Sánchez-Bayo and Wyckhuys 2019). Agriculture recently utilizes genetically-uniform monocultures, repeated application of synthetic fertilizers and pesticides, removed plant diversity such as trees and shrubs to allow machinery movement and further diverted waterways and wetlands for irrigation (Sánchez-Bayo and Wyckhuys 2019), all of which would severely decrease diversity of insect populations by creating uniform habitat. Breeding-ground factors, such as habitat loss, exposure to toxins such as pesticides, phenological asynchrony, and other climate change impacts in North America, may be compounding precipitous declines in these, and possibly other species, of aerial insectivores.

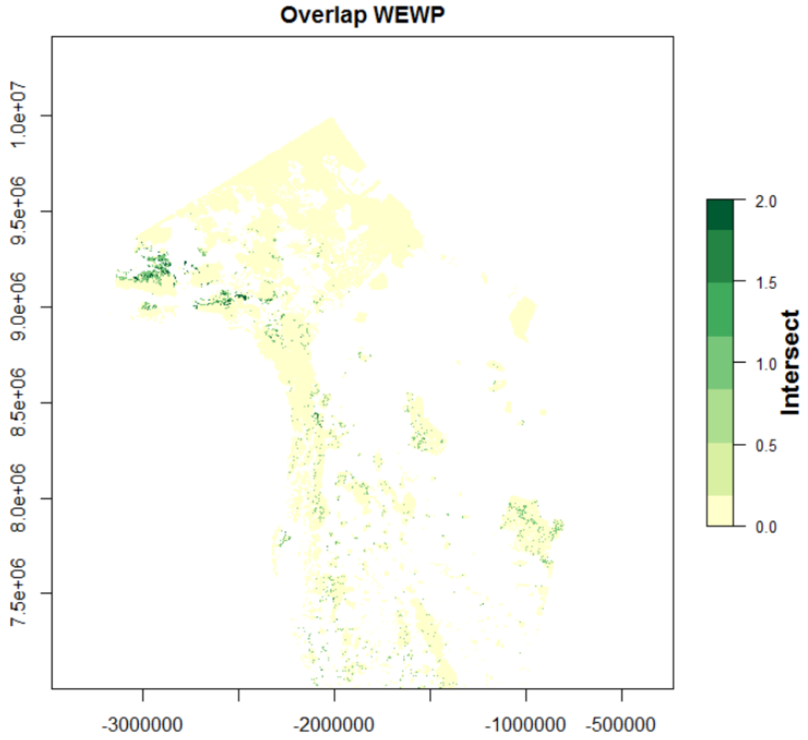
Diversity and abundance of almost all organisms are declining globally, and evidence is mounting that insects are declining faster than other taxonomic groups such as plants and birds (Sánchez-Bayo and Wyckhuys 2019), making full recovery of aerial insectivorous birds unlikely. Bird populations of most taxonomic groups or guilds are declining, with one in eight species threatened with extinction globally (BirdLife BirdLifeInternational 2018). The boreal region of western Canada supports relatively high predicted abundances of both the OSFL and WEWP in current and future projected time periods, bolstering the need to address the comparatively low amount of protected area in the Canadian boreal using quantitative data and identification of refugia areas with relatively high certainty. In addition to the many calls and needs for further data and greater understanding of impacts of climate change in conservation and management, curbing global warming would have an exponential impact on the preservation of populations from extinction. Each incremental reduction in warming will positively impact hundreds of species (Bellard et al. 2012). In addition to societal shifts towards addressing the critical need to curb global climate change, increased awareness of the impacts of human land use patterns, such as intensive and unsustainable agricultural practices, the devastating impacts of invasive species on endemics and entire ecosystems, and the pressures of an exponentially expanding human population globally, are slowly, but progressively, providing the simplest and best possible refuge for biodiversity: understanding and appreciation that leads to conservation action.

5.2 Figures

Figure 5-1A,B. Projected refugia from climate change and IUCN protected Areas. Projected refugia were calculated from gains in predicted abundance (above the median abundances from the baseline time period) of habitat (shown in blues) predicted from BRTs at 4-km resolution between baseline climatic conditions (2071-2100) and assuming a high (RCP8.5) greenhouse gas emission trajectory (assuming no time lag from vegetation change). Protected Areas of North America polygons were obtained from the Commission for Environmental Cooperation (2017) and six IUCN categories are denoted by shade of green: darker green indicates higher levels of protection (For example, Category I and II are strict nature reserves or national parks respectively, and Category VI is a protected area with sustainable use of natural resources, see https://www.iucn.org/theme/protected-areas/about/protected-area-categories for full definitions). The plots below represent areas of overlap between current protected areas and areas of high predicted refugia potential for each species, where darker green indicates area of overlap between predicted climate change refugia and existing protected areas (of any classification).




Protected areas and areas of high refugia potential OSFL


Overlap WEWP

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APPENDICES

Appendix 1 Land cover, topographical and climate variables

Table A1. Land cover, disturbance and topographical variables and layers used to generate boosted regression tree models for Olive-sided Flycatcher and Western Wood-Pewee abundance and distribution in Northwestern North America.

Variable	Description	Resolution	Extent	Source
NALC1	17 levels of land cover: Conifer Dense, Agriculture, Barren, ConifOpen, ConifSparse, DecidDense, DecidOpen, DecidSparse, Developed, Grass, Mixed (3), Shrub, Wet (3)	250 m	Canada/USA	NALCMS[1]
NALC2	9 levels of land cover: Conifer, Agriculture, Barren, Deciduous, Developed, Grass, Mixed, Shrub, Wet	250 m	Canada/USA	NALCMS[1]
LCC05	37 levels of land cover	250 m	Canada	LCCMC[2]
Vegetation layers	Temperate Needle, Taiga Needle Forest, Temperate Deciduous, Mixed Forest, Temperate Shrub, Shrub Lichen Moss, Grass Lichen Moss, Barren Lichen Moss Wetland	250 m	Canada/USA	NALCMS[1]
Height	Canopy Height (m)	1 km	Canada	GMFCH[3]
Forest Loss	Stand-replacement disturbance, 0 – 16 primarily between 2000 and 2016	30 m	Global	Global Forest Change[4]
Fire Size and Year Since Fire		30 m		Derived from CWDFIS[5]
d2Road	Perpendicular distance to road			BAM
CTI-90	Combined Topographical Index			BAM
Elv90	Elevation			BAM
Slope	Slope (Rad)	90 m	USA/Can	NALCMS[1]
TOPO30	Topography layer	30 m	North America	USGS, Institute for Bird Populations[6]

[1] North American Land Cover Monitoring System (Commission for Environmental Cooperation 2014) http://www.cec.org/tools-and-resources/north-american-environmental-atlas/north-american-land-change-monitoring-system

[2] Land Classification Cover Map of Canada 2005 (Natural Resources Canada 2016) https://www.nrcan.gc.ca/earth-sciences/land-surface-vegetation/land-cover/north-american-landcover/9146

[3] Global Map of Forest Canopy Height (Simard et al. 2011; Oak Ridge National Laboratory 2014)

[4] Hansen et al. 2013

[5] Canadian Wildland Database Fire Information System; Natural Resources Canada 2014)

[6] Phil Nott, The Institute for Bird Populations https://databasin.org/maps [accessed Dec 2018]

Table A2. Climate layers and variables used to generate boosted regression tree models for Olive-sided Flycatcher and Western Wood-Pewee abundance and distribution in Northwestern North America.

Variable	Description	Resolution	Extent	Source
Climate layers	7 layers: bFFP, MAR, MSP, MWMT, NFFD, SHM, Tave_sm For baseline and two future time periods under two emission scenarios (RCP4.5 and 8.5)	1 km	North America	AdaptWest[1]
Climate data	2 covariates: PAS and TD Baseline time period only			BAM biophysical database
InsectOffset	Difference between current and peak insect abundance temperature			Derived from data in Chapter IV
ArrivalTemp	Difference between recorded and species-specific arrival date temperature			Derived from data in Chapter IV

[1]Wang et al. 2015

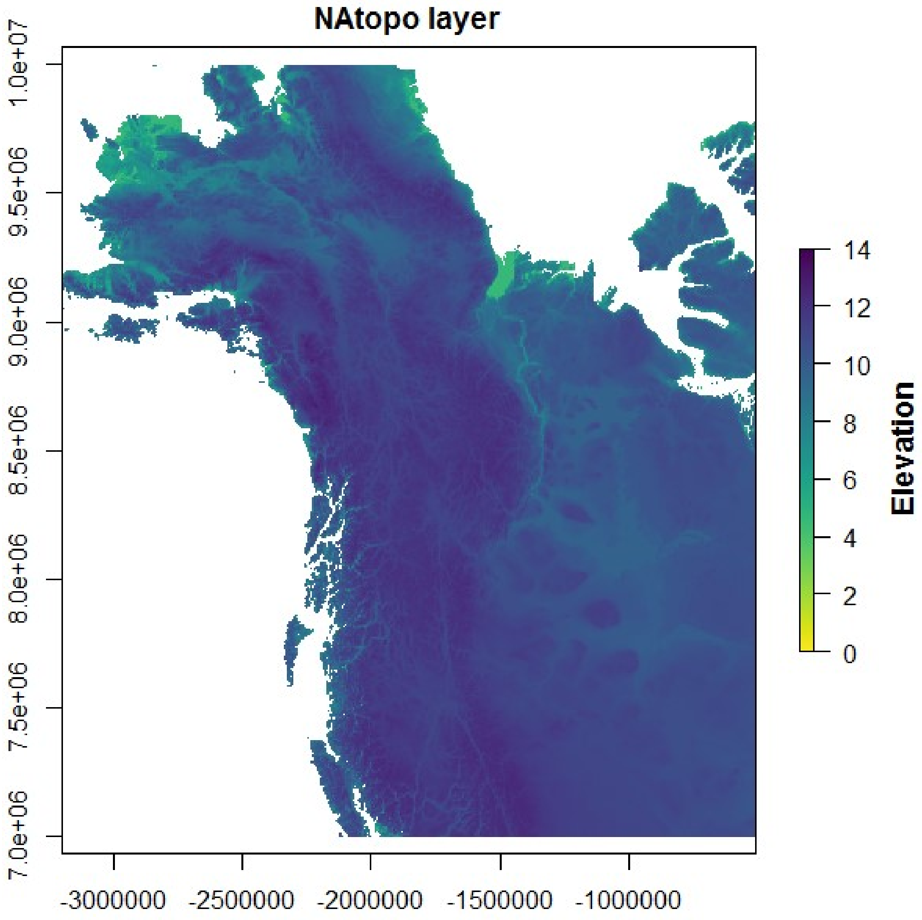

Figure A1. North American topography layer used in boosted regression tree models, from Pacific Northwest Topography, databasin (USGS TOPO30, Phil Nott, The Institute for Bird Populations 2018), originally in 1 km^2, resampled to 4 km^2.

Appendix 2 Optimization of number of trees used in boosted regression tree models

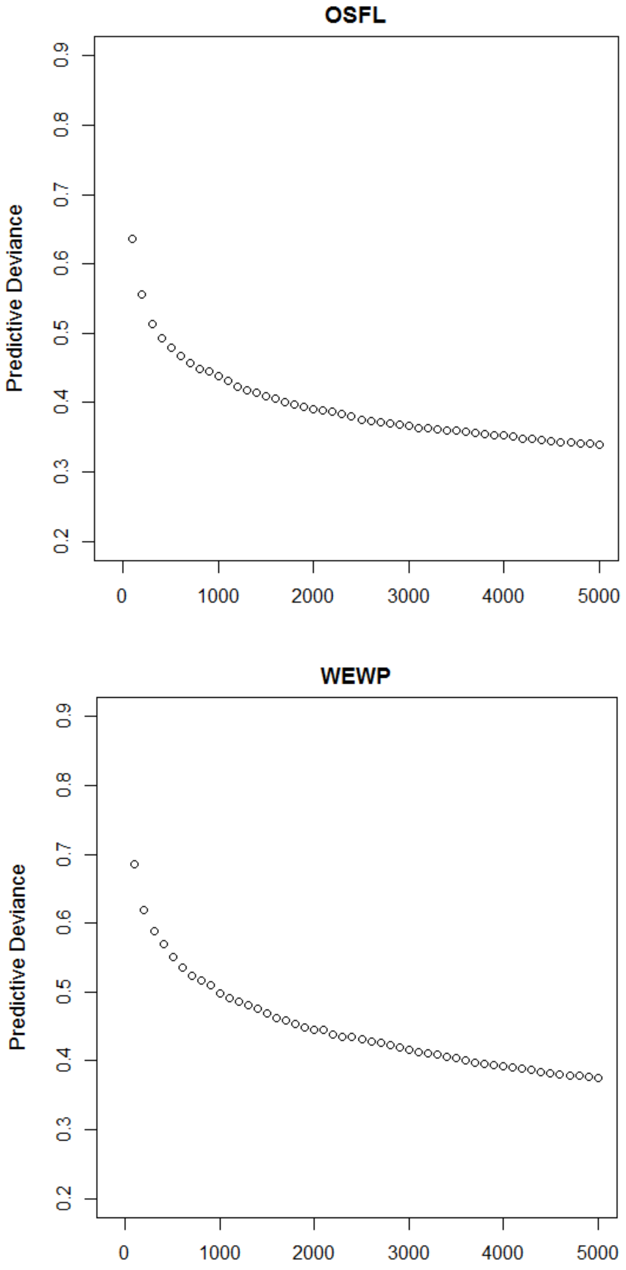

Figure A2. Optimization for the number of trees used in boosted regression tree models for the Olive-sided Flycatcher (OSFL) and the Western Wood-Pewee (WEWP).

Appendix 3 Historical mean temperatures near Whitehorse, YT

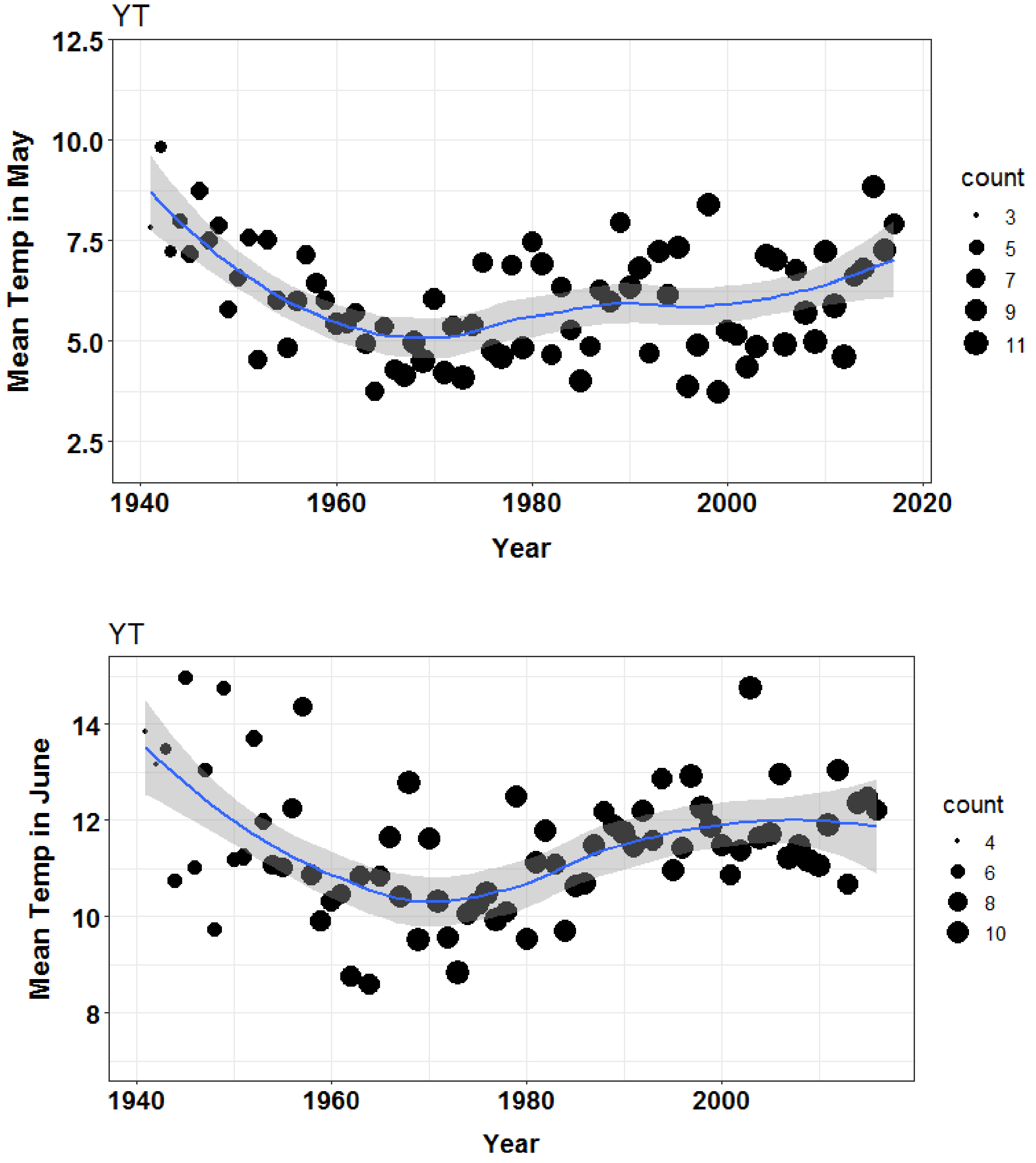

Figure A3. Mean temperature in May and June from 1941 until 2017 at Whitehorse weather station ("Whitehorse") operated by ECCC (https://climate-change.canada.ca/climate-data/#/ Station ID 2101303). Line is a polynomial regression fitted for illustrative purposes only.