WETLAND- AND LANDSCAPE-LEVEL EFFECTS ON SCOTER (*MELANITTA* SPP.), SCAUP (*AYTHYA* SPP.), AND MACROINVERTEBRATES IN WETLANDS OF THE CENTRAL MACKENZIE VALLEY, NORTHWEST TERRITORIES

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ABSTRACT

North American breeding populations of scoters (*Melanitta* spp.) and scaup (*Aythya* spp.), which nest predominantly in the rapidly changing boreal forest, were over 20% lower 2005–2014 in the western boreal forest compared to long-term averages (1955–2014), yet habitat needs for these duck species remain poorly documented. The purpose of my research is to predict impacts of ongoing environmental changes on waterfowl food supplies in northern areas and to prioritize key habitats for conservation of these species. At a key waterfowl breeding site in Canada's boreal forest, I tested three main hypotheses: (i) trophic enrichment – Wetlands located in areas burned by recent wildfires would be characterized by higher nutrient and productivity levels, and unique macroinvertebrate communities, versus those wetlands in unburned areas; (ii) foraging habitat limitation – Variables describing foraging habitat availability would be the best predictors of scoter and scaup occurrence; and (iii) scale dependency – The spatial scales at which landscape variables affected duck occurrence would correspond with home range size.

To test my first hypothesis, I measured levels of nitrogen, phosphorous, and chlorophyll-*a* concentrations, as well as macroinvertebrate community characteristics, in burned and unburned wetlands. Consistent with my predictions, total phosphorous and chlorophyll-*a* levels were approximately two-fold higher in burned than in unburned wetlands, although this effect was seasonally variable. Conversely, total nitrogen levels were similar in burned and unburned wetlands. For macroinvertebrate community composition, results were not as expected – on average, samples from burned and unburned wetlands contained similar taxa in similar abundances. To test my second and third hypotheses, I applied a multi-scale regression approach, using aerial breeding waterfowl survey data and remotely sensed landscape composition variables on unburned wetlands to evaluate relationships between landscape variables and habitat use. As predicted, wetland size correlated strongly and positively with scoter and scaup occurrence. In contrast, the amount of different land cover types correlated only weakly with occurrence. For scoters, the most important landscape variables were total number and area of waterbodies/km^2, while the proportion wetland cover was the most important landscape variable for scaup followed by total waterbody area/km^2. However, for both scoter and scaup, some of these relationships were negative, contrary to my predictions. I also found that scoters had a larger average scale of effect than scaup, as expected based on the size of their home ranges.

Taken together, these results suggest that wetland ecosystems in the northwestern boreal forest are resilient to, and may even benefit from, moderate to severe fires under current climate conditions. However, fire impacts on aquatic ecosystems are likely to intensify as the climate warms, such that this resilience may not be maintained in coming decades. The results also suggest that scoter and scaup foraging habitat is limited in the study site and that wetland-level conservation for scoter and scaup pairs should be informed primarily by wetland characteristics (e.g., wetland size and amphipod abundance) and less so by landscape composition (e.g., proportion coniferous forest cover) surrounding wetlands. In addition, the findings indicate that future landscape-level predictive modelling for these duck species should include species-specific, scale-optimized variables and should focus on home range selection.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 General background

The boreal forest of North America (hereafter the boreal), a region spanning almost 6 million km^2, contains the largest intact forest and wetland blocks on the planet and supports 1.65–3 billion breeding birds annually (Wells and Blancher 2011, Badiou et al. 2013). Nonetheless, habitat alteration caused by industrial activity and climate change is widespread in the region and is expected to intensify (Wells 2011). Industrial activity in the boreal includes forestry, mining, oil and gas, and hydropower projects, and climate change impacts include advancing spring dates, and increasing mean temperatures leading to increased droughts, forest fires, and tree-killing insect outbreaks (Drever et al. 2012, Wells et al. 2020). As mounting evidence indicates that such changes are affecting ecosystem structure and function, including forest-dwelling and aquatic bird species, the need for boreal forest conservation becomes increasingly urgent (Schindler and Lee 2010, Badiou et al. 2013, Berteaux 2013, Wells et al. 2020).

In particular, the western boreal forest (western boreal) is critical for North American waterfowl populations, supporting 12–15 million breeding ducks comprised of 23 species (Slattery et al. 2011). However, multiple duck species with more than half their population breeding in the western boreal are below conservation targets (Slattery et al. 2011). Compounding this problem, our understanding of drivers of breeding waterfowl distributions in the boreal remains limited, especially for sea ducks (tribe Mergini), such as white-winged scoter (*Melanitta deglandi*) and surf scoter (*Melanitta perspicillata*), but also for scaup (*Aythya* spp.; Prairie Habitat Joint Venture 2014, Sea Duck Joint Venture Management Board 2014).

The western boreal supports 80% and 67%, respectively, of the North American breeding populations of scoters and scaup, which have declined and remain below population targets set out by the North American Waterfowl Management Plan (Slattery et al. 2011, North American Waterfowl Management Plan 2012). The combined North American breeding scoter population (white-winged scoter, surf scoter, and black scoter) has declined since the 1950s in North America, although the exact population size is unknown because existing breeding surveys occur too early for these late-nesting species and do not adequately cover their core breeding area (Sea Duck Joint Venture 2015, Reed et al. 2016). In 2014, the western boreal scoter population was 23% lower than the long-term average (1955–2014) and 42% lower than conservation targets (Prairie Habitat Joint Venture 2014). The combined North American breeding scaup population (lesser scaup and greater scaup) declined from 5.7–7.6 million birds in the 1970s to 3.25 million birds in 2006 but showed signs of recovery in 2013 with a population estimate of 4.2 million (Zimpfer et al. 2013, Austin et al. 2014). In 2019, the North American scaup population (3.6 million) was still 28% lower than the long-term average (5.0 million, 1955–2018; U.S. Fish and Wildlife Service 2019).

Projections for the western boreal indicate that the area may warm 40% more than the global average, and, in some parts of the boreal, wildfire occurrence is expected to increase 50% by the end of the 21st century (Soja et al. 2007, Flannigan et al. 2009). Already, evidence that these changes may be limiting the recovery of breeding scoter and scaup populations is growing. For example, warming may impact scoter and scaup populations by advancing spring dates, as snow cover duration is positively related to scoter and scaup population growth rates (Drever et al. 2012). Climate change may also affect critical food sources for breeding scoters and scaup; reduced surface water area and changes in wetland chemistry of boreal wetlands in Alaska have been linked to declines in amphipods, a key macroinvertebrate prey item for breeding scoter and scaup (Corcoran et al. 2009, Anteau et al. 2020, Brown and Fredrickson 2020). Potential effects of increased wildfires in the western boreal on scoter and scaup populations are less clear. White-winged scoter densities were lower on wetlands surrounded by burned or sparse tundra vegetation in the Mackenzie Delta region (Haszard 2004), but fire appeared to have no effect on abundance of waterbird young, including scoter and scaup ducklings, on wetlands in the boreal forest of Alaska (Lewis et al. 2014). Climate change, including changes in timing of seasonal events, and the occurrence of wildfire, therefore remain major conservation challenges in the western boreal.

Though the effects of wildfires on wetland ecosystems and associated duck populations are not well understood, there is a general consensus that (i) fire in the upland impacts the productivity of aquatic systems, (ii) effects of fire increase with extent and severity of burn, and (iii) effects typically last for two to three years (McCullough et al. 2019, Pretty et al. 2021). As described by Pretty et al. (2021) in their study of fire and macroinvertebrate communities in

Canadian subarctic lakes, runoff from burned catchments tends to be enriched in nutrients, leading to higher concentrations of total nitrogen, total phosphorous, and dissolved organic carbon in waterbodies that drain burned landscapes (Garcia and Carignan 1999, 2005, Lamontagne et al. 2000, McEachern et al. 2000, Allen et al. 2005, Kelly et al. 2006, Wagner et al. 2014). Increases in nutrients have been linked to increases in primary productivity (Garcia and Carignan 2005, Kelly et al. 2006, Silins et al. 2014), which have in turn been linked to short-term increases in zooplankton biomass (Patoine et al. 2000). Longer-term changes to benthic macroinvertebrate communities have also been documented, likely explained by increased primary and secondary productivity and the overall effects of disturbance, and often marked by increases in generalist species like amphipods, as well as predator taxa (Scrimgeour et al. 2001, Bladon et al. 2014). However, the effects of fire on waterbodies are highly dependent on ecological context, including lake, landscape, fire and local weather characteristics (McCullough et al. 2019). For example, drought, waterbody surface area, watershed topography, soil properties, abundance and connectivity of waterbodies, water residence time, and fire extent, severity, location, and history can all mediate the response of waterbodies to fire (Mccoll and Grigal 1977, Schindler et al. 1996, Fergus et al. 2017, McCullough et al. 2019). McCullough et al. (2019) discuss these factors in more detail and suggests that large fires near waterbodies and tributaries generally have greater effects on waterbodies than small, distant fires (Pettit and Naiman 2007).

Scoter and scaup habitat conservation may be informed by improved knowledge of the effects of fire on wetlands, and by knowing which landscapes are most likely to support high breeding densities of these species. To date, most research on the effects of fire on aquatic ecosystems examines streams and wetlands in the western USA (Bixby et al. 2015). Conversely, studies of the effects of fire on boreal wetland nutrients and macroinvertebrates are limited and have inconsistent outcomes. Fire resulted in increased wetland productivity in a boreal subarctic plateau in northern Alberta but not in two more northerly sites in Alaska and the Northwest Territories (Scrimgeour et al. 2001, Haszard and Clark 2007, Lewis et al. 2014).Time since fire and pre-fire nutrient concentrations may have influenced the lack of increased productivity at these northern boreal sites; nutrients were measured three years post-fire in the Northwest Territories study, while pre-fire nutrient levels were abnormally high in the Alaska study. Currently, there are no such studies of fire impacts on nutrient-poor northern boreal wetlands one to two years after fire, especially those examining impacts on breeding waterfowl (Haszard and Clark 2007, Lewis et al. 2014). Scoter and scaup habitat associations in the boreal require further study though because existing studies are either single scale, based on ill-timed counts, or both (Savard and Lamothe 1991, Décarie et al. 1995, Fast et al. 2004, Haszard 2004, Walsh et al. 2006, Perry et al. 2006, Safine and Lindberg 2008, Takekawa et al. 2011, Brook et al. 2012, Barker et al. 2014, Lewis et al. 2015, Gurney et al. 2017). In sum, previous research leaves fundamental uncertainties surrounding the habitat needs of boreal-breeding scoter and scaup and the responses of their macroinvertebrate prey to wildfire, a dominant and increasingly common disturbance across the boreal region.

1.2 Thesis objectives and organization

The broad objective of this research is to inform wetland and waterfowl conservation programs in the boreal forest by (i) addressing unresolved questions surrounding responses of boreal wetlands to wildfire and (ii) better identifying habitat characteristics important to boreal-nesting white-winged scoters, surf scoters, and scaup. I address this objective in two data chapters (Chapters 2 and 3) and a synthesis chapter (Chapter 4). Because Chapters 2 and 3 are written in manuscript style in preparation for publication, certain sections of this thesis contain repeated material. I use water samples, macroinvertebrate counts, and wildfire history to test for an effect of fire on water chemistry, aquatic macroinvertebrate community composition, and scaup abundance (Chapter 2). Additionally, I use landscape composition variables and accurate, optimally timed aerial counts of breeding white-winged scoter, surf scoter, and scaup pairs to evaluate the distributions of these duck species at multiple spatial scales in the northwestern boreal forest of Canada (Chapter 3).

1.2.1 Study area and study species

I conducted this research in Ts'udé Niljné Tuyeta, a 10,060 km² Indigenous Protected Area with cultural and ecological importance to the Sahtú Dene and Métis, particularly the K'asho Got'ine Dene and Métis of Fort Good Hope, located in the Central Mackenzie Valley of the Northwest Territories. Specifically, the study focuses on wetlands within an important waterfowl area in Ts'udé Niljné Tuyeta—the Ramparts River wetlands (Ramparts; 4,692 km^2), which is known to support high densities of waterfowl, especially scoter and scaup (Latour et al. 2008; Figure 1.1). Past breeding pair surveys indicated that scoter and scaup were the most abundant species in the Ramparts, representing 1% of the estimated Canadian populations of nesting scoter and scaup (Ducks Unlimited Canada 1997). The Ramparts is a low-lying, postglacial lakebed surrounding the lower Ramparts and upper Ontaratue Rivers, and underlain by discontinuous permafrost (Heginbotton 2000, Latour et al. 2008). Primarily located within the Taiga Plains ecozone, the Ramparts area contains a high density of lakes, ponds, and wetlands, where wetlands are characterized by peat plateau bogs and fens, including open black spruce (*Picea mariana*) bogs, ericaceous shrublands, floating bogs, and sedge wetlands (Canadian Wildlife Service 2007, Latour et al. 2008). Vegetation in this ecozone consists primarily of open, slow-growing black spruce, shrub species such as dwarf birch (*Betula nana*), Labrador tea (*Rhododendron groenlandicum*), and willow, and understory species such as bearberry (*Arctostaphylos uva-ursi*), mosses, and sedges (Ecological Stratification Working Group 1995). Wildfire is the main natural disturbance in the Ramparts, and the area was partially burned in 2017 and 2018 (Canadian Wildlife Service 2007). In the northern part of the Ramparts, the fire-affected area was large, and severely burned only once in the last ten years (2017), whereas the more southerly Ramparts was characterized by smaller fires that moderately burned in both 2017 and 2018 (Matthew Coyle, Government of the Northwest Territories, personal communication).

White-winged and surf scoters (hereafter scoters) are large diving ducks that breed on freshwater wetlands and lakes in the boreal forest of Canada and Alaska, and winter primarily along the coasts of the northern Pacific and northern Atlantic oceans (Anderson et al. 2020, Brown and Fredrickson 2020). Scoters are highly philopatric and among the latest waterfowl species to initiate their nests, arriving and initiating clutches in the western boreal forest in early to mid-June (Drever et al. 2012; M. Ross, *unpublished report*). White-winged scoter females nesting for the first time return to their hatching site, and adult female white-winged and surf scoters use the same approximate nest site in consecutive years (Takekawa et al. 2011, Anderson et al. 2020, Brown and Fredrickson 2020). Scoters are ground-nesting species that usually nest far from water in dense cover, sometimes under conifers, and often on islands (Anderson et al. 2020, Brown and Fredrickson 2020). During the breeding season, the two species often co-occur on wetlands where their core breeding ranges overlap and have similar diets consisting mostly of aquatic insects and invertebrates, as well as molluscs (Haszard and Clark 2007, Drever et al. 2012, Anderson et al. 2020, Brown and Fredrickson 2020). In particular, breeding scoters are strongly associated with large ponds rich in amphipods (Haszard and Clark 2007, Lewis et al.

2015). Both scoter species are single-brooded and generally long-lived with a low reproductive output, like most sea ducks (Anderson et al. 2020, Brown and Fredrickson 2020).

Lesser scaup and greater scaup are abundant, widespread, medium-sized diving ducks that breed on wetlands and lakes across the boreal forest and parklands from central Alaska through Manitoba (Anteau et al. 2020). During winter, lesser scaup primarily use lakes, reservoirs, and estuaries along the south Atlantic Coast, Gulf Coast, and Pacific Coast (Anteau et al. 2020). Like scoters, lesser scaup are late-nesting species, arriving at breeding areas in late May to early June and initiating clutches in June (Drever et al. 2012, Anteau et al. 2020). Lesser scaup nest closer to water than scoters, building nests adjacent to or over water, as well as in the uplands, typically in tall living vegetation under shrubs and on islands (Anteau et al. 2020). Scoter and lesser scaup also share a similar prey base—namely aquatic invertebrates and molluscs—and show the same preference for larger waterbodies abundant in amphipods (Fast et al. 2004, Drever et al. 2012, Lewis et al. 2015). Lesser scaup will renest following nest failure, but like scoters and other sea ducks, they have lower reproductive rates than other duck species (Anteau et al. 2020).

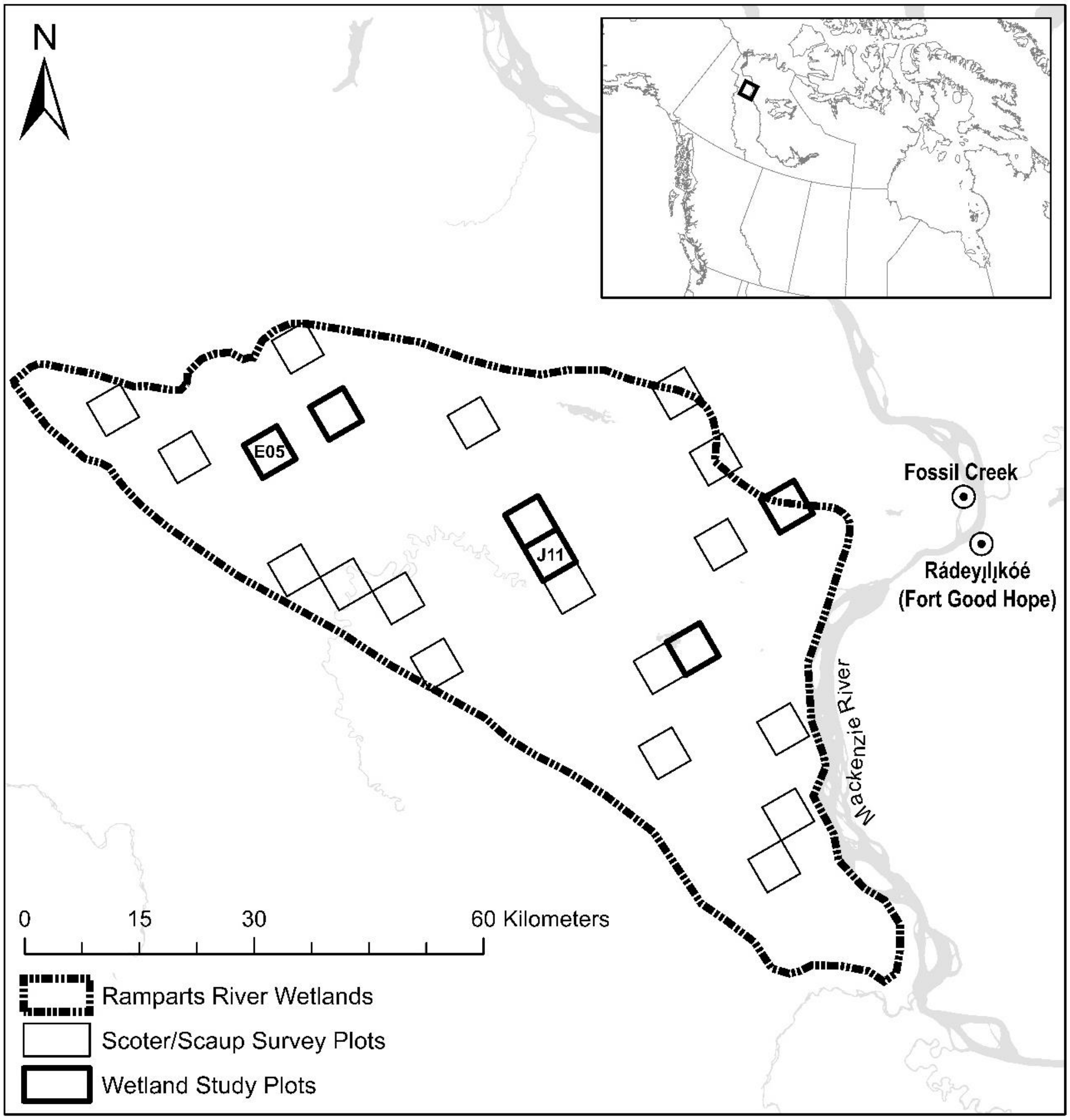

Figure 1.1. Map of the Ramparts River wetlands study area, Northwest Territories, Canada. The Canadian Wildlife Service conducted breeding surveys of scoter and scaup by helicopter in 2017 in 20 survey plots containing 1288 unique wetlands. I collected data from 39 unique wetlands within these plots in 2018–2019 (11 of which were in recently burned areas [n = 6 in E05, n = 5 in J11]) and 13 unique wetlands near Fossil Creek in 2017.

CHAPTER 2. RESPONSES OF MACROINVERTEBRATES AND BREEDING SCAUP (*AYTHYA* SPP.) TO WILDFIRE IN CANADA’S BOREAL FOREST

2.1 Introduction

Wildfire is a common natural disturbance in many forested regions of the globe, with a broad range of effects on ecosystem structure and function (Giglio et al. 2006, Grimm et al. 2013, Cunillera-Montcusí et al. 2019). Terrestrial effects of fire, such as changes to vegetation structure, soil properties, and runoff dynamics often impact freshwater systems, and elevated nutrient and sediment inputs to aquatic ecosystems following wildfire are well-documented (Bladon et al. 2014, McCullough et al. 2019). For example, after a burn in the surrounding landscape, concentrations of nitrogen and phosphorous often increase in lakes for up to two to three years post-burn, which can lead to increased primary production in these systems (Carignan et al. 2000, McEachern et al. 2000, Scrimgeour et al. 2001, Kelly et al. 2006). These fire-induced increases in primary production can, in turn, affect higher trophic levels across a broad suite of aquatic habitats, including macroinvertebrates and the avian fauna that forage on them. The specific effects of wildfire on higher trophic levels, however, are variable, with some studies reporting enrichment (i.e., increased macroinvertebrate abundance, possibly leading to increased bird abundance), and others suggesting potential deleterious effects, such as reductions in foraging efficiency due to changes in water colour and clarity (McEachern et al. 2000, Haszard and Clark 2007, Lewis et al. 2015).

Throughout the boreal forest biome (hereafter the boreal), wildfire is typically the dominant form of ecosystem disturbance, altering both landscape structure and species composition of plant, mammal, bird, and insect communities (Turetsky and St. Louis 2006, Jager et al. 2021). Wildfire size and frequency have increased during recent decades, especially in the boreal of Alaska and western Canada, and further increases are predicted (Soja et al. 2007, Wells et al. 2020). Specifically, in some parts of the boreal, area burned is predicted to double and wildfire occurrence is expected to increase 50% by the end of the 21st century (Flannigan et al. 2009). The boreal contains at least 60% of the earth's surface freshwater, and 25% of the world's wetlands occur in Canada's boreal (Schindler and Lee 2010). Multiple impacts from climate change, such as permafrost degradation, reductions in surface water area, and changes in phytoplankton and macroinvertebrate communities are already threatening these ecosystems (Riordan et al. 2006, Corcoran et al. 2009, Roach et al. 2011).

Despite the rapid increase in fire activity, studies of fire-induced trophic enrichment in boreal lakes and wetlands remain limited, often with contrasting results, and there is limited information on how fire will influence wetland-dependent wildlife, such as waterfowl. For example, in the Caribou Mountains, a boreal subarctic plateau in northern Alberta, nutrient (reactive phosphorus) and productivity measures (chlorophyll-*a*, insect and zooplankton biomass) were higher and water was darker in colour in burned lakes than in reference lakes one to two years following a wildfire (Scrimgeour et al. 2001). In contrast, in the Yukon Flats of boreal Alaska, wildfire did not affect concentrations of nutrients (total nitrogen, total phosphorus) or chlorophyll-*a* levels measured in lakes. Although some zooplankton (Crustacea: Amphipoda) did occur at higher densities in burned lakes than in reference lakes at this site, fire had no detectable effect on abundance of waterfowl offspring; instead, the number of young decreased across the entire study area following the wildfire (Lewis et al. 2014). Similar to Alaska, nutrient concentrations (total nitrogen, total phosphorus) in boreal wetlands of the Mackenzie Delta, Northwest Territories (NT) did not vary between unburned and burned wetlands three years post-fire (Haszard and Clark 2007). However, for up to two years following a wildfire, density of white-winged scoter (*Melanitta deglandi*) pairs was lower on wetlands surrounded by burned or sparse tundra vegetation than on wetlands surrounded by dense forest, possibly due in part to altered macroinvertebrate food webs or increased concentrations of dissolved organic carbon leading to darker water (Haszard 2004).

To help clarify the uncertainty regarding cascading effects of fire on wetland ecosystems in the North American boreal and thereby inform wetland and waterfowl conservation programs in this region, I conducted field studies at a key waterfowl area in the Central Mackenzie Valley, NT (Latour et al. 2008). Specifically, I tested the trophic enrichment hypothesis, whereby fires enrich aquatic nutrients, which in turn elevates aquatic production across multiple trophic levels from primary producers to consumers. To test this hypothesis, I evaluated nutrient levels, productivity, colour, macroinvertebrate community composition, and abundance of a key waterfowl taxon, scaup (*Aythya* spp.), in the context of recent (within the previous two years) wildfires. I predicted that, relative to unburned wetlands, recently burned wetlands would have

(i) higher levels of total nitrogen, total phosphorus, and chlorophyll-*a*; (ii) darker coloured water; (iii) greater relative abundances and percent compositions of the macroinvertebrate Amphipoda, and (iv) higher densities of scaup, which feed primarily on amphipods (Haszard and Clark 2007, Lewis et al. 2014). Scaup are ideal models for studying trophic impacts of wildfire on boreal wetlands, as they nest predominantly in boreal areas and depend on freshwater macroinvertebrates for successful reproduction (Anteau et al. 2020). Recent studies also suggest that failure of scaup populations to reach conservation targets may be related to changes in wetland food webs on boreal breeding grounds, further highlighting the need to understand links between wildfire, changes in boreal wetlands, and abundance of waterfowl (Corcoran et al. 2009, Slattery et al. 2011, Drever et al. 2012).

2.2 Methods

2.2.1 Study area

I evaluated the effects of recent wildfire on water chemistry, macroinvertebrates, and scaup on wetlands within Ts'udé Nilįné Tuyeta, a 10,060 km² Indigenous Protected Area with cultural and ecological importance to the Sahtú Dene and Métis, particularly the K'asho Got'ine Dene and Métis of Fort Good Hope. Specifically, within Ts'udé Nilįné Tuyeta, I collected data in the Ramparts River wetlands (hereafter the Ramparts), a 4,660 km^2 area approximately 35 km west of Fort Good Hope, NT, at 66°15'N, 130°00'W, which is known to support high waterfowl densities (Salter et al. 1974, Ducks Unlimited Canada 1997). The Ramparts is a low-lying, postglacial lakebed surrounding the lower Ramparts and upper Ontaratue Rivers, underlain by discontinuous permafrost (Heginbotton 2000, Latour et al. 2008). Primarily located within the Taiga Plains ecozone, the Ramparts area contains a high density of lakes, ponds, and wetlands, where wetlands are characterized by peat plateau bogs and fens including open black spruce (*Picea mariana*) bogs, ericaceous shrublands, floating bogs, and sedge wetlands (Canadian Wildlife Service 2007, Latour et al. 2008). Vegetation in this ecozone consists primarily of open, slow-growing black spruce forest, shrub species such as dwarf birch (*Betula nana*), Labrador tea (*Rhododendron groenlandicum*), and willow, and understory species such as bearberry (*Arctostaphylos uva-ursi*), mosses, and sedges (Ecological Stratification Working Group 1995). The region is characterized by short, cool summers and long, cold winters. Wildfire is the main natural disturbance in the Ramparts (Canadian Wildlife Service 2007), and the area was partially burned in 2017 and 2018. The more northern burned area was large and severely burned only once in the last ten years (2017), while the more southerly fire location was smaller and moderately burned in 2017 and 2018 (Matthew Coyle, Government of the Northwest Territories, personal communication; Figure 2.1).

2.2.2 Wetland selection

I selected 39 wetlands that were spread across six different 5 x 5 km survey plots in the Ramparts. The plots were non-randomly selected to represent the range of predicted plot-level scoter and scaup densities in the Ramparts (Canadian Wildlife Service [CWS], *unpublished data*). I non-randomly selected 5–12 wetlands stratified into six categories within each of these plots based on wetland surface area and wildfire history (Table A.1). Specifically, I categorized wetlands as either small (≤ 2.6 ha), medium (2.7–13.5 ha), or large (> 13.5 ha), and as either burned (located in an area that burned once or twice, one to two years before the sampling date) or unburned (located in an area that either had not burned since 1965 or burned > 40 years before the sampling date). I also included 13 small, unburned wetlands located near Fossil Creek, for a total of 52 unique wetlands. These 13 wetlands were sampled primarily because they could be easily accessed without use of a helicopter.

2.2.3 Sample collection

I accessed the study site in May and June 2017–2019 using a Bell 206LR helicopter equipped with floats. I measured water parameters and collected water and macroinvertebrate samples from study wetlands immediately after spring thaw (May 20–25) and approximately one month later (June 17–22), closer to the peak growing period for vegetation in the region. On arriving at study wetlands, the pilot landed the helicopter in the center of the wetland and reduced the rotor speed to avoid disturbing the water column. I used a water quality meter (YSI ProDSS) to measure conductivity, pH, temperature, and percent dissolved oxygen (DO), and I collected one litre grab samples from wetland surfaces to be analysed for nutrients (total nitrogen, TN and total phosphorus, TP), productivity (chlorophyll-*a*, Chl-*a*), dissolved organic carbon (DOC), and colour (Col). In 2019, I measured depth at each sampling site by lowering a weighted rope marked with 10 cm intervals to the bottom of wetlands. I stored water samples in a cool dark location immediately following collection until analyses were conducted (Taiga Labs in Yellowknife, NT).

In 2018 and 2019, I collected freshwater macroinvertebrates by pulling a kick net (363 μm mesh size) 2 m horizontally at a 10–20 cm depth in the center of wetlands, once per wetland.

Macroinvertebrates were counted and identified to the Family level by Cordillera Environmental Consulting in British Columbia in 2018 and by technicians in the field in 2019. Samples were processed on the day of collection or refrigerated and processed within 24 hours of collection. I rinsed sample containers into white sorting trays to count and identify individuals, using a dissecting microscope when necessary, aiming to match the taxonomic resolution achieved in 2018 (Thorp and Covich 2001, Merritt et al. 2008).

2.2.4 Waterfowl survey

I also recorded the abundance of all waterbirds detected on the wetlands I sampled for chemistry and macroinvertebrates June 17–19, 2019 (n = 30). I surveyed the perimeters of each of these study wetlands and flew additional center transects on wetlands that were too large to survey from the shoreline adequately (Ducks Unlimited Canada 2015, *unpublished protocol*). Surveys were flown approximately 15–50 m above ground level at speeds of a hover to 100 km/h in good light conditions (between one hour after sunrise and one hour before sunset). I was the lone observer, located in the front left of the float-equipped helicopter. I identified most individuals to species and sex; however, I identified all scaup to the genus level (*Aythya* spp.) because high scaup densities made differentiating between lesser and greater scaup impractical. Most of the observed scaup were presumed to be lesser scaup, because scaup counts in the boreal are ~89% lesser scaup, and of the speciated scaup observed by the Canadian Wildlife Service in 2017 waterfowl surveys in the Ramparts, all were lesser scaup (Afton and Anderson 2001; M. Ross, *unpublished report*). To estimate the number of scaup pairs per study wetland, I converted observed counts of scaup to an index of indicated breeding pairs (IBPs). I took the number of IBPs to be the number of observed pairs plus the number of males observed in all other groups containing four or fewer males (Gilliland et al. 2009). Observations containing five or more males were excluded from analyses because individuals in groups of this size may not be local breeders (Brook et al. 2012).

2.2.5 Statistical analyses

2.2.5.1 Nutrients, productivity, and colour

I used general linear mixed models with normal errors to test for differences in nutrients, productivity, and colour between burned and unburned wetlands while accounting for the non-independence of study wetlands from the same plot (function *lmer* R package *lme4* version 1.1.23, Bates et al. 2015). To increase the power to detect an effect of fire on wetland chemistry, I pooled the data from all three years (2017–2019; number of unique wetlands = 52, number of samples = 121). I created separate *a priori* candidate model sets for each response variable of interest (TP, TN, Chl-*a*, and Col). I determined the optimal random effect structure (either plot or study wetland nested within plot) using Akaike's Information Criterion corrected for small sample size (*AICc*; Zuur et al. 2009; R package *MuMIn* version 1.43.17, Bartoń 2020). I selected a set of predictor variables that are known or hypothesized to influence water chemistry of wetlands: sampling year, sampling month, wetland size class, and burn category (burned/unburned). I also considered plausible interactions between burn and other predictors in my model set. Specifically, I modeled an interaction between burn and month because seasonal events such as spring snowmelt and summer rains that increase runoff and erosion rates can increase inputs of dissolved and particulate forms of nutrients and carbon to wetlands (Bladon et al. 2014; dissolved organic carbon [DOC] is strongly correlated with colour in the study wetlands; Figure A.1). As well, a burn effect might be less detectable in months when background nutrient, productivity, or colour levels are higher (Lewis et al. 2014). I also included an interaction between burn and size class in my model sets because fire-derived inputs of nutrients and carbon may be more diluted in larger water bodies (McColl and Grigal 1975).

The candidate model sets for each of the four response variables consisted of six increasingly complex models. I began with a statistical null model containing only the random effect. Next, I created a biological null model containing year, month, or both that best explained the temporal variation of the response variable (determined using *AICc*). The next most complex model contained burn—the variable of interest. I then added a burn-month interaction term. I also created a similar model containing size class and a burn-size class interaction. Lastly, I created the global model, which contained all fixed terms and interaction terms described above. TP, TN, and Chl-*a* were log-transformed to meet model assumptions of constant variance and normal errors. I based inferences on the best-approximating model in each candidate model set, which I identified using a model selection approach based on *AICc* (Burnham and Anderson 2002).

2.2.5.2 Macroinvertebrate community composition

To compare macroinvertebrate communities in burned and unburned wetlands, I used non-metric multidimensional scaling (NMDS) and environmental fitting (R package *vegan* version 2.5-6, Oksanen et al. 2019). A preliminary NMDS plot of all samples showed strong separation by year, so I began by comparing invertebrate communities in burned and unburned communities in 2018 and 2019 separately. These analyses revealed no separation by burn in either year, so I pooled data from 2018 and 2019 to increase the power to detect an effect of burn on macroinvertebrate communities (number of unique wetlands = 39, number of samples = 108). To achieve model convergence, I excluded taxa that were observed in less than 3.7% of samples (i.e., < 4 samples out of the 108 samples, which represented 28 of the 46 observed taxa). I also excluded some individuals not identified to a low enough taxonomic resolution for these analyses (typically the family level; 2.4 % of observed individuals). The community ordination was conducted along three axes and was based on Bray-Curtis dissimilarities and standardized macroinvertebrate abundances (number per sample; function *metaMDS* R package *vegan* version 2.5-6, Oksanen et al. 2019). The standardizations included both a Wisconsin double standardization and a square root transformation. Each sampling event was included as a unique community in the NMDS (n = 108).

I fit the burn variable (burned/unburned) to the ordination, along with a set of control variables identified from the literature as the most likely wetland drivers of macroinvertebrate abundance (function *envfit* R package *vegan* version 2.5-6, Oksanen et al. 2019). Control variables included DO, temperature (Temp), TN, nitrogen to phosphorous ratio (N-P), Chl-*a*, wetland size class (SizeClass), year, and month. Although TP and pH influence macroinvertebrate abundance as well, I excluded them from this analysis because they correlated with other, more relevant variables (pH & temperature: $r = 0.59$; TP and Chl-*a*: $r = 0.63$; TP and N-P: $r = -0.55$). Correlations among the remaining variables were weaker ($|r| < 0.41$). For all dimensions, the fit and significance of burn and the control variables were determined using permutations (function *envfit* R package *vegan* version 2.5-6, Oksanen et al. 2019). I used a backward selection approach to remove uninformative variables (false discovery rate corrected p-value < 0.10).

In addition, I compared the mean abundance (hereafter relative abundance) and percent composition of all observed macroinvertebrate taxa, including rare taxa excluded from the NMDS analysis. I use the term relative abundance to distinguish from more accurate detection-corrected estimates of wetland macroinvertebrate abundance, which I did not measure in this study. I calculated mean relative abundance as the mean number of individuals of a taxon per sweep sample. I calculated percent composition as the total number of individuals of a taxon across all samples, divided by the total number of individuals of all observed taxa across all samples.

2.2.5.3 Scaup abundance

To test for an effect of fire on breeding scaup abundance, I analysed the number of scaup IBPs on study ponds using a generalized linear mixed model with a negative binomial error structure that accounted for non-independence of study wetlands from within the same plot (function *glmer.nb* R package *lme4* version 1.1.23, Bates et al. 2015). More specifically, I modelled the scaup IBPs by including study wetland surface area as an offset in the model because scaup are more likely to occur on larger wetlands in the study area (Lewis et al. 2015), and scaup abundance can be expected to be higher on wetlands that have more space and resources available. I created an *a priori* candidate model set designed to test for effects of wildfire on scaup abundance while controlling for other potentially important wetland variables. To reduce the risk of overfitting the models, I selected only two independent variables for inclusion in the model set, along with burn. To do so, I used likelihood ratio tests (LRT's) to compare the explanatory power of alternative models, each containing the random term, the offset, and the variable of interest (function *lrtest* R package *lmtest* version 0.9.38, Zeileis and Hothorn 2002). Only two of the tested variables were influential: wetland depth (p-value = 0.05) and N-P (p-value = 0.04).

After confirming that depth and N-P were not strongly correlated ($r < 0.1$), I selected a biological null model by determining the relative support (as indicated by *AICc*) of a depth model, an N-P model, and a combined depth and N-P model (R package *MuMIn* version 1.43.17, Bartoń 2020). The combined model had the most support; therefore, the final candidate model set consisted of three models, all containing the random term and offset: the statistical null (intercept-only), the biological null (depth and N-P), and the biological null with burn added (depth, N-P, and burn). Due to sample size constraints, I did not consider non-linear effects. I used a model selection approach based on *AICc* to select the best-approximating model in each candidate model set (Burnham and Anderson 2002). All three analyses (water chemistry, macroinvertebrate, and scaup abundance) were performed using Program R version 3.6.2 (R Core Team 2019).

2.3 Results

2.3.1 Nutrients, productivity, and colour

2.3.1.1 Phosphorous

Estimated mean marginal TP was higher in burned wetlands (43.06 µg/L, 95% CI: 15.28, 70.85; Table 2.2) than in unburned wetlands (22.18 µg/L, 95% CI: 10.78, 33.57), but only in May (P = 0.0915), not June (P = 0.7943; Figure 2.2). The top model for TP contained the fixed terms year, month, burn and an interaction term between burn and month, as well as wetland nested within plot as a random effect (Table 2.1). Because it accounted for 82% of model weight, I based inferences on this model alone. Marginal and conditional R^2_{GLMM} estimates were 0.21 and 0.70, respectively, suggesting that a substantial proportion of the explained variation in TP can be attributed to unmeasured variables that varied with plot.

***2.3.1.2 Chlorophyll-*a**

Like TP, Chl-*a* was higher in burned wetlands (7.39 µg/L, 95% CI: 2.87, 11.91; Table 2.4) than in unburned wetlands (3.27 µg/L, 95% CI: 1.85, 4.69) in May (P = 0.0476) but not in June (p = 0.6694; Figure 2.3). The top model for Chl-*a* contained the fixed terms year, month, burn and an interaction term between burn and month, like TP, as well as plot as a random effect (Table 2.3). Again, I based inferences on the most parsimonious model because it explained most of the variation in Chl-*a* in the sample (ω_i = 0.91). Marginal and conditional R^2_{GLMM} estimates were 0.23 and 0.27, respectively, suggesting that most of the explained variation can be attributed to the fixed effects.

2.3.1.3 Nitrogen and colour

In contrast to the findings for TP and Chl-*a*, burn had no detectable effect on TN or colour in study wetlands. In both TN and colour model sets, the top model contained only a single temporal variable (year or month; Table 2.5, Table 2.6). The next most parsimonious model in both model sets contained burn in addition to year or month and was within 2 *AICc* units of the top model. Therefore, burn was uninformative in both model sets because it did not reduce the deviance enough to overcome the 2-unit penalty for one additional parameter (Arnold 2010).

2.3.2 Macroinvertebrate community composition

Ordination analyses were based on 108 samples containing observations of 18 taxa (23,557 individuals total). The analyses did not detect differences in macroinvertebrate community composition between burned and unburned wetlands. Specifically, there was little separation by burn category along any of the three axes (NMDS1 & 2: $R^2 = 0.012$, P = 1.000; NMDS1 & 3: $R^2 = 0.009$, P = 1.000: NMDS2 & 3: $R^2 = 0.005$, P = 1.000; Table A.3; Figure 2.4), and Amphipoda appeared to contribute equally to burned and unburned communities. Indeed, the relative abundance and percent composition of Amphipoda were similar in burned (1.9 [95% CI: -0.1, 3.8], 0.7%; Table 2.7) and unburned (7.3 [95% CI: 3.5, 11.1], 3.7%) wetlands.

2.3.3 Scaup abundance

A total of 155 scaup IBPs were observed on 13 of the 30 wetlands surveyed for waterbirds in 2019. Burn had no detectable independent effect on scaup IBPs (Table 2.8). The top model contained depth and N-P and had a model weight of 0.55. The next most parsimonious model contained burn in addition to depth and N-P, but the effect of burn was negligible (Δ *AICc* = 1.46, $\omega_i = 0.26$, Burn $\beta = 1.16$, 95% CI: -0.58, 3.08). Marginal and conditional R^2_{GLMM} estimates for the top model were both 0.51, suggesting that all the explained variation can be attributed to the fixed effects.

2.4 Discussion

To test the trophic enrichment hypothesis, I compared abiotic and biotic characteristics of 28 unburned and 11 recently burned wetlands in the Ramparts River wetlands of the northwestern boreal forest of North America. I detected elevated TP and Chl-*a* in burned wetlands in early spring but did not detect effects of fire on macroinvertebrate community composition or scaup abundance. These results suggest that the scope of nutrient enrichment that occurred in the study wetlands following wildfire was limited and that enrichment did not influence higher trophic levels.

2.4.1 Nutrients, productivity, and colour

TP and Chl-*a* were approximately 2-fold higher in burned than in unburned wetlands in May but not in June, whereas TN and colour were similar in burned and unburned wetlands, regardless of sampling month. The results for TP and Chl-*a* support the trophic enrichment hypothesis, which predicted that recently burned wetlands would be more nutrient-rich and productive than unburned wetlands, whereas the result for TN was inconsistent with this hypothesis. The result for colour was also unexpected, as I predicted burned wetlands would be darker in colour than unburned wetlands.

The higher TP observed in burned wetlands is consistent with previous studies of boreal shield lakes, boreal subarctic lakes, and a montane cordillera lake (Carignan et al. 2000, McEachern et al. 2000, Scrimgeour et al. 2001, Kelly et al. 2006). This phenomenon is generally explained by increased nutrient exports from burned terrestrial areas to lakes (Scrimgeour et al. 2001). More specifically, the increased runoff and erosion that occurs in burned areas often leads to increased nutrient loadings in nearby aquatic systems (Smith et al. 2011). I likely observed higher TP in burned wetlands in May but not June because of the greater erosion rates that would be expected during snowmelt in early spring, which occurs from late March to early May in the Mackenzie River basin (Quinton and Hayashi 2005, Bladon et al. 2014, Yang et al. 2015). May samples were collected several weeks after snowmelt, whereas June samples were collected more than a month later. In addition, the vegetation growth that occurred between May and June sampling periods may have contributed to the limited effect of fire on nutrient levels in June because nutrient uptake by growing plants likely removed much of the nutrients released by wildfires (McColl and Grigal 1975; Figure A.2–Figure A.**5**).

The similar TN concentrations observed in burned and unburned Ramparts wetlands are perhaps not surprising given the high degree of nitrogen retention that has been observed in other peatland areas following fire. Nitrogen concentrations are often higher in burned lakes than in unburned lakes in the boreal two to three years following fire (Carignan et al. 2000, McEachern et al. 2000). However, McEachern et al. (2000) found that fire caused more significant increases in TP than TN in lakes in the boreal subarctic natural subregion of northern Alberta, a poorly drained, peatland-dominated region underlain by discontinuous permafrost, comparable to the Ramparts study area (Natural Regions Committee 2006). Similar findings of nitrogen retention and phosphorous export were observed in burned fens in the Experimental Lakes Area of the Canadian Shield (Bayley et al. 1992). Such nitrogen retention in peatlands may occur because peatland vegetation tends to be N limited, which was the case in Alberta, where plant tissues in marshes and fens had TN:TP ratios of <14 (Bayley and Mewhort 2004).

Pre-fire nutrient concentrations may have influenced the findings for nitrogen as well. Specifically, fire-induced changes in nitrogen may have gone undetected if the changes did not exceed background variation in nitrogen. Such a result was reported from lakes in the Yukon Flats basin of interior Alaska, where fire-induced changes in nutrients were likely undetectable because the study lakes were naturally nutrient-rich (Lewis et al. 2014). In the Ramparts, TN varied considerably within and between years and plots, and the study wetlands appear to be nitrogen-sufficient and phosphorous-limited. Phosphorous limitation is considered likely when lake nitrogen to phosphorous ratios exceed 20:1, and average TN:TP was 81:1 in unburned wetlands and 48:1 in burned wetlands in the Ramparts (Maberly et al. 2020). Previous studies confirm that forest-tundra lakes and upland wetlands in the Mackenzie River basin are generally nitrogen-sufficient and phosphorous-limited (Haszard and Clark 2007, Ogbebo et al. 2009). Moreover, phosphorous is the limiting nutrient in almost all freshwater systems (Kalff 2002).

The heightened Chl-*a* observed in burned wetlands is consistent with previous studies documenting higher Chl-*a* concentrations in burned boreal subarctic and montane cordillera lakes due to elevated nutrients (Scrimgeour et al. 2001, Kelly et al. 2006). Higher Chl-*a* concentrations following nutrient pulses are explained by the fact that primary productivity in lakes is limited by nitrogen and phosphorous availability, especially phosphorous availability, because increases in Chl-*a* require an increase in one or both nutrients (Schindler 1977). The strong association between phosphorous and Chl-*a*, specifically, is typical across aquatic ecosystems and has previously been observed in forest-tundra lakes of the Mackenzie River basin (Kalff 2002, Ogbebo et al. 2009).

Colour, a correlate of DOC in the study wetlands as in other northern peatlands, was similar in burned and unburned wetlands in the Ramparts, despite multiple studies documenting increased carbon in boreal lakes following wildfire (Carignan et al. 2000, McEachern et al. 2000, Scrimgeour et al. 2001). However, there is evidence that DOC influxes to wetlands following wildfire may be limited compared to that of lakes. For example, in the Caribou Mountains, DOC concentrations were similar across fens, regardless of whether fens received drainage from burned or unburned areas (McEachern et al. 2000). Though only three fens were included in the Caribou Mountain study, the results suggest that there may be important differences in fire impacts on water chemistry between boreal lakes, which are generally larger and deeper, and shallower and smaller wetlands.

2.4.2 Macroinvertebrate community composition

Under the trophic enrichment hypothesis, and because wildfire was associated with greater nutrient concentrations and productivity in study wetlands in May, I expected to find differences in macroinvertebrate community composition between burned and unburned wetlands. However, my results were not consistent with this prediction. In addition, the relative abundance and percent composition of Amphipoda was similar across burned and unburned wetlands, which contrasted with my prediction that generalist taxa like Amphipoda would predominate in burned wetlands.

These unexpected results may relate to the magnitude of the differences in nutrients (TP) and productivity (Chl-*a*) between burned and unburned wetlands, the coarse index of macroinvertebrate abundance I used, or the timing of macroinvertebrate collections. The observed 2-fold difference in TP and Chl-*a* between burned and unburned wetlands in the study area may not have been large enough to translate into a difference in the macroinvertebrate communities in these two wetland types. Alternatively, the magnitude of the differences was biologically relevant, but I could not capture community-level differences using my coarse measure of macroinvertebrate abundance. A more accurate estimate of macroinvertebrate abundance would incorporate multiple samples, collected in open water, emergent vegetation, and submergent vegetation zones because macroinvertebrate presence and abundance vary with aquatic vegetation (Gregg and Rose 1985). Or, perhaps a different metric such as macroinvertebrate biomass would have yielded different results (Scrimgeour et al. 2001, Patoine et al. 2000). It is also possible that my macroinvertebrate collections (late May and late June) were ill-timed to capture differences in macroinvertebrate community composition between burned and unburned wetlands.

2.4.3 Scaup abundance

Burn had no detectable effect on scaup IBPs on wetlands in our study area. This result is inconsistent with the trophic enrichment hypothesis, which predicted that waterbird species that feed on macroinvertebrates and show a preference for Amphipoda would be more abundant on burned wetlands. However, it was unsurprising given the similar macroinvertebrate community composition and Amphipoda abundance and percent composition in burned and unburned wetlands. Further, wetland nutrients and productivity (TP and Chl-*a*) were only higher in burned wetlands in May, whereas scaup were surveyed in June (approximately one month later) when the majority of scaup would have recently settled at nesting sites in the Northwest Territories (Anteau et al. 2020).

Recently burned wetlands appeared to provide adequate nesting habitat for scaup. In the Northwest Territories, scaup typically nest in dense sedge cover 1 m from water, though emergent vegetation is sometimes used (Anteau et al. 2020). Despite the recent wildfire, burned ponds in our study area generally had substantial shoreline and emergent vegetation in the years following the fire (M. S. Tanguay, University of Saskatchewan, personal observation; Figure A.3, Figure A.**5**). This mismatch between peak fire impacts and the settling date of scaup, and the seemingly adequate nesting habitat available on and around burned ponds the spring following a wildfire, suggests that overall, settling scaup are unlikely to be impacted by forest fires that occurred the previous summer. This apparent resilience of scaup to fires is consistent with a boreal-wide, population-level study that found no immediate or lagged effects of fire on duck abundance (Lewis et al. 2016).

Importantly, my inability to detect an effect of recent forest fire on scaup pairs is not conclusive evidence that wildfires do not impact breeding scaup for several reasons. First, my uncorrected metric of scaup abundance may be inaccurate because it does not account for imperfect detection. However, detection was likely high, as it was for breeding scoters and scaup on boreal wetlands in Alaska (91% for scoters and 90% for scaup; Lewis et al. 2015), which reflects the tendency of scoter and scaup to use the centers of large waterbodies—often the most visible zones during aerial surveys. Second, I cannot rule out the potential effects of helicopter disturbance on my survey results. For example, helicopter disturbance can sometimes cause waterbirds to flush from their initial positions and land elsewhere on the same wetland or a nearby wetland, which could affect survey results. Third, I do not know pre-fire scaup abundance, so it is possible that fire did have an important effect on scaup pairs that the after-only study design I applied was unable to detect. Lastly, scaup pair abundance in June may be driven more by other factors such as available nesting habitat or competition among pairs for breeding sites than by wetland productivity, as I measured it, meaning scaup abundance may be a weak metric for testing the trophic enrichment hypothesis. Perhaps duckling abundance or survival would be more sensitive and reflective of any changes in wetland productivity since ducklings are produced on wetlands.

2.4.4 Conclusions

Recently burned wetlands had significantly higher concentrations of TP and Chl-*a* than unburned wetlands in May in the years immediately following wildfire. However, these heightened nutrient and productivity levels did not appear to translate into a significant shift in wetland macroinvertebrate community composition nor an increased abundance or dominance of Amphipoda. Scaup IBPs were similar on burned and unburned wetlands as well, possibly because breeding scaup pairs in June are not reflective of increased wetland productivity, or because changes in TP and Chl-*a* were restricted to the early spring period and did not extend into June when the majority of scaup settled on our study ponds. Such a temporal mismatch between fire impacts and scaup arrival seems likely given the return to similar TP and Chl-*a* levels observed on burned and unburned wetlands in June. Although, it is possible that much of the TP and Chl-*a* observed in May but not June could have been incorporated into macroinvertebrates by the time scaup pairs arrived, such that the trophic enrichment hypothesis is supported in June.

The limited effect of wildfires on abundance of breeding scaup pairs and their macroinvertebrate prey one to two years post-fire on our study wetlands is consistent with similar studies conducted in the boreal forest of interior Alaska and the Mackenzie River Delta region. These studies found that wetland water chemistry and waterbird abundance were unaffected by moderate to severe wildfires during the three years immediately following the fires (Haszard and Clark 2007, Lewis et al. 2014, 2016). In combination with previous research, our results suggest that wetland ecosystems in the northwestern boreal forest are resilient to and may even benefit from moderate to severe fires under current climate conditions. However, fire impacts on aquatic ecosystems are likely to intensify as the climate warms, such that this resilience may not be maintained in coming decades.

Mean annual temperatures in the Canadian boreal are predicted to be 4–5°C higher by 2100 (Price et al. 2013). Wildfire occurrence is predicted to increase 25% in Canada by 2030 and 75% by the end of the 21st century in response to increased drought (Wotton et al. 2010). Warming might impact phytoplankton biomass via reduced ice cover, thawing permafrost, and increased water temperatures, enhancing algal growth, productivity, and nutrient cycling (Ogbebo et al. 2009). However, eutrophication and associated phytoplankton blooms can negatively impact water quality in aquatic ecosystems by reducing water transparency and oxygen content (Ogbebo et al. 2009). Warmer temperatures can be especially detrimental in areas of discontinuous permafrost like the Ramparts, where even small increases in ground heating could cause substantial changes to wetland hydrology (Rouse 2000). Further, wildfires might contribute to permafrost thaw by removing insulating soil layers and exposing soil to greater warming (Riordan et al. 2006). Thus, continued monitoring of the impacts of climate warming and associated increases in wildfires on boreal wetlands is critical to identifying and mitigating future threats to these ecosystems.

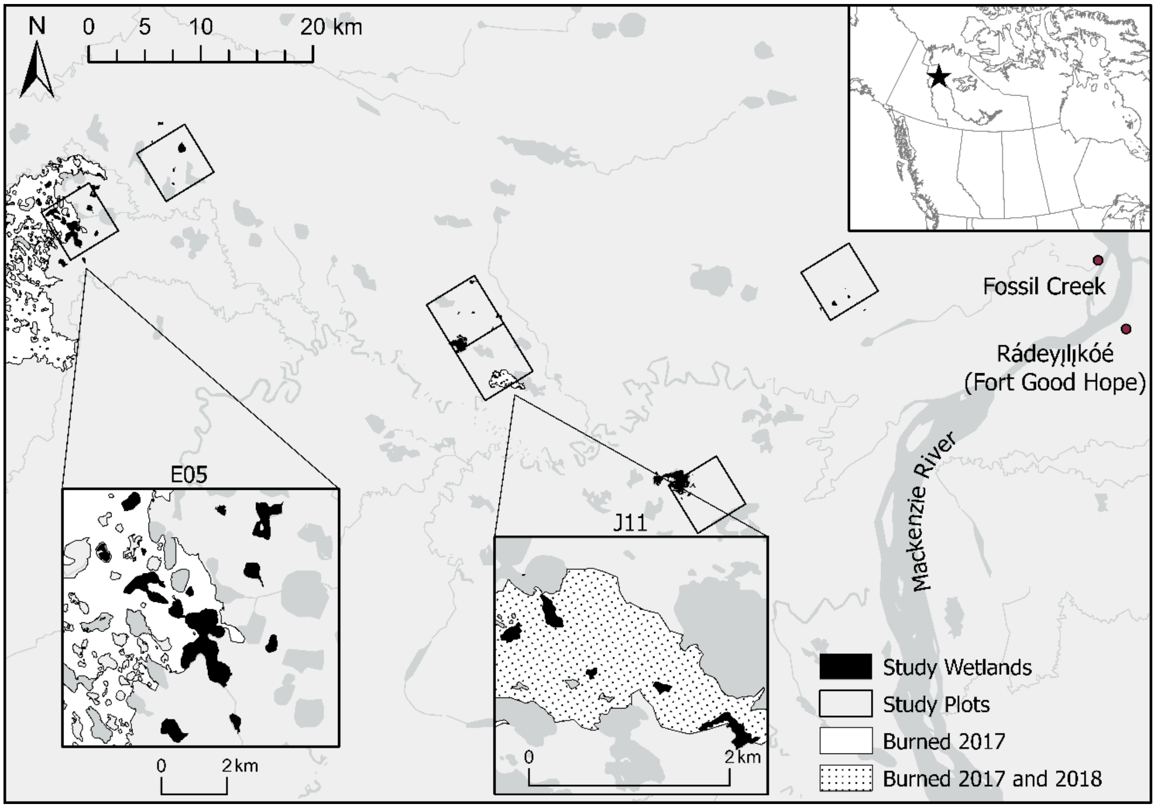

Figure 2.1. Map of the Ramparts River wetlands study area. I collected data from 52 unique wetlands, 11 of which were in recently burned areas (n = 6 in E05, n = 5 in J11), and 13 of which were located near Fossil Creek and sampled in June 2017 only.

Table 2.1. Phosphorous model selection table.

Model	k	logLik	Δ *AICc*	ω*i*
Year + Month + Burn + Burn:Month	9	-100.19	0.00	0.82
Year + Month + Burn + Burn:Month + SizeClass + Burn:SizeClass	13	-97.13	3.66	0.13
Year + Month + Burn	8	-104.85	6.97	0.03
Year + Month	7	-106.34	7.66	0.02
Year + Month + Burn + SizeClass + Burn:SizeClass	12	-101.60	10.07	0.01
Null	4	-124.70	37.73	0.00

Note: All candidate models include wetland nested within plot as a random effect (the null model contains only the random effect).

Table 2.2. Estimated marginal mean phosphorous (95% confidence interval) in burned and unburned wetlands in May and June (µg/L). P-values are for within-month contrasts between burned and unburned wetlands.

	Unburned	Burned	Contrast p-value
May	22.18 (10.78, 33.57)	43.06 (15.28, 70.85)	0.0915
June	16.69 (8.55, 24.84)	17.89 (6.35, 29.43)	0.7943

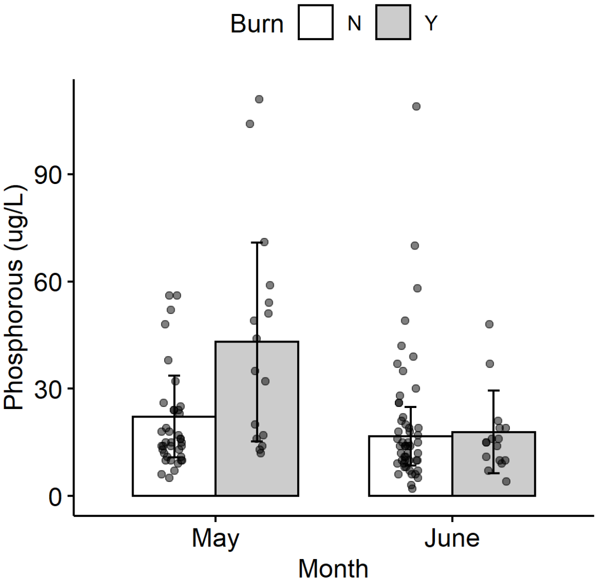

Figure 2.2. Estimated marginal mean phosphorous in burned and unburned wetlands in May and June. Error bars are 95% confidence intervals.

Table 2.3. Chlorophyll-*a* model selection table.

Model	k	logLik	Δ *AICc*	ω*i*
Year + Month + Burn + Burn:Month	8	-132.18	0.00	0.91
Year + Month + Burn + Burn:Month + SizeClass + Burn:SizeClass	12	-130.45	6.17	0.04
Year + Month + Burn	7	-136.63	6.61	0.03
Year + Month	6	-138.37	7.83	0.02
Year + Month + Burn + SizeClass + Burn:SizeClass	11	-134.98	12.76	0.00
Null	3	-148.40	21.35	0.00

Note: All candidate models include plot as a random effect (the null model contains only the random effect).

Table 2.4. Estimated marginal mean chlorophyll-*a* (95% confidence interval) in burned and unburned wetlands in May and June (µg/L). P-values are for within-month contrasts between burned and unburned wetlands.

	Unburned	Burned	Contrast p-value
May	3.27 (1.85, 4.69)	7.39 (2.87, 11.91)	0.0476
June	2.86 (1.90, 3.82)	2.56 (1.00, 4.13)	0.6694

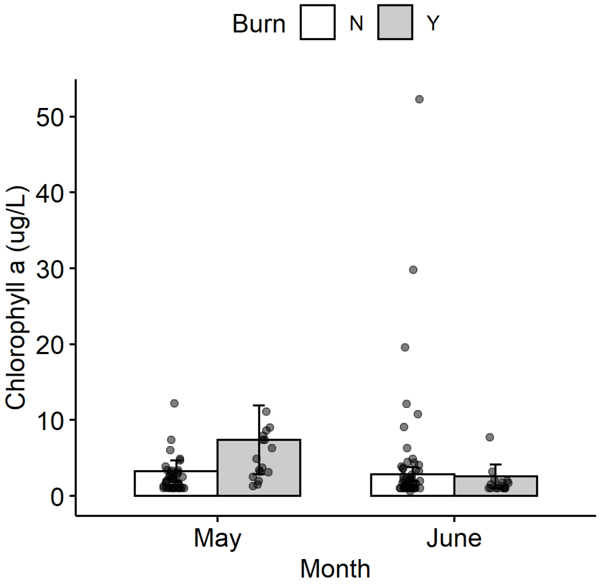

Figure 2.3. Estimated marginal mean chlorophyll-*a* in burned and unburned wetlands in May and June. Error bars are 95% confidence intervals.

Table 2.5. Nitrogen model selection table.

Model	k	logLik	Δ *AICc*	ω*i*
Year	6	-12.35	0.00	0.59
Year + Burn	7	-12.00	1.55	0.27
Year + Month + Burn + Burn:Month	9	-11.00	4.20	0.07
Null	4	-16.99	4.89	0.05

Notes: All candidate models include wetland nested within plot as a random effect (the null model contains only the random effect). Models ranking below the null were excluded from the table.

Table 2.6. Colour model selection table.

Model	k	logLik	Δ *AICc*	ω*i*
Month	5	-287.76	0.00	0.55
Month + Burn	6	-287.45	1.86	0.22
Null	4	-290.24	2.58	0.15

Notes: All candidate models include wetland nested within plot as a random effect (the null model contains only the random effect). Models ranking below the null were excluded from the table.

Figure 2.4. Separation of macroinvertebrate taxa by burn along axes 1 and 2 (panel a), 1 and 3 (panel b), and 2 and 3 (panel c) with 95% confidence interval ellipses for unburned (hollow points, dotted lines) and burned wetlands (solid points and lines).

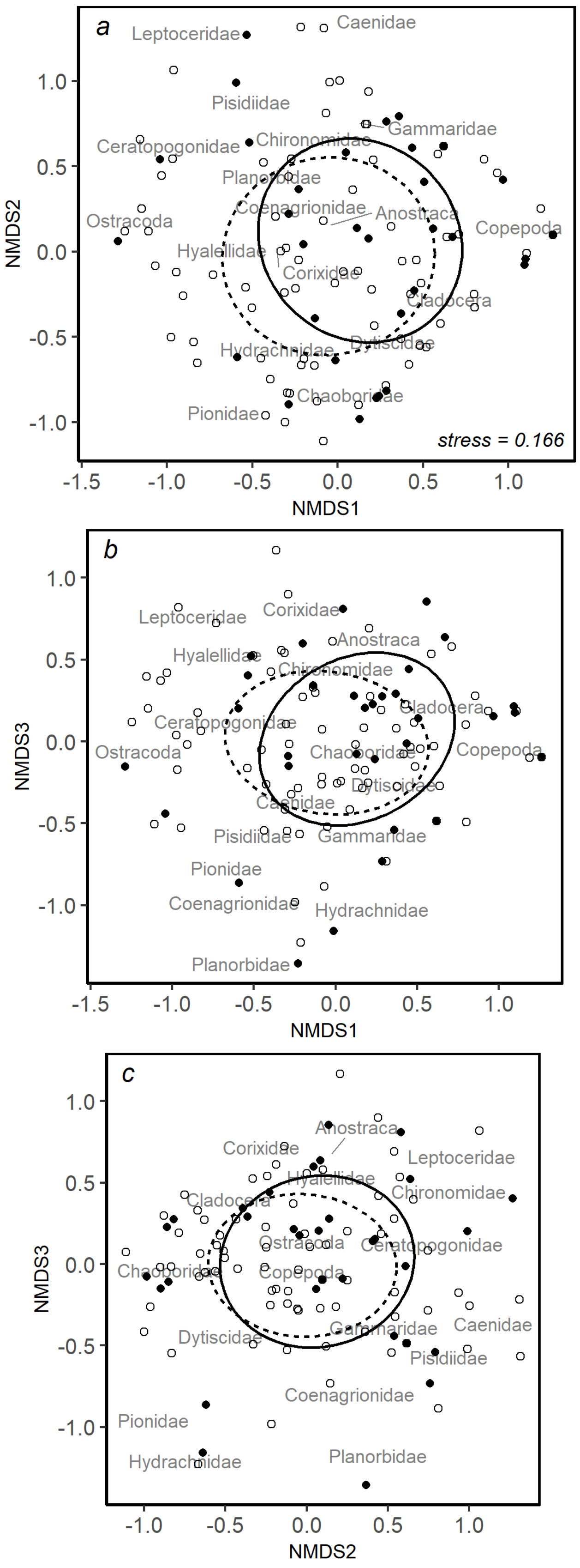

Table 2.7. Mean relative abundance per sample (with standard errors and 95% confidence intervals) and overall percent composition of observed macroinvertebrate taxa, based on pooled data from 2018 and 2019, in order of relative abundance on unburned wetlands.

	UNBURNED				BURNED			
Taxa	Mean	SE	95%CI	%Comp	Mean	SE	95%CI	%Comp
Copepoda	85.1	25.2	34.6, 135.5	44.0	40.8	17.2	6.4, 75.2	14.3
Cladocera	72.5	31.3	9.9, 135.2	37.6	205.2	140.8	-76.4, 486.8	72.1
Anostraca	14.0	8.1	-2.2, 30.2	7.2	10.2	5.0	0.2, 20.3	3.6
Chaoboridae	8.3	1.7	4.9, 11.7	4.3	5.7	2.4	0.9, 10.5	2.0
Amphipoda	7.3	1.9	3.5, 11.1	3.7	1.9	1.0	-0.1, 3.8	0.7
Gammaridae	3.9	1.3	1.2, 6.6	2.0	0.9	0.4	0.1, 1.7	0.3
Hyalellidae	3.4	1.4	0.5, 6.2	1.7	1.0	0.6	-0.2, 2.2	0.4
Chironomidae	2.9	1.2	0.6, 5.3	1.5	13.1	8.8	-4.4, 30.7	4.6
Caenidae	0.5	0.3	-0.1, 1	0.2	0.1	0.0	0, 0.1	0.0
Lynceidae	0.5	0.5	-0.5, 1.5	0.3	0.0	0.0	0, 0	0.0
Pionidae	0.4	0.1	0.1, 0.6	0.2	0.4	0.3	-0.1, 0.9	0.1
Pisidiidae	0.4	0.3	-0.1, 1	0.2	0.5	0.4	-0.2, 1.3	0.2
Dytiscidae	0.2	0.1	0, 0.5	0.1	0.0	0.0	0, 0.1	0.0
Ostracoda	0.2	0.0	0.1, 0.3	0.1	0.1	0.0	0, 0.1	0.0
Leptoceridae	0.1	0.1	0, 0.3	0.1	0.1	0.1	-0.1, 0.3	0.0
Ceratopogonidae	0.1	0.0	0, 0.2	0.1	0.8	0.7	-0.7, 2.3	0.3
Corixidae	0.1	0.1	0, 0.3	0.1	0.1	0.1	0, 0.3	0.0
Coenagrionidae	0.1	0.1	0, 0.2	0.0	0.2	0.1	-0.1, 0.4	0.1
Planorbidae	0.1	0.1	0, 0.2	0.0	0.1	0.0	0, 0.1	0.0
Baetidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Siphlonuridae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Glossosomatidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Hydropsychidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Phryganeidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Chrysomelidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Culicidae	0.0	0.0	0, 0.1	0.0	0.1	0.1	-0.1, 0.2	0.0
Empididae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Simuliidae	0.0	0.0	0, 0	0.0	0.1	0.1	-0.1, 0.2	0.0
Tipulidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Notonectidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Corduliidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Arrenuridae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Eylaidae	0.0	0.0	0, 0.1	0.0	0.0	0.0	0, 0	0.0
Hydrachnidae	0.0	0.0	0, 0.1	0.0	0.0	0.0	0, 0.1	0.0
Lebertiidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Limnesiidae	0.0	0.0	0, 0	0.0	0.1	0.1	-0.1, 0.3	0.0
Mideidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Mideopsidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Oxidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Physidae	0.0	0.0	0, 0.1	0.0	0.0	0.0	0, 0	0.0
Valvatidae	0.0	0.0	0, 0.1	0.0	0.0	0.0	0, 0.1	0.0

	UNBURNED				BURNED			
Taxa	Mean	SE	95%CI	%Comp	Mean	SE	95%CI	%Comp
Glossiphoniidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Enchytraeidae	0.0	0.0	0, 0	0.0	4.6	4.6	-4.5, 13.7	1.6
Naididae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Tardigrada	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0	0.0
Cicadellidae	0.0	0.0	0, 0	0.0	0.0	0.0	0, 0.1	0.0
Nematoda	0.0	0.0	0, 0	0.0	0.1	0.0	0, 0.1	0.0

Table 2.8. Model selection table for indicated breeding scaup pairs on study wetlands in June 2019.

Model	k	logLik	Δ *AICc*	ω*i*
Depth + N-P	5	-56.32	0.00	0.55
Depth + N-P + Burn	6	-55.48	1.46	0.26
Null	3	-60.20	2.18	0.19

Note: All candidate models include plot as a random effect and the log of study wetland surface area as an offset (the null model contains only the random effect and the offset).

CHAPTER 3. MULTI-SCALE LANDSCAPE EFFECTS ON OCCURRENCE OF BREEDING SCOTERS (*MELANITTA* SPP.) AND SCAUP (*AYTHYA* SPP.) IN CANADA'S BOREAL FOREST

3.1 Introduction

Species distributions are typically assumed to reflect variation in habitat quality, and, species-based habitat models, by identifying the biotic and abiotic features that drive habitat use, allow resource managers to predict species distributions and to prioritize habitats for conservation (Jones 2001, Johnson 2007, Pressey et al. 2007, Kuhn et al. 2011). For example, higher densities of breeding birds in the northern hemisphere are frequently associated with higher-quality habitats, particularly in areas undisturbed by human activity (Bock and Jones 2004). As such, studies of avian habitat selection have clear conservation applications, and the literature is extensive, covering a range of species, life cycle phases, and geographic areas (De La Cruz et al. 2014, Herse et al. 2017, Fiss et al. 2021). Our understanding of the drivers of species distributions, however, is often incomplete, mainly because optimal analytical and design approaches, such as multi-scale models that incorporate each covariate at spatial scales relevant to the focal species, are not always realized (Wiens 1989, Graf et al. 2005).

The scale of effect for a covariate, defined as the spatial scale at which the covariate best predicts a species' response such as abundance or occurrence, is often species- and variable-dependent (Wiens 1989, Holland et al. 2004, McGarigal et al. 2016). Therefore, a common approach to addressing scale in species-landscape association studies is to identify the scale of effect for each covariate independently, and then combine the covariates into a multi-scale, multi-variable model (e.g., Timm et al. 2016, Wan et al. 2017, Bosco et al. 2019). Models of this type often outperform single-scale equivalents (Boscolo and Metzger 2009, Kuhn et al. 2011, Timm et al. 2016); for example, multi-scale habitat selection models for Mexican spotted owls (*Strix occidentalis lucida*) explained a greater proportion of deviance and had better predictive performance than equivalent single-scale models (Timm et al. 2016).

The boreal forest of North America (hereafter the boreal), a region spanning almost 6 million km^2, contains the largest intact forest and wetland blocks on the planet and supports

1.65–3 billion breeding birds annually (Wells and Blancher 2011, Badiou et al. 2013). However, because of habitat loss and degradation, as well as ongoing changes in climate, the continental population of boreal-breeding birds declined by 33% between 1970 and 2017 (Wells et al. 2016, Rosenberg et al. 2019). Species that are uniquely dependent on boreal habitat, such as Rusty Blackbird (*Euphagus carolinus*), Olive-sided Flycatcher (*Contopus cooperi*), and Canada Warbler (*Cardellina canadensis*), have shown especially steep declines (Wells et al. 2016, Rosenberg et al. 2019). Therefore, the need for boreal conservation is urgent—habitat alteration is widespread in the region and expected to intensify (Wells 2011, Badiou et al. 2013).

With respect to North American populations of waterfowl, the western boreal forest (western boreal) is particularly important, supporting 12–15 million breeding ducks of 23 species including multiple species with more than half their population breeding in the boreal (Slattery et al. 2011). The four most abundant boreal-breeding ducks in Canada are below continental conservation targets, or 1970s population levels (Slattery et al. 2011). Despite these missed population targets, our understanding of drivers of breeding waterfowl distributions in the boreal remains limited, especially for sea ducks (tribe Mergini), such as white-winged scoter (*Melanitta deglandi*) and surf scoter (*Melanitta perspicillata*), but also for scaup (*Aythya* spp.; Prairie Habitat Joint Venture 2014, Sea Duck Joint Venture Management Board 2014). The boreal supports 80% and 67% of the North American breeding populations of scoter and scaup, respectively, both of which have declined and remain below population objectives set out by the North American Waterfowl Management Plan (Slattery et al. 2011, North American Waterfowl Management Plan 2012, U.S. Fish and Wildlife Service 2019). Such declines are likely due in part to climate-related habitat changes on their boreal breeding grounds (Corcoran et al. 2009, Drever et al. 2012). However, studies of habitat association for breeding scoter and scaup in the boreal are limited, and primarily focus on presumed breeding locations or broad-scale survey plots or transects (Décarie et al. 1995, Takekawa et al. 2011, M. Ross [*unpublished report*]) rather than on individual ponds (but see Lewis et al. 2015). Notably, to my knowledge, no existing studies use a multi-scale approach, in which environmental covariates are scale-optimized and combined into a multi-scale model. Further, several studies use observations from surveys performed before late-nesting species like scoter and scaup have settled in nesting areas (Adde et al. 2021, e.g., Lemelin et al. 2010, Barker et al. 2014). Therefore, fundamental uncertainties surrounding relationships between landscape characteristics and breeding scoter and scaup distributions in the boreal continue to persist.

The objective of this research is to identify landscape-level correlates of breeding scoter and scaup occurrence on ponds during the early nesting period using a multi-scale approach that addresses the scale-dependency of habitat selection. Specifically, I focus on a two-part research question: (1) which landscape characteristics are associated with scoter and scaup occurrence on boreal ponds, and (2) at which scale do these associations occur? To address these questions, I use scale-optimized landscape covariates and optimally timed observations of breeding white-winged scoter, surf scoter, and scaup pairs to evaluate the occurrence of these species across boreal ponds within a key waterfowl area in the Central Mackenzie Valley of the Northwest Territories (Latour et al. 2008, Reed et al. 2020).

Previous studies suggest that – in a given study area – scoter and scaup prefer large ponds during the breeding season, possibly due to optimal food resources often associated with increasing pond size (Toft and Trauger 1982, Fast et al. 2004, Haszard 2004, Walsh et al. 2006, Lewis et al. 2015). For example, scoter and scaup densities were higher in 5 x 5 km plots containing more waterbodies and greater waterbody area, up to a threshold, in a habitat selection study conducted across the northern boreal (M. Ross, *unpublished report*). These associations are likely explained by the fact that boreal-breeding scoter and waterfowl species typically use several wetlands during the reproductive period to meet the differing energetic needs of the nesting and brood-rearing period (Krapu 1974, Dwyer et al. 1979, Haszard 2004, Baldassarre and Bolen 2006). Likewise, a study conducted in boreal Alaska reported that pond size was the strongest predictor of scoter and scaup brood occurrence, possibly linked to improved foraging habitat (Lewis et al. 2015). Accordingly, under the principles of this foraging habitat limitation hypothesis, I predicted that scoter and scaup would be more likely to occur on larger ponds surrounded by more waterbodies and waterbody area.

Lastly, I tested the non-mutually exclusive prediction that scoter and scaup would be more likely to occur on ponds surrounded by more nesting habitat. For scoters, I characterized nesting habitat as the amount of coniferous forest cover and shoreline, as scoters nest in dense, forested cover, often on islands (Safine 2005, Brown and Fredrickson 2020). I characterized scaup nesting habitat as the amount of shoreline habitat, as scaup nest along waterbody margins (Corcoran et al. 2007, Anteau et al. 2020). Finally, scales of effect often vary by species and habitat components and are generally assumed to be linked to movement distances for waterfowl and other organisms (Webb et al. 2010, Beatty et al. 2014, Jackson and Fahrig 2015, McGarigal et al. 2016). Under the scale dependency hypothesis, I predicted that the scale of effect of landscape covariates would be larger for scoters than for scaup because breeding scoters have larger home ranges than breeding scaup (S. Gilliland, CWS, *unpublished data*; Anteau et al. 2020).

3.2 Methods

3.2.1 Study area and waterfowl surveys

I evaluated landscape correlates of breeding scoter and scaup pair occurrence within Ts'udé Nilı̨né Tuyeta, a 10,060 km² Indigenous Protected Area with cultural and ecological importance to the Sahtú Dene and Métis, particularly the K'asho Got'ine Dene and Métis of Fort Good Hope, located in the Central Mackenzie Valley of the Northwest Territories (NT). Specifically, we focused on a 4,692 km^2 area within Ts'udé Nilı̨né Tuyeta that is known to support high densities of waterfowl—the Ramparts River wetlands (hereafter the Ramparts; Figure 3.1). The eastern edge of the Ramparts is 35 km west of Fort Good Hope, NT, at 66°15'N, 130°00'W (Latour et al. 2008). The area surrounds the lower Ramparts and upper Ontaratue Rivers. It contains a high density of lakes, ponds, and wetlands, where wetland types include open black spruce (*Picea mariana*) bogs, ericaceous shrublands, floating bogs, and sedge wetlands (Latour et al. 2008). Past breeding pair surveys indicated that scoter and scaup were the most abundant waterfowl species in the Ramparts, representing 1% of the estimated Canadian populations of nesting scoter and scaup (Ducks Unlimited Canada 1997).

To index breeding scoter and scaup pair occurrence on ponds during the early nesting period, I used breeding pair survey data for white-winged scoter, surf scoter, and scaup collected by the Canadian Wildlife Service (CWS) in the study area June 10–16, 2017. To select dates for this survey, CWS researchers determined arrival and departure dates of scaup and scoters from satellite telemetry data, and nest initiation dates from brood surveys by back-dating from brood age. The telemetry data was accessed in 2016 from the Sea Duck Joint Venture's satellite telemetry database and included locations recorded 1 April to 1 September for white-winged scoter, surf scoter, and black scoter in eastern and western North America. Brood data was collected during brood surveys conducted in the early 1990's and 2007 in Quebec and Labrador. The CWS survey was structured using a 5 km x 5 km grid of cells overlaid across the Ramparts study area, 20 of which (i.e., survey plots) were selected to be surveyed. CWS used a stratified-random sampling approach to select these survey plots to ensure that they were representative of the range of habitats and predicted breeding scoter pair abundance in the study area (where predicted pairs were based on a previous habitat model for scoters breeding in Labrador and Northern Quebec; Roy et al. *unpublished data*). The final sample of survey plots covered 500 km^2 (11%) of the study area and had adequate spatial coverage of the Ramparts to ensure that subsequent analyses could detect spatial patterns that might be present but not explained in prior habitat models.

CWS survey crews, comprised of three trained biologists, conducted aerial surveys of the 20 plots by a Bell 407 helicopter using a double dependent observer approach with a single front seat observer and two rear seat observers, allowing them to measure detectability (Nichols et al. 2000). The front-seat observer reported observations to the rear-seat observers, who then reported any observations missed by the front-seat observer. The helicopter flew 15–50 m above ground from a hover to 100 km/h, while observers surveyed all water within survey plots; where ponds were intersected by a plot border, they were only partially surveyed. Observers recorded GPS-linked observations of ducks. For each observation, observers recorded the number of males and females, which were entered as pairs if they were deemed as such, or large groups if they were not deemed to be local breeders. Surveys did not occur in heavy precipitation, low visibility, or winds exceeding 40 km/h.

3.2.2 Data processing

To select the study ponds for the present study, I used ArcGIS 10.7.1 (Environmental Systems Research Institute, Redlands, California, USA) and the 1:50,000 waterbody layer from Natural Resource Canada's CanVec topographical map reference (v 6.18). I defined study ponds as all ponds within the 20 surveyed plots, excluding those that were partially surveyed. To calculate the total number of scoter and scaup pairs per study pond, I converted raw counts of white-winged scoter, surf scoter, lesser scaup, and unidentified scaup (presumed to be lesser scaup since scaup counts in the boreal are ~89% lesser scaup, and of the speciated scaup observed, all were lesser scaup [Afton and Anderson 2001; M. Ross, *unpublished report*]) to an index of indicated breeding pairs (hereafter IBPs). I took the number of IBPs to be the number of males observed, for all observations composed of four or fewer males (Gilliland et al. 2009). Observations containing five or more males were excluded from analyses because individuals in groups of this size may not be local breeders (Brook et al. 2012). I overlayed IBPs onto the study pond layer and excluded any pairs associated with partially surveyed ponds. I assigned each pair to the nearest study pond and calculated the total number of pairs of surf scoter, white-winged scoter, and pooled scaup (lesser scaup and unidentified scaup) associated with each study pond.

Using ArcGIS 10.7.1, I extracted pond size and a set of landscape composition variables identified in the literature as potential predictors of scoter distributions. Data sources included Natural Resource Canada's 1:50,000 scale CanVec topographical map reference (v 6.18) and Ducks Unlimited Canada's Hybrid Wetland Layer (HWL). The HWL is a raster layer that classifies the Canadian land base into three broad cover types (water, wetlands, and upland) using a 25 m pixel resolution (N. Jones, *unpublished report*). More specifically, I extracted the total number and area of waterbodies (WB_Count, WB_Area), the total number and length of watercourses (WC_Count, WC_Length), and the total shoreline length within buffers surrounding pond perimeters from CanVec layers (see below for explanation of buffer sizes). Within the same buffers, I extracted the proportion of the buffer covered by water, wetland, and dense, sparse, and open coniferous forest from the Hybrid Wetland Layer (H20_Prop, WL_Prop, CD_Prop, CS_Prop, CO_Prop). I also extracted the surface area of each study pond (SP_Area) from the CanVec waterbody layer. Lastly, I calculated a shoreline density index (SDI) as a measure of shoreline complexity within buffers using the following formula (Hutchinson 1957):

$$\mathrm{SDI} = \frac{\text{total shoreline length}}{2\pi\sqrt{\left(\frac{\text{average waterbody area}}{\pi}\right) \times \text{total number of waterbodies}}} \quad \text{................(3.1)}$$

Using this index, more complex shorelines had SDI values greater than one, less complex shorelines had values below 1, and values of 1 contained the total shoreline length that one would expect if all waterbodies in the buffer were perfect circles. I normalized WB_Count, WB_Area, WC_Count, and WC_Length by buffer area because buffers varied in size. In other words, I entered these variables into models as ratios (value divided by buffer area). I calculated the total coniferous forest cover (CF_Prop) in buffers by taking the sum of dense, sparse, and open coniferous forest. Based on breeding scoter and scaup movement patterns, I extracted these landscape variables within 210 m, 438 m, 1085 m, and 1960 m of pond perimeters (Table 3.1).

3.2.3 Statistical analyses

The study taxa occurred on a low percentage of the 1,288 study ponds (rates of occurrence were 1.3%, 1.7%, and 16.1%, for white-winged scoter, surf scoter, and scaup, respectively). Therefore, for my primary analysis, I chose to (1) pool white-winged scoter and surf scoter IBPs to increase the power to detect landscape effects on scoters, and (2) analyze the presence/absence of scoters and scaup on study ponds, rather than abundance. I converted pair abundance data to a binary response variable (0 if total IBP = 0; 1 if total IBP ≥ 1) and used mixed-effect logistic regression models to account for the non-independence of study ponds from the same survey plot and the binary nature of our response variable (R package *glmmTMB* version 1.0.2.1, Brooks et al. 2017). I chose not to account for imperfect detection of scoter and scaup pairs because analyses by the CWS, including the Ramparts survey data and additional survey data from the northern boreal, indicate that the total detection from the helicopter (two to three observers) was high (~98%; Christian Roy, personal communication). I analyzed scoter and scaup occurrence in identical but separate analyses. Additionally, I performed similar regression analyses on the original pair abundance data to gain preliminary insights into potential parallels between patterns of occurrence and abundance for scoter and scaup pairs in the study area. Abundance models were mixed-effect negative binomial regression models suitable for analyzing overdispersed count data collected from spatially clumped study units (Brooks et al 2017).

3.2.3.1 Scales of effect

Before selecting landscape variables for inclusion in a global model for each species group (i.e., pooled scoter and pooled scaup; hereafter species), I identified the scale of effect for each variable for each species. I determined the optimal scale for a given variable by comparing *AICc* support for biological null models containing the variable across the four spatial scales (R package *MuMIn* version 1.43.17, Bartoń 2020). More specifically, all models included survey plot as a random effect and SP_Area as a fixed effect in addition to the landscape variable of interest, and I compared support for four models for each variable, using one model for each scale of measurement (210 m, 438 m, 1085 m, 1960 m).

3.2.3.2 Multi-scale multi-variable models

I selected variables for inclusion in a global multi-scale, multi-variable model for each species by considering sample-size limitations first, followed by correlations and variance inflation factors (VIFs, Zuur et al. 2010). I was limited to six variables in scoter models because scoters occurred on only 31 study ponds, and the minimum recommended events per predictor variable for logistic regression is five (Vittinghoff and McCulloch 2007). Therefore, I selected a set of landscape variables to include in the global scoter and global scaup models believed to be most influential based on current literature: WB_Count, WB_Area, WL_Prop, CF_Prop, and SDI. Pearson correlation coefficients and VIFs for this set of variables, including SP_Area, were below the standard cut-off values of 0.6 and 2.5, respectively (maximum r = 0.35; maximum VIF = 1.5), at both scoter and scaup scales of effect (Allison 1999, Zuur et al. 2010). I calculated z-scores for SP_Area and the selected landscape variables to enable direct comparison of variable coefficients. I confirmed that the global model for each species met the assumptions of logistic regression models (R package *DHARMa* version 0.3.3.0, Hartig 2021). I did not consider curvilinear effects because model diagnostics indicated that the models' residuals were linear on the logit scale (Osborne 2015).

I also determined the relative importance of pond size and landscape variables in predicting scoter and scaup occurrence by calculating the sum of Akaike weights across all models containing a given variable (function *importance* R package *MuMIn* version 1.43.17, Bartoń 2020). I calculated importance values from a candidate model set composed of all possible variable combinations (2^6 or 64 unique combinations), where I included each covariate in an equal number of models (function *dredge* R package *MuMIn* version 1.43.17, Bartoń 2020). In addition, I calculated model-averaged coefficients for all covariates included in the 95% confidence set of models (function *model.avg* R package *MuMIn* version 1.43.17, Bartoń 2020). I used the Hosmer-Lemeshow test to evaluate the fit of the top model for each species (function *HLtest* R Package *vcdExtra* version 0.7.5, Friendly et al. 2021), and I calculated the predictive power of these top models using two pseudo-R^2 measures (McFadden and McKelvey-Zavoina; function *PseudoR2* R Package *DescTools* version 0.99.41, Signorell et al. 2021). I performed all analyses using Program R version 3.6.2 (R Core Team 2019).

3.3 Results

3.3.1 Pond size and landscape effects

3.3.1.1 Scoter

Scoter pairs were more likely to occur on larger ponds (SP_Area β = 0.85, 95% CI: 0.55, 1.15; Table 3.2; Figure 3.2) surrounded by more waterbody area/km^2 within 1960 m of pond perimeters (WB_Area β = 0.69, 95% CI: 0.22, 1.17), fewer waterbodies/km^2 within 438 m (WB_Count β = -1.00, 95% CI: -1.71, -0.29) and less complex shorelines within 1085 m (SDI β = -0.74, 95% CI: -1.34, -0.14). Importance values and 95% confidence intervals surrounding parameter estimates indicate that SP_Area was the most important variable (importance = 100%), followed by WB_Count_438 (importance = 96%), which was closely followed by WB_Area_1960 and SDI_1085 (importance = 89% and 86%, respectively). The proportion wetland cover and coniferous forest cover surrounding ponds did not influence scoter occurrence (WL_Prop_1085 β = -0.12, 95% CI: -0.89, 0.66; CF_Prop_210 β = 0.03, 95% CI: -0.49, 0.55). Marginal and conditional R^2_{GLMM} estimates for the top scoter model were identical (0.45), suggesting that unmeasured variables that varied with survey plot explained no more variation in scoter occurrence probability than the variables of interest. The top model, with the random effect omitted, fit the data adequately (Hosmer-Lemeshow test p = 0.95). A supplementary analysis indicated a weak negative quadratic effect of pond size on scoter pair abundance where abundance peaked at 160 hectares (SP_Area β = 0.73, 95% CI: 0.54, 0.92; SP_Area^2 β = -0.02, 95% CI: -0.03, -0.01; Table B.6, Table B.7, Figure B.1). Additionally, the analysis showed that associations between scoter pair abundance and landscape composition were nearly identical to those described above for scoter pair occurrence.

3.3.1.2 Scaup

Scaup pairs were more likely to occur on larger ponds (SP_Area β = 0.80, 95% CI: 0.50, 1.10; Table 3.3; Figure 3.3) surrounded by more irregular shorelines within 210 m (SDI β = 0.10, 95% CI: -0.06, 0.27), less waterbody area/km^2 within 210 m (WB_Area β = -0.25, 95% CI: -0.45, -0.05), fewer waterbodies/km^2 within 438 m (WB_Count β = -0.20, 95% CI: -0.42, 0.02), and less wetland cover within 1960 m (WL_Prop β = -0.42, 95% CI: -0.73, -0.12). Importance values and 95% confidence intervals surrounding parameter estimates indicate that SP_Area was the most important variable (importance = 100%), followed by WL_Prop_1960 (importance = 90%) and WB_Area_210 (importance = 73%). WB_Count_438 and SDI_210 were much less important (importance = 34% and 14%, respectively). The proportion coniferous forest cover surrounding ponds did not influence scaup occurrence (CF_Prop β = -0.10, 95% CI: -0.44, 0.24). Marginal and conditional R^2_{GLMM} estimates for the top scaup model were 0.18 and 0.39, respectively, suggesting that the variables of interest and unmeasured variables that varied with survey plot explained a similar amount of variation in scaup occurrence probability. The top model, with the random effect omitted, fit the data adequately (Hosmer-Lemeshow test p = 0.53). A supplementary analysis indicated a negative quadratic effect of pond size on scaup pair abundance where abundance peaked at 150 hectares (SP_Area β = 0.51, 95% CI: 0.39, 0.62;

SP_Area^2 $\beta = -0.02$, 95% CI: -0.02, -0.01; Table B.8, Table B.9, Figure B.2). Additionally, the analysis showed that associations between scaup pair abundance and landscape composition were nearly identical to those described above for scaup pair occurrence.

3.3.2 Scales of effect

Three of the above variables had clear scales of effect: WB_Count (210/438 m), WB_Area (1085/1960), and SDI (1085; Table B.2). The average value of these scales of effect is 977 m. The other two variables (WL_Prop and CF_Prop) had equal support across three or more scales (210 m, 438 m, 1085 m, and 1960 m models had ΔAICc < 2). Similarly, scales of effect for scaup were clear for three variables (WB_Count [438 m], WB_Area [210 m], and SDI [210]; Table B.4) and ambiguous for two variables (WL_Prop and CF_Prop). Scales of effect for scoter and scaup pair abundance were identical to those identified above for pair occurrence.

3.4 Discussion

Landscape composition around breeding ponds correlated weakly with scoter and scaup occurrence, whereas pond size correlated strongly and positively with occurrence of both species. This suggests that scoter and scaup select breeding ponds based primarily on those ponds' characteristics rather than characteristics of the landscape surrounding them. One possible explanation for this finding is that these ducks perceive and base settling decisions on landscape characteristics at a larger spatial scale than that examined here (i.e., the home range); if this is the case, selected home ranges should contain the landscape needed to support the entire breeding season, from laying and incubation to brood-rearing (i.e., preferred amounts of aquatic and upland habitats). Thus, pond selection within the home range in mid-June in the Northwest Territories, when scoter and scaup pairs have already settled within their home ranges, may be based primarily on pond-level characteristics necessary to support the laying, incubation, and brood-rearing phases of the breeding season rather than landscape characteristics.

3.4.1 Pond size

The positive association between scoter and scaup occurrence and pond size was consistent with my prediction based on previous research demonstrating that scoter and scaup prefer large ponds during the breeding season in the boreal (Toft and Trauger 1982, Fast et al. 2004, Haszard 2004, Walsh et al. 2006, Lewis et al. 2015). Although larger ponds may be more likely to support scoter and scaup simply because they provide more habitat, the positive association between pond size and pair occurrence may also relate to a biologically based preference, in that pond size often correlates positively with pond depth and amphipod abundance (Fast et al. 2004), an important food item for these diving species (Anteau et al. 2020, Brown and Fredrickson 2020). Larger ponds, however, are limited in our study area, as in other boreal regions (e.g., interior Alaska; Lewis et al. 2015). Although scoter and scaup reached an occurrence probability of 100% on ponds of 120 ha and 82 ha, respectively (Figure 3.2, Figure 3.3), most of the study ponds (75%) were smaller than 1.6 ha (Figure B.3). Further, supplementary analyses revealed that scoter and scaup pair abundances were highest on 160 ha and 150 ha ponds, respectively (Table B.7, Figure B.1, Table B.7, Figure B.2). In addition, surveys of a subset of 39 ponds in the Ramparts study area in June 2018 and 2019 showed that amphipods occurred on only 17 ponds (44%) in early June. Lewis et al. (2015) suggested that the rarity of large ponds containing amphipods in the boreal forest likely leads to strong selection for these ponds by breeding scoters and scaup.

3.4.2 Landscape effects

3.4.2.1 Scoter

Although landscape effects were weak overall, the total number and area of waterbodies per km^2 (at the 438 and 1960 m scales, respectively) were the two most important landscape predictors of scoter occurrence, followed closely by shoreline density index at the 1085 m scale. As predicted, scoters were more likely to occur on ponds surrounded by more total waterbody area/km^2. This positive relationship is consistent with a preliminary study of breeding scoter habitat selection across 5 x 5 km plots in the northern boreal, whereby plots with more waterbody area had a higher density of scoter pairs, up to a threshold waterbody area (M. Ross, *unpublished report*). A similar effect occurred in the Hudson Bay Lowlands, where sites occupied by scoter pairs tended to be covered with a greater number of small (≤ 100 ha) waterbodies within 250 m than those plots without scoters (Brook et al. 2012). This finding provides some support for the foraging habitat limitation hypothesis, which predicted that scoters would be more likely to occur on larger ponds surrounded by more waterbodies and waterbody area.

Contrary to my expectations under the foraging habitat limitation hypothesis, scoters were more likely to occur on ponds surrounded by fewer waterbodies/km^2. In contrast to this finding, M. Ross (*unpublished report*) found that surf scoter pair density was higher in plots that contained more waterbodies up to a threshold number of waterbodies. Differences in scale may explain the unexpected negative association in our study – whereas I included waterbodies/km^2 in the scoter model at the 438 m scale, M. Ross (*unpublished report*) measured them at the much larger scale of 5 x 5 km plots. Takekawa et al. (2011) reported a similar scale-dependent discrepancy, where breeding surf scoters tended to settle in areas with fewer waterbodies within 2 x 2 km and more waterbodies within 4 x 4 km. This apparent discrepancy may arise because scoter use several wetlands during the reproductive period to meet the differing energetic and nutritional needs of egg-laying, incubation, and brood-rearing (Krapu 1974, Dwyer et al. 1979, Haszard 2004, Baldassarre and Bolen 2006). Thus, scoters may tend to settle in areas that contain many waterbodies at a coarse scale to increase the likelihood that they will have access to adequate resources throughout the various phases of the breeding season, from nesting to brood-rearing while simultaneously preferring that their primary breeding ponds be surrounded by more non-aquatic landscape containing many potential nesting spots.

Scoters were more likely to occur on ponds surrounded by less complex shorelines in our study area. Similarly, at the pond level in the Mackenzie Delta region of the boreal forest, white-winged scoter abundance was lower on ponds with irregular shorelines (Haszard 2004). I included shoreline complexity in scoter models mainly as a proxy for island habitat because scoters are known to nest on islands; as such, I expected to find a positive correlation between shoreline complexity and scoter occurrence probability (Brown and Fredrickson 2020). However, it is possible that shoreline index across the study area was driven more by differences in waterbody shapes and sizes than by the presence or absence of islands. For example, waterbodies with more irregular shorelines tend to have numerous bays that are too shallow for scoters to dive. As well, lower shoreline density indices may have corresponded with landscapes containing larger waterbodies, primarily because pond buffers that intersect several larger waterbodies will have lower shoreline density values than expected relative to the waterbody area they contain (M. Ross, *unpublished report*). Therefore, pond size preferences may have contributed to the apparent negative association with shoreline complexity since scoters prefer larger ponds.

Proportion wetland and coniferous forest cover had no significant effect on scoter occurrence. Existing scoter studies show mixed findings regarding wetland cover; in 5 x 5 km and 10 x 10 km forested plots in the boreal region of Quebec, there was no evidence of the use of open wetlands (meadow marshes, densely vegetated emergent marshes, riparian fens, or bogs, with <25% tree cover) by surf scoter pairs (Lemelin et al. 2010). Similarly, in Canada's eastern boreal forest and subarctic regions, 4 x 4 km plots surrounding presumed surf scoter nests contained little to no marsh or swamp cover (Perry et al. 2006). In contrast, white-winged scoter pair density increased with proportion wetland cover in forested and transitional northern boreal areas, up to a threshold proportion (M. Ross, *unpublished report*).

The limited effect of coniferous forest cover was more surprising than that of wetland cover. I expected a positive correlation between coniferous forest cover and scoter occurrence based on multiple studies. Scoters are known to nest in dense cover, and in the northern boreal forest, surf scoters nest in black spruce cover and their presence is positively associated with tree cover and negatively associated with treeline (Takekawa et al. 2011, Brown and Fredrickson 2020). Moreover, presumed surf scoter nest sites in Canada's eastern boreal forest and subarctic regions were located in 2 x 2 km plots that were 66% forest and 11% tundra, on average (Perry et al. 2006). Similarly, M. Ross (*unpublished report*) reported a positive linear relationship between forest cover and surf scoter pair density. M. Ross (*unpublished report*) also reported a negative quadratic relationship between plot-level coniferous forest cover and white-winged scoter pair density, noting that white-winged scoters were generally absent from open habitats with few trees.

Proportions of wetland cover and coniferous forest cover varied considerably across the study area (SD WL_Prop = 13.8–19.9%; SD CF_Prop = 15.7–18.7%; Table B.1), so a lack of variability cannot explain the unimportance of these variables. Instead, it may be that ponds in the Ramparts are surrounded by optimal amounts of wetland and coniferous forest cover for white-winged scoters. Mean percentages of wetland cover (21.5–22.7%) and coniferous forest cover (23.9–24.5%) surrounding Ramparts study ponds are similar to percentages associated with peak pair density in 5 x 5 km plots in the northern boreal (Table B.1; white-winged scoter density was highest when ~25% of the plot was covered by wetlands and 30% was covered by coniferous forest; M. Ross [*unpublished report*]). The ideal proportions of wetland and coniferous forest cover in the landscapes surrounding study ponds suggest that selection for these variables may be weak in the Ramparts. This contrasts with the patchy distribution of large ponds I observed in the Ramparts (i.e., those more likely to support scoters). Lewis et al. (2015) reported a similar availability of nesting habitat and scarcity of foraging ponds in the Yukon Flats of Alaska, which, like the Ramparts, consists of pristine boreal forest.

3.4.2.2 Scaup

Contrary to my prediction that total number and area of waterbodies per km^2 would be the most important predictors of scaup occurrence, proportion wetland cover was the most important, followed in order by total area and total number of waterbodies per km^2. I also expected these variables to correlate positively with scaup occurrence, but found that scaup were more likely to occur on ponds surrounded by less waterbody and wetland cover while marginally more likely to occur on ponds surrounded by fewer waterbodies. These findings provide limited support for the foraging habitat limitation hypothesis.

These three results appear to be inconsistent with previous findings as well. The strongest predictors of lesser scaup density reported by M. Ross (*unpublished report*) were the number and area of waterbodies. Similarly, Lemelin et al. (2010) reported positive associations between scaup and open waterbody habitat and wetland cover. Indeed, breeding scaup appear to select wetland complexes, as opposed to singular ponds, to support both the nesting and brood-rearing phases (Anteau et al. 2020). In contrast, results from the present study suggest that scaup in the Ramparts study area are more strongly associated with ponds surrounded by limited aquatic habitat. Since scaup may move broods more than 1 km to rearing habitat, they may not be limited to nesting on tightly clustered ponds that together provide the variety of resources needed for nesting and brood-rearing phases of the breeding season (Corcoran et al. 2007).

As I suggested for scoter, these unexpected findings may also be due in part to differences in scale because the direction of relationships between animal occupancy and landscape variables can vary depending on the scale of measurement (Jackson and Fahrig 2015). The largest scale examined in the present study (1960 m) is considerably smaller than that used in previous studies (5 x 5 km–10 x 10 km plots; Lemelin et al. 2010, M. Ross [*unpublished report*]). Differences in study area characteristics and survey timing may have also played a role in these unexpected results. M. Ross (*unpublished report*) mainly included forest-tundra transitional habitats, whereas the Ramparts study area is primarily forested. Lemelin et al. (2010) based their analyses on surveys conducted before scaup settled in nesting areas.

The two least important variables were shoreline complexity and the proportion of coniferous forest cover. Scaup were marginally more likely to occur on ponds surrounded by more complex shorelines. This finding likely reflects the nesting ecology of scaup, as scaup in the Northwest Territories nest on islands and 0.5–1 m from water along waterbody shorelines

(Vermeer 1968, Long 1970, Brown 1987, Fournier and Hines 2001, Corcoran et al. 2007). Importantly, high densities of lesser scaup nests occur on islands of floating buckbean (*Menyanthes trifoliata*) in the Northwest Territories (Anteau et al. 2020). This association with floating vegetation suggests that the effect of shoreline complexity might have been stronger if I had included perimeters of floating vegetation mats in the shoreline density index calculation.

Coniferous forest cover did not affect scaup occurrence probability. Given the sedge and grass cover that typically characterize scaup nests in the northwestern boreal forest, I might have expected scaup occurrence to be higher on ponds surrounded by less coniferous forest cover (Fournier and Hines 2001, Corcoran et al. 2007). Indeed, Lemelin et al. (2010) found that scaup pairs selected against forested shorelines. However, based on June 2018 and 2019 surveys of a subset of 39 ponds spread across the Ramparts study area, many ponds surrounded by coniferous forest uplands also had grass or sedge margins (M. S. Tanguay, University of Saskatchewan, personal observation).

3.4.3 Scales of effect

Although our models did not indicate strong effects of scale, some findings are worth noting. For example, landscape factors affected scoter abundance at a larger average scale than scaup, as predicted by the scale dependency hypothesis. Thus, the scale of effect probably relates to movement distances because breeding scoters appear to occupy a larger core movement area than breeding scaup. The average core use area for nesting white-winged scoter and surf scoter hens in the boreal forest was approximately 12 km^2 (radius ≈ 2000 m; S. Gilliland, CWS, *unpublished data*). In contrast, the average minimum home range of nesting lesser scaup hens in southwestern Manitoba was < 1 km^2 (radius ≈ 500 m; Hammell 1973, as cited in Allen [1986]). It is more likely that scales of effects are caused by differences in movement patterns between the two groups of duck species and not differences in timing of breeding because scoter and scaup have similar breeding schedules in the boreal forest (Anderson et al. 2020, Anteau et al. 2020, Brown and Fredrickson 2020). Therefore, researchers should consider movement distances when selecting spatial scales for species-landscape association studies, including waterfowl habitat selection studies (e.g., Webb et al. 2010, Beatty et al. 2014).

Scales of effect also depended on which landscape variable was considered for both scoter and scaup, suggesting it may be overly simplistic to select a single scale when modelling habitat selection on the landscape. Most notably, total waterbody area/km^2 and shoreline complexity had much larger scales of effect than did the total number of waterbodies/km^2 for scoter. Therefore, total waterbody area and shoreline complexity on the landscape might be a general cue of suitable breeding habitat for prospecting scoters as they arrive on the breeding grounds, when distances traveled for daily foraging flights are still relatively long (Beatty et al. 2014). In contrast, the smaller scale at which total number of waterbodies/km^2 affected scoter presence suggests that scoters may assess waterbody density later in the season, perhaps while on short nest scouting or foraging flights within the home range (Beatty et al. 2014). This result illustrates the importance of using scale-optimized landscape variables in species-habitat studies to ensure that important landscape effects do not go undetected.

3.4.4 Conclusions

Scoter and scaup were likely to occur on larger wetlands, potentially because large wetlands have the surface area, food resources, and ideal depths to support more breeding scoters and scaup. Supplementary analyses, though preliminary, also suggested that scoter and scaup densities are highest on 150-160-hectare wetlands in the Ramparts. Selection for larger wetlands was likely further strengthened by the rarity of large wetlands in the study area. In contrast, scoter and scaup distributions were only weakly related to landscape composition, suggesting that selection of landscapes by scoters and scaup likely occurs at a higher level than that examined here (i.e., home range or second-order selection; Johnson 1980). The most important landscape variables were the total number and area of waterbodies per km^2 (followed closely by shoreline complexity) for scoters and the proportion of wetland cover and total waterbody area/km^2 for scaup. Scaup occurrence was also weakly related to the total number of waterbodies/km^2 and shoreline complexity. However, some of the relationships were unexpectedly negative (most notably, the relationship between scoters and the total number of waterbodies per km^2, and the relationship between scaup and the total number and area of waterbodies per km^2). Differences in support among scales were not substantial, but selection of breeding location occurred over a larger spatial area for scoters than for scaup. Nonetheless, our results confirm that scales of effect for scoter- and scaup-landscape relationships are highly variable. As such, future landscape-level predictive modelling for these duck species should include species-specific, scale-optimized variables and perhaps focus on home range selection.

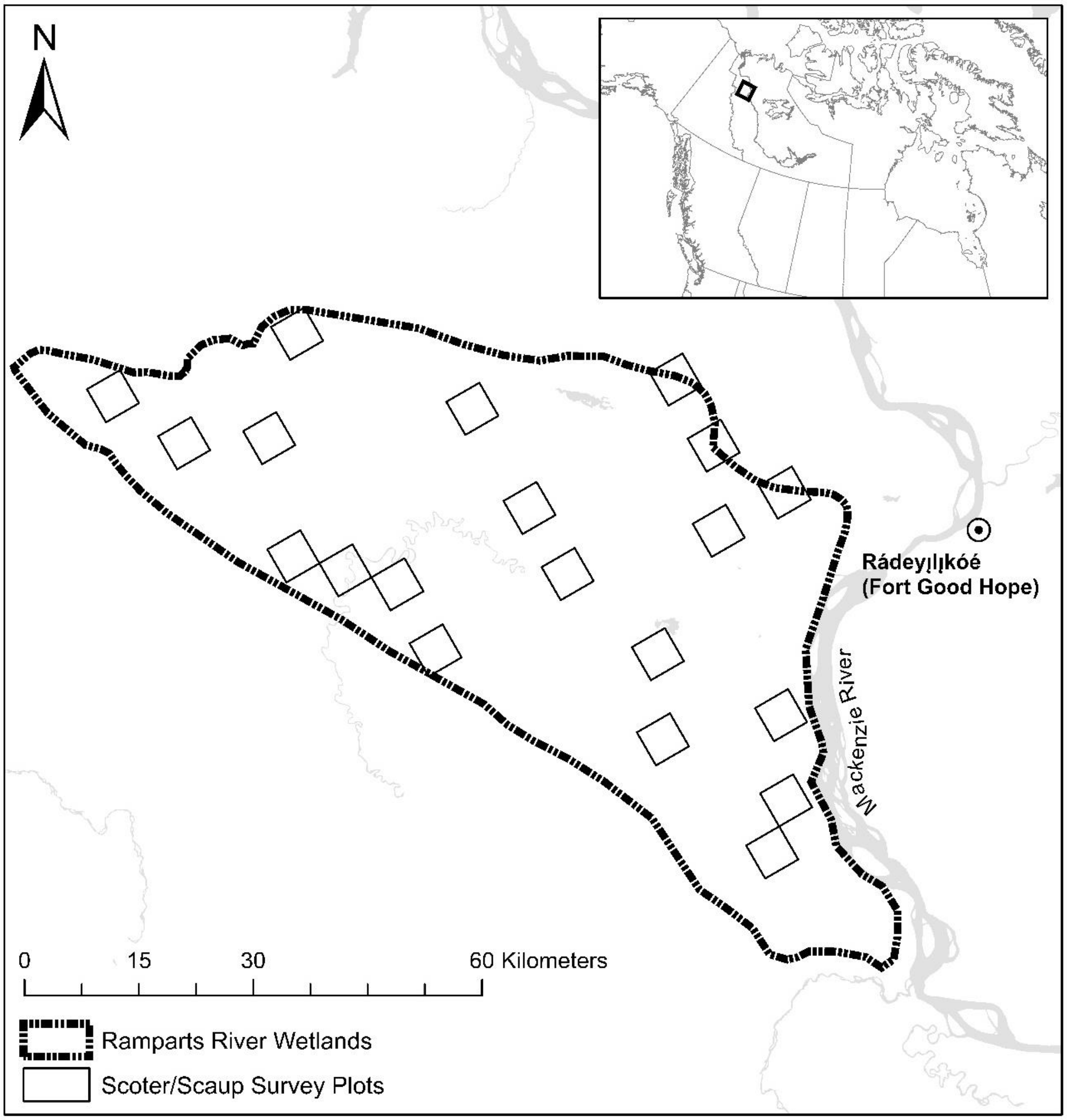

Figure 3.1. Map of the Ramparts River wetlands study area. The Canadian Wildlife Service conducted breeding surveys of scoter and scaup by helicopter in 2017 in 20 survey plots containing 1288 unique wetlands.

Table 3.1. Scales of measurement of landscape covariates and rationale for selected scales.

Scale (m)	Rationale
210	The average nesting distance from water for white-winged scoters on the Yukon Flats National Wildlife Refuge, Alaska (Safine and Lindberg 2008).
438	Intermediate scale between 210 m and 438 m that approximates scaup home range size (the radius of the average minimum home range of lesser scaup in Manitoba was 532 m; (Hammell 1973, as cited in Allen 1986).
1085	Intermediate scale between 210 m and 1960 m included to increase the likelihood of detecting landscape effects (Jackson and Fahrig 2015).
1960	The estimated radius of the average core use area of breeding scoter hens (where each core use area was a polygon containing 50% of the recorded locations for a given scoter [Namgail et al. 2011; S. Boyd & J. Evenson, *unpublished data*])

Note: Scale refers to the buffer distance from study wetland perimeters.

Table 3.2. Standardized model-averaged parameter estimates (in log odds) and importance values for covariates included in all-subsets candidate scoter occurrence model set.

Parameter	Estimate (95% CI)	Importance
Intercept	-4.86 (-5.60, -4.12)	-
SP_Area	0.85 (0.55, 1.15)	100%
WB_Count_438	-1.00 (-1.71, -0.29)	96%
WB_Area_1960	0.69 (0.22, 1.17)	89%
SDI_1085	-0.74 (-1.34, -0.14)	86%
WL_Prop_1085	-0.12 (-0.89, 0.66)	27%
CF_Prop_210	0.03 (-0.49, 0.55)	20%

Note: The estimates and associated 95% confidence intervals were calculated from models in the 95% confidence set of the all-subsets set (Table A.4).

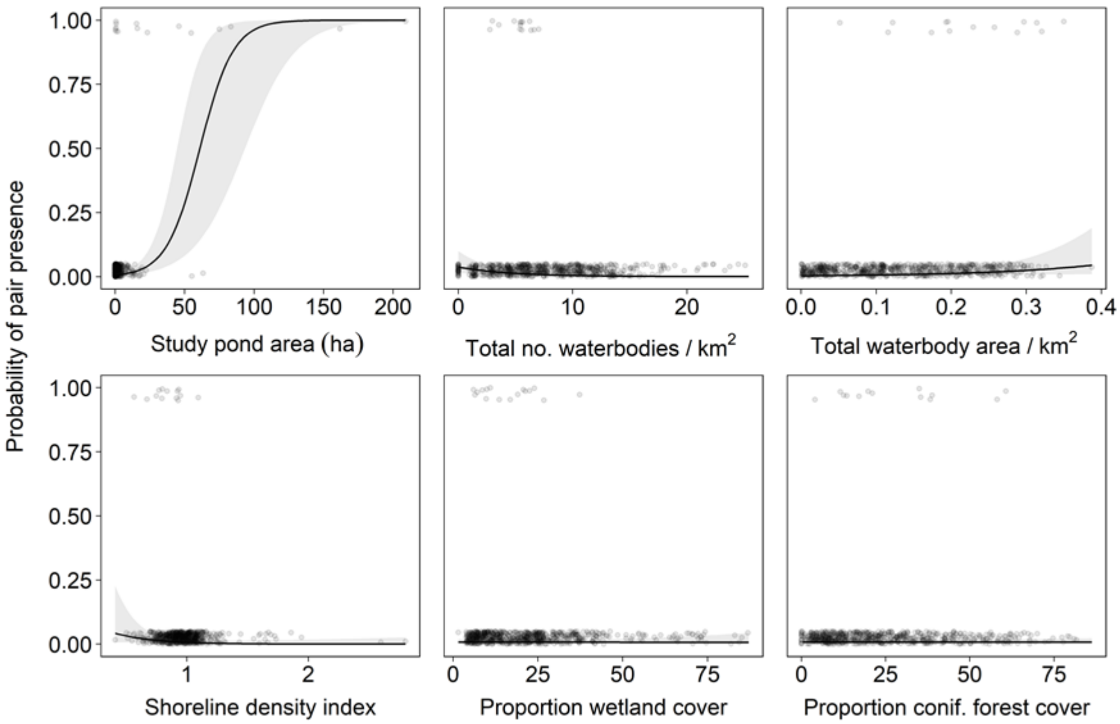

Figure 3.2. Relationships between the predicted probability of scoter presence on ponds and pond size and landscape composition covariates.

Table 3.3. Standardized model-averaged parameter estimates (in log odds) and importance values for covariates included in all-subsets candidate scaup occurrence model set.

Parameter	Estimate (95% CI)	Importance
Intercept	-1.92 (-2.45, -1.40)	-
SP_Area	0.80 (0.50, 1.10)	100%
WL_Prop_1960	-0.42 (-0.73, -0.12)	90%
WB_Area_210	-0.25 (-0.45, -0.05)	73%
WB_Count_438	-0.20 (-0.42, 0.02)	34%
CF_Prop_1085	-0.10 (-0.44, 0.24)	16%
SDI_210	0.10 (-0.06, 0.27)	14%

Note: The estimates and associated 95% confidence intervals were calculated from models in the 95% confidence set of the all-subsets set (Table A.6).

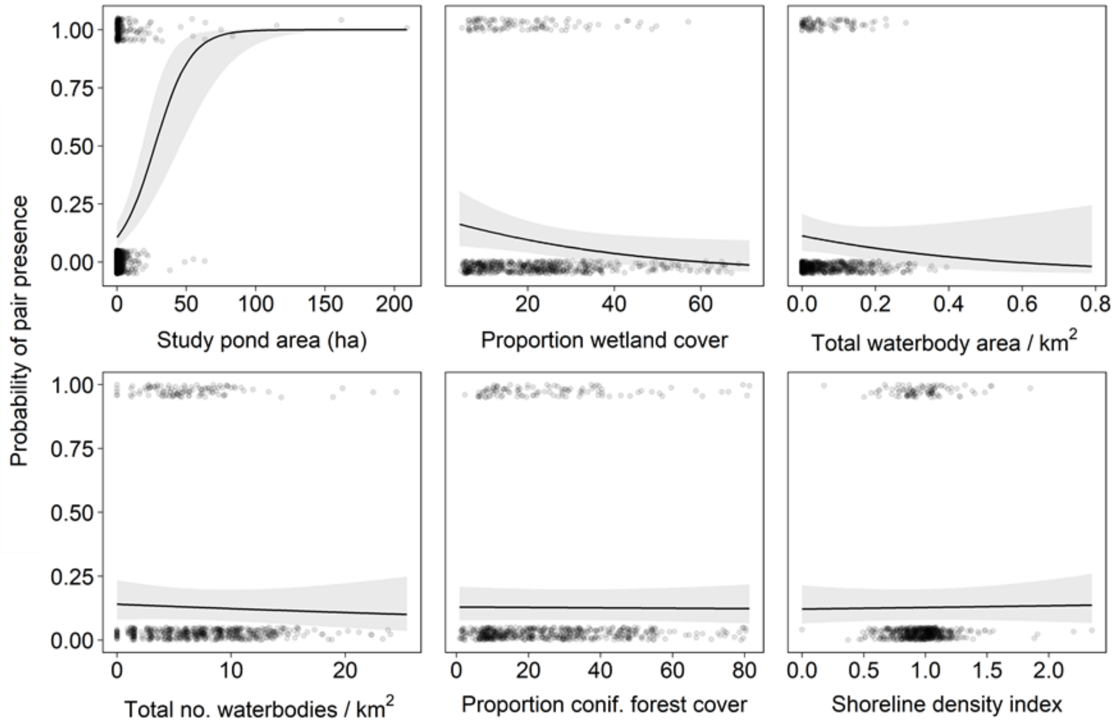

Figure 3.3. Relationships between the predicted probability of scaup presence on ponds and pond size and landscape composition covariates.

CHAPTER 4. SYNTHESIS

The western boreal forest (western boreal) supports 80% and 67% of the North American breeding populations of scoter (*Melanitta* spp.) and scaup (*Aythya* spp.), both of which have declined and remain below population objectives set out by the North American Waterfowl Management Plan (Slattery et al. 2011, North American Waterfowl Management Plan 2012, U.S. Fish and Wildlife Service 2019). Such declines are likely due in part to climate-related habitat changes on boreal breeding grounds, but specific hypotheses relating to these declines are largely untested (Corcoran et al. 2009, Drever et al. 2012). The western boreal is projected to warm 40% more than the global average (Soja et al. 2007). Multiple climate change impacts, such as earlier springs, increased wildfire size and frequency, reductions in surface water area, and changes in phytoplankton and macroinvertebrate communities, are already threatening boreal wetland ecosystems (Riordan et al. 2006, Corcoran et al. 2009, Drever et al. 2012, Wells et al. 2020). Climate change is currently the main conservation challenge in the northwestern boreal forest, but industrial development is likely to increase in this region and may impact duck populations. For comparison, population trends of ground-nesting duck species in the more southerly Boreal Plains ecozone of the western boreal have declined from 1960–2007, being most negative in areas with high seismic line, well pad, and pipeline density (Singer et al. 2020).

My research helps predict impacts of ongoing habitat changes while identifying important habitats for conservation of scoters and scaup by identifying key wetland and landscape correlates of breeding scoter and scaup distributions, as well as potential impacts of wildfire on scaup distributions and their macroinvertebrate prey in the northwestern boreal forest of North America.

4.1 Major findings

In Chapter 2, I tested the trophic enrichment hypothesis, evaluating nutrient levels, productivity, colour, macroinvertebrate community composition, and abundance of a key waterfowl taxon, scaup (*Aythya* spp.), on phosphorous-limited wetlands in the context of recent (within the previous two years) wildfire in the northwestern boreal. I predicted that, relative to unburned wetlands, recently burned wetlands would have (i) increased levels of total nitrogen, total phosphorus, and chlorophyll-*a*; (ii) darker coloured water; (iii) greater relative abundances and percent compositions of Amphipoda, and (iv) higher densities of scaup. I found that recently burned wetlands had significantly higher concentrations of total phosphorous and chlorophyll-*a* than unburned wetlands in May in the years immediately following wildfire. However, these heightened nutrient and productivity levels did not appear to translate into a significant shift in wetland macroinvertebrate community composition nor an increased abundance or dominance of Amphipoda. Indicated breeding scaup pair abundance was similar on burned and unburned wetlands as well, possibly because breeding scaup pairs in June are not reflective of increased wetland productivity, or because changes in total phosphorous and chlorophyll-*a* were restricted to the early spring period and did not extend into June when the majority of scaup settled on our study ponds. Such a temporal mismatch between fire impacts and scaup arrival seems likely given the return to similar total phosphorous and chlorophyll-*a* levels observed on burned and unburned wetlands in June. Although, it is possible that much of the total phosphorous and chlorophyll-*a* observed in May but not June could have been incorporated into macroinvertebrates by the time scaup pairs arrived, such that the trophic enrichment hypothesis is supported in June. In sum, I detected nutrient enrichment but found little evidence of trophic enrichment one to two years post-wildfire in wetlands of the Central Mackenzie Valley, Northwest Territories.

In Chapter 3, I tested the foraging habitat limitation and scale dependency hypotheses using scale-optimized landscape covariates and optimally timed aerial observations of breeding white-winged scoter (*Melanitta deglandi*), surf scoter (*Melanitta perspicillata*), and scaup pairs (Reed et al. 2020). I evaluated the occurrence of these duck species across boreal wetlands within the spatial area of their home range (third-order selection; Johnson 1980) in a key waterfowl area in the Central Mackenzie Valley of the Northwest Territories (Latour et al. 2008). I predicted that scoter and scaup would be more likely to occur on larger wetlands surrounded by more waterbodies and waterbody area, and that landscape effects would be stronger at a larger spatial scale for scoters than for scaup. I found that scoters and scaup were likely to occur on larger wetlands, potentially because large wetlands have the surface area and resources needed to support more ducks, as well as ideal depths and food resources for breeding scoters and scaup. Supplementary analyses, though preliminary, also suggested that scoter and scaup densities were highest on 150-160-hectare wetlands in the Ramparts. Selection for larger wetlands was likely further strengthened by the rarity of large wetlands in the study area. In contrast, scoter and scaup distributions were only weakly related to wetlands' landscape composition, suggesting that selection of landscape composition by scoter and scaup likely occurs at a higher level than that examined here (i.e., home range or second-order selection; Johnson 1980). The most important landscape variables were total number and area of waterbodies per km^2 (followed closely by shoreline complexity) for scoters, and the proportion of wetland cover and total waterbody area/km^2 for scaup. Scaup occurrence was also weakly related to the total number of waterbodies/km^2 and shoreline complexity. However, some of the relationships were unexpectedly negative (most notably, the relationship between scoter and the total number of waterbodies per km^2 and the relationship between scaup and the total number and area of waterbodies per km^2). Differences in support among scales were not substantial, but selection of breeding location occurred over a larger spatial area for scoter than for scaup. To conclude, these results provide some support for the foraging habitat limitation and scale dependency hypotheses.

Overall, I found that wetland ecosystems in the northwestern boreal forest appear resilient to moderate to severe wildfires under current climate conditions and that they may even benefit from nutrient pulses and subsequent increases in primary productivity following wildfire. However, fire impacts on aquatic ecosystems are likely to intensify as the climate warms, such that this resilience may not be maintained in coming decades. Specifically, warming might impact phytoplankton biomass via reduced ice cover, thawing permafrost, and increased water temperatures, enhancing algal growth, productivity, and nutrient cycling, possibly reducing water quality in aquatic ecosystems by reducing water transparency and oxygen content (Ogbebo et al. 2009). In boreal Alaska and western Canada, where climate warming is predicted to be 40% higher compared to the global average, the average area burned per decade is predicted to double by 2041–2050 and increase 3.5–5.5 times by the last decade of the 21st century (Soja et al. 2007, Balshi et al. 2009). Thus, continued monitoring of the impacts of climate warming and associated increases in wildfires on boreal wetlands is critical to identifying and mitigating future threats to these ecosystems. My results also suggest that conservation planning in the northern boreal forest should prioritize complexes of large (possibly 160-hectare) wetlands for scoters. Whereas for scaup, large (possibly 150-hectare) wetlands with few waterbodies and limited waterbody cover in the immediate surroundings, as well as little wetland cover, should be prioritized. However, the greater importance of wetland size in the scoter and scaup models suggests that wetland-level conservation for scoter and scaup pairs in the northwestern boreal forest should be informed primarily by wetland characteristics (e.g., wetland size and amphipod abundance) and less so by the landscape characteristics surrounding wetlands (e.g., proportion coniferous forest cover). Selection of landscape composition by scoter and scaup likely occurs at a higher level than that examined here. Still, the results confirm that scales of effect for scoter- and scaup-landscape relationships are highly variable. As such, future landscape-level predictive modelling for these ducks should include species-specific, scale-optimized variables and perhaps focus on home range selection.

4.2 Future research

I recommend continued monitoring of wetland parameters in Ts'udé Nilįné Tuyeta so that future research has a baseline against which to measure climate change impacts. For example, such baseline data would allow researchers to compare wetland parameters measured before and after fire using a robust before-after-control-impact study that tests for an effect of fire on wetland parameters while controlling for pre-existing differences between burned and unburned wetlands (e.g., Lewis et al. 2014). Additionally, a quality baseline dataset would allow long-term analyses of wetland parameters that could test for potential reductions in surface water area and changes to macroinvertebrate communities like those already documented in subarctic Alaska (Riordan et al. 2006, Corcoran et al. 2009). Simultaneous monitoring of breeding scoter and scaup pair density, brood density, and duckling quality and survival in the Ramparts River wetlands area of Ts'udé Nilįné Tuyeta, where there is a high density of wetlands and waterfowl, would allow future research on the linkages between climate change impacts on wetlands and duck productivity and population trends.

I also recommend that future scoter and scaup habitat selection studies be conducted over a larger area to increase sample sizes and the power to detect potentially weak landscape effects. Larger study areas are justified in the boreal where waterfowl, including scoter and scaup, nest at relatively low densities. A larger study area is vital if future research is to model scoter and scaup species separately (i.e., *Melaniita deglandi, M. perspicillata, Aythya affinis,* and *A. marila*), which I recommend. In addition, I suggest such regional studies focus on second-order selection (i.e., selection of the home range; Johnson 1980), as I suspect these species are more likely to perceive and base settling decisions on coarse, landscape-level habitat information at this level of selection rather than during the process of wetland selection (i.e., third-order selection; Johnson 1980). Lastly, as shown in Chapter 3, a multi-scale approach is warranted, in which each covariate enters the model at its scale of effect. Until accessible methods of true scale optimization are readily available to ecologists (as described by McGarigal et al. [2016]), I suggest including a large range of scales encompassing the home range of the study species, separated by small intervals (Jackson and Fahrig 2015). Broad-scale habitat selection studies like these can increase the specificity and effectiveness of future habitat conservation measures to support scoter and scaup breeding populations.

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APPENDIX A

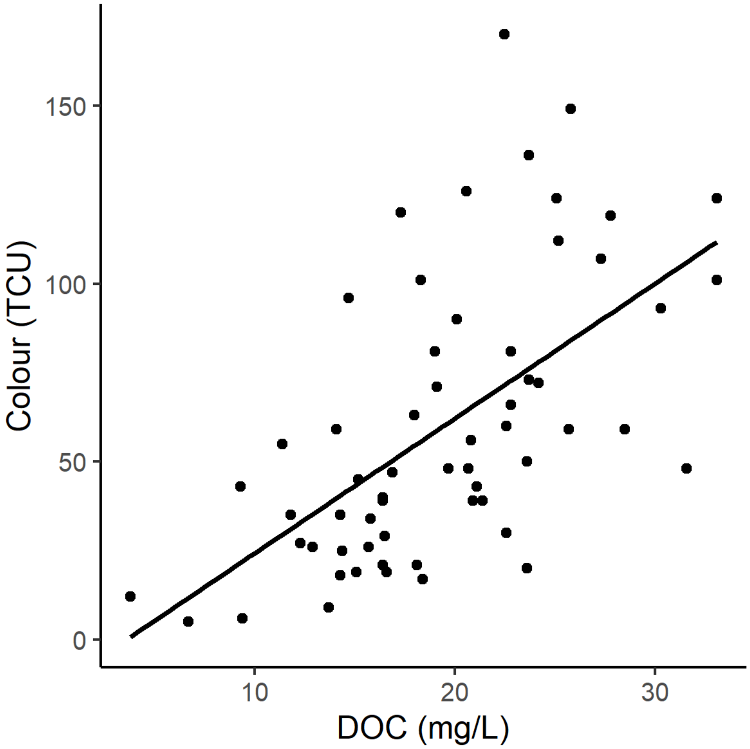

Figure A.1. Correlation between colour and DOC in 2019 (Pearson *r* = 0.6).

Figure A.2. Example study wetlands in the burned area of J11 in the Ramparts River wetlands, May 2019. The area was burned by small, moderate-severity wildfires in 2017 and 2018. The estimated start date of the 2017 fire was September 7, and it was called out on October 26 at a final area of 294 ha. The estimated start date of the 2018 fire was June 13, and it was called out on August 13 at a final area of 87 ha. The bottom panels of Figure A.2 and Figure A.3 depict the same wetland.

Figure A.3. Example study wetlands in the burned area of J11 in the Ramparts River wetlands, June 2019. The area was burned by small, moderate-severity wildfires in 2017 and 2018. The estimated start date of the 2017 fire was September 7, and it was called out on October 26 at a final area of 294 ha. The estimated start date of the 2018 fire was June 13, and it was called out on August 13 at a final area of 87 ha. The bottom panels of Figure A.2 and Figure A.3 depict the same wetland.

Figure A.4. Example study wetlands in the burned area of E05 in the Ramparts River wetlands, May 2018. The area was burned by a large, high-severity wildfire in 2017. The estimated start date of the fire was June 20, and it was called out on August 28 at a final area of 25,661 ha.

Figure A.5. Example study wetlands in the burned area of E05 in the Ramparts River wetlands, June 2018. The area was burned by a large, high-severity wildfire in 2017. The estimated start date of the fire was June 20, and it was called out on August 28 at a final area of 25,661 ha.

Table A.1. Sample sizes in the two burn categories (recently burned and not recently burned) and three wetland size classes (SizeClass: small, medium, and large) sampled in 2017, 2018, and 2019.

Burn category	Year	n Small	n Medium	n Large	Total
Unburned	2017	13	0	0	13
	2018	10	12	14	36
	2019	16	14	10	40
Burned	2017	0	0	0	0
	2018	2	4	6	12
	2019	10	4	6	20
	TOTAL	51	34	36	121

Note: The number of samples is twice the number of study wetlands because wetlands were sampled once in May and once in June (except in 2017 when wetlands were only sampled in June).

Table A.2. Summary statistics of wetland variables in Chapter 2. N = 121 for all variables except DO (n = 114), Col (n = 60), and Depth (n = 30).

Variable (abbr.)	Units	Mean (SD)	Range
Size	Hectares (ha)	27.4 (62.0)	0.002–358.9
Depth	Meters (m)	1.5 (1.5)	0.3–7.0
Temperature (Temp)	Degrees Celsius (ºC)	14.5 (5.6)	4.2–25.4
pH		6.9 (0.9)	4.7–9.1
Dissolved oxygen (DO)	Percent of air saturation (%)	93.0 (22.0)	40.7–164.0
Total nitrogen (TN)	Micrograms per liter (µg/L)	1022.0 (390.3)	220.0–2390.0
Total phosphorous (TP)	Micrograms per liter (µg/L)	22.7 (20.2)	2.0–111.0
Nitrogen:Phosphorous (N-P)		72.4 (56.3)	8.2–330.0
Chlorophyll-*a* (Chl-*a*)	Micrograms per liter (µg/L)	3.6 (5.9)	0.6–52.3
Colour (Col)	True colour units (TCU)	59.8 (39.6)	5.0–170.0
Dissolved organic carbon (DOC)	Milligrams per liter (mg/L)	22.1 (9.0)	3.8–72.3

Table A.3. Separation of macroinvertebrate communities by burn history.

Variable	Axes	R^2	P-value
Burn	Axes 1,2	0.012	1.000
Year	Axes 1,2	0.239	0.011
Month	Axes 1,2	0.034	0.097
Temp	Axes 1,2	0.105	0.006
Nitrogen	Axes 1,2	0.141	0.006
Burn	Axes 1,3	0.009	1.000
Year	Axes 1,3	0.305	0.011
Temp	Axes 1,3	0.072	0.126
Nitrogen	Axes 1,3	0.135	0.006
DO	Axes 1,3	0.148	0.006
Burn	Axes 2,3	0.005	1.000
Month	Axes 2,3	0.073	0.017
DO	Axes 2,3	0.151	0.008
Size Class	Axes 2,3	0.061	0.046

Table A.4. DOC model selection table.

Model	k	logLik	Δ *AICc*	ω*i*
Year + Month	7	-350.64	0.00	0.61
Year + Month + Burn	8	-350.30	1.61	0.27
Year + Month + Burn + Burn:Month	9	-350.12	3.58	0.10
Year + Month + Burn + SizeClass + Burn:SizeClass	12	-348.94	8.50	0.01
Year + Month + Burn + Burn:Month + SizeClass + Burn:SizeClass	13	-348.76	10.65	0.00
Null	4	-389.49	71.06	0.00

Note: All candidate models include wetland nested within plot as a random effect (the null model contains only the random effect).

APPENDIX B

Table B.1. Summary statistics of wetland and landscape variables included in scoter and scaup occurrence analyses (n = 1288 for all variables).

Variable (abbr.)	Units	Scale	Mean (SD)	Range
Study pond area (SP_Area)	Hectares (ha)	-	2.7 (10.2)	0.02–209.0
Total number of waterbodies (WB_Count)	Total number / km^2	210	11.0 (8.6)	0.0–55.3
		438	7.4 (4.6)	0.0–25.4
		1085	5.1 (2.7)	0.0–16.3
		1960	4.3 (2.2)	0.2–13.5
Total waterbody area (WB_Area)	Total area (km^2) / km^2	210	0.1 (0.1)	0.0–0.8
		438	0.1 (0.1)	0.0–0.6
		1085	0.1 (0.1)	0.0–0.5
		1960	0.1 (0.1)	0.0–0.4
Proportion wetland cover (WL_Prop)	-	210	22.7 (19.9)	0.0–98.2
		438	22.1 (17.6)	0.4–96.8
		1085	21.7 (15.6)	1.5–87.1
		1960	21.5 (13.8)	4.2–71.2
Proportion total coniferous forest (CF_Prop)	-	210	23.9 (18.7)	0.0–85.9
		438	24.3 (18.6)	0.0–87.1
		1085	24.3 (17.3)	0.8–81.3
		1960	24.5 (15.7)	1.4–79.0
Shoreline density index (SDI)	-	210	1.0 (0.2)	0.0–2.4
		438	1.0 (0.2)	0.4–3.2
		1085	1.0 (0.2)	0.4–2.8
		1960	1.0 (0.2)	0.4–2.6

Table B.2. Model selection table for scale-optimization phase of scoter occurrence modeling process. Only three covariates (bolded) had clear scales of effect.

Model	k	logLik	Δ AICc	ω*i*
(1|Plot) + SP_Area + WB_Count_438	**4**	**-97.89**	**0.00**	**0.48**
(1|Plot) + SP_Area + WB_Count_210	**4**	**-98.33**	**0.86**	**0.31**
(1|Plot) + SP_Area + WB_Count_1085	4	-99.06	2.33	0.15
(1|Plot) + SP_Area + WB_Count_1960	4	-100.04	4.29	0.06
(1|Plot) + SP_Area + WB_Area_1960	**4**	**-98.29**	**0.00**	**0.52**
(1|Plot) + SP_Area + WB_Area_1085	**4**	**-98.82**	**1.06**	**0.30**
(1|Plot) + SP_Area + WB_Area_438	4	-99.72	2.86	0.12
(1|Plot) + SP_Area + WB_Area_210	4	-100.52	4.46	0.06
(1|Plot) + SP_Area + WL_Prop_1085	4	-99.11	0.00	0.36
(1|Plot) + SP_Area + WL_Prop _1960	4	-99.52	0.81	0.24
(1|Plot) + SP_Area + WL_Prop _438	4	-99.62	1.01	0.22
(1|Plot) + SP_Area + WL_Prop _210	4	-99.81	1.40	0.18
(1|Plot) + SP_Area + CF_Prop_210	4	-100.09	0.00	0.32
(1|Plot) + SP_Area + CF_Prop _1085	4	-100.42	0.65	0.23
(1|Plot) + SP_Area + CF_Prop _1960	4	-100.43	0.68	0.23
(1|Plot) + SP_Area + CF_Prop _438	4	-100.47	0.76	0.22
(1|Plot) + SP_Area + SDI_1085	**4**	**-97.04**	**0.00**	**0.60**
(1|Plot) + SP_Area + SDI_210	4	-98.39	2.70	0.15
(1|Plot) + SP_Area + SDI_438	4	-98.47	2.86	0.14
(1|Plot) + SP_Area + SDI_1960	4	-98.74	3.41	0.11

Table B.3. Model selection table for all possible scoter occurrence model subsets (n = 64). The 95% confidence set of models (bolded) was used to calculate model-averaged parameter estimates.

CF_Prop (210)	WL_Prop (1085)	SDI (1085)	SP_Area	WB_Area (1960)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	**NA**	**-0.74**	**0.84**	**0.68**	**-1.03**	**6**	**-92.38**	**0.00**	**0.46**
NA	**-0.05**	**-0.74**	**0.84**	**0.67**	**-1.02**	**7**	**-92.52**	**2.30**	**0.14**
0.04	**NA**	**-0.73**	**0.84**	**0.68**	**-1.02**	**7**	**-92.84**	**2.95**	**0.11**
NA	**NA**	**NA**	**0.86**	**0.79**	**-1.02**	**5**	**-95.19**	**3.62**	**0.08**
0.02	**-0.03**	**-0.73**	**0.84**	**0.67**	**-1.01**	**8**	**-92.86**	**5.01**	**0.04**
NA	**NA**	**-0.84**	**0.94**	**NA**	**-0.72**	**5**	**-95.96**	**5.14**	**0.04**
NA	**-0.42**	**-0.82**	**0.93**	**NA**	**-0.68**	**6**	**-95.20**	**5.65**	**0.03**
NA	**-0.03**	**NA**	**0.86**	**0.78**	**-1.01**	**6**	**-95.29**	**5.83**	**0.02**
0.10	**NA**	**NA**	**0.86**	**0.79**	**-0.98**	**6**	**-95.56**	**6.36**	**0.02**
NA	**-0.55**	**-0.81**	**0.96**	**NA**	**NA**	**5**	**-97.38**	**7.99**	**0.01**
-0.15	-0.50	-0.82	0.92	NA	-0.73	7	-95.37	8.01	0.01
0.03	NA	-0.83	0.94	NA	-0.71	6	-96.41	8.07	0.01
NA	NA	-0.77	0.94	0.46	NA	5	-97.47	8.17	0.01
0.11	0.02	NA	0.87	0.80	-0.98	7	-95.54	8.35	0.01
NA	NA	-0.83	0.98	NA	NA	4	-98.67	8.56	0.01
NA	-0.42	-0.76	0.94	0.34	NA	6	-96.88	9.02	0.01
0.28	NA	-0.73	0.94	0.48	NA	6	-97.34	9.92	0.00
NA	NA	NA	0.95	NA	-0.68	4	-99.51	10.24	0.00
NA	-0.45	NA	0.94	NA	-0.63	5	-98.65	10.53	0.00
0.03	-0.53	-0.80	0.96	NA	NA	6	-97.73	10.70	0.00
0.21	NA	-0.81	0.98	NA	NA	5	-98.79	10.82	0.00
0.18	-0.29	-0.74	0.94	0.39	NA	7	-97.02	11.30	0.00
NA	NA	NA	0.96	0.53	NA	4	-100.14	11.49	0.00
NA	-0.59	NA	0.98	NA	NA	4	-100.48	12.17	0.00
NA	-0.43	NA	0.95	0.42	NA	5	-99.52	12.27	0.00
0.33	NA	NA	0.96	0.57	NA	5	-99.78	12.80	0.00
NA	NA	NA	1.00	NA	NA	3	-101.89	12.98	0.00
-0.10	-0.50	NA	0.94	NA	-0.66	6	-98.90	13.04	0.00
0.06	NA	NA	0.95	NA	-0.65	5	-99.91	13.05	0.00
0.25	-0.26	NA	0.96	0.50	NA	6	-99.49	14.23	0.00
0.07	-0.55	NA	0.98	NA	NA	5	-100.81	14.86	0.00
0.24	NA	NA	1.00	NA	NA	4	-101.93	15.08	0.00
NA	NA	-0.64	NA	0.88	-1.23	5	-123.43	60.08	0.00
NA	-0.03	-0.64	NA	0.87	-1.22	6	-123.74	62.73	0.00
-0.02	NA	-0.64	NA	0.88	-1.24	6	-124.09	63.43	0.00
NA	NA	NA	NA	0.97	-1.24	4	-126.53	64.27	0.00
-0.04	-0.05	-0.65	NA	0.86	-1.23	7	-124.27	65.81	0.00
NA	0.01	NA	NA	0.97	-1.24	5	-126.81	66.84	0.00
0.02	NA	NA	NA	0.97	-1.23	5	-127.14	67.50	0.00
0.03	0.02	NA	NA	0.97	-1.23	6	-127.30	69.85	0.00
NA	NA	-0.69	NA	NA	-0.93	4	-130.45	72.12	0.00

CF_Prop (210)	WL_Prop (1085)	SDI (1085)	SP_Area	WB_Area (1960)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	-0.43	-0.70	NA	NA	-0.88	5	-129.57	72.37	0.00
-0.23	-0.55	-0.70	NA	NA	-0.93	6	-129.56	74.36	0.00
-0.05	NA	-0.69	NA	NA	-0.95	5	-130.96	75.14	0.00
NA	NA	NA	NA	NA	-0.93	3	-133.66	76.52	0.00
NA	-0.41	NA	NA	NA	-0.87	4	-132.90	77.02	0.00
-0.20	-0.51	NA	NA	NA	-0.92	5	-132.98	79.18	0.00
-0.06	NA	NA	NA	NA	-0.95	4	-134.13	79.47	0.00
NA	NA	-0.67	NA	0.57	NA	4	-134.63	80.47	0.00
NA	-0.47	-0.67	NA	0.44	NA	5	-133.68	80.58	0.00
NA	-0.61	-0.70	NA	NA	NA	4	-134.89	80.99	0.00
0.25	NA	-0.65	NA	0.60	NA	5	-134.59	82.41	0.00
NA	NA	-0.70	NA	NA	NA	3	-136.91	83.01	0.00
0.11	-0.39	-0.66	NA	0.48	NA	6	-134.06	83.37	0.00
NA	NA	NA	NA	0.61	NA	3	-137.24	83.67	0.00
NA	-0.47	NA	NA	0.50	NA	4	-136.34	83.89	0.00
-0.04	-0.64	-0.70	NA	NA	NA	5	-135.36	83.94	0.00
NA	-0.63	NA	NA	NA	NA	3	-137.96	85.12	0.00
0.27	NA	NA	NA	0.66	NA	4	-137.11	85.44	0.00
0.16	NA	-0.70	NA	NA	NA	4	-137.27	85.74	0.00
0.15	-0.37	NA	NA	0.55	NA	5	-136.64	86.51	0.00
NA	NA	NA	NA	NA	NA	2	-139.91	87.02	0.00
-0.02	-0.64	NA	NA	NA	NA	4	-138.44	88.09	0.00
0.16	NA	NA	NA	NA	NA	3	-140.27	89.74	0.00

Table B.4. Model selection table for scale-optimization phase of scaup occurrence modeling process. Only three covariates (bolded) had clear scales of effect.

Model	k	logLik	Δ AICc	ω*i*
(1|Plot) + SP_Area + WB_Count_438	**4**	**-506.10**	**0.00**	**0.71**
(1|Plot) + SP_Area + WB_Count_210	4	-507.47	2.73	0.18
(1|Plot) + SP_Area + WB_Count_1085	4	-508.20	4.19	0.09
(1|Plot) + SP_Area + WB_Count_1960	4	-509.71	7.22	0.02
(1|Plot) + SP_Area + WB_Area_210	**4**	**-506.55**	**0.00**	**0.67**
(1|Plot) + SP_Area + WB_Area_1960	4	-507.52	1.92	0.26
(1|Plot) + SP_Area + WB_Area_438	4	-509.39	5.67	0.04
(1|Plot) + SP_Area + WB_Area_1085	4	-509.42	5.74	0.04
(1|Plot) + SP_Area + WL_Prop_1960	4	-505.49	0.00	0.41
(1|Plot) + SP_Area + WL_Prop _1085	4	-505.78	0.58	0.30
(1|Plot) + SP_Area + WL_Prop _438	4	-506.29	1.60	0.18
(1|Plot) + SP_Area + WL_Prop _210	4	-506.83	2.69	0.11
(1|Plot) + SP_Area + CF_Prop _1085	4	-508.96	0.00	0.29
(1|Plot) + SP_Area + CF_Prop _1960	4	-509.03	0.14	0.27
(1|Plot) + SP_Area + CF_Prop _438	4	-509.21	0.50	0.23
(1|Plot) + SP_Area + CF_Prop _210	4	-509.29	0.66	0.21
(1|Plot) + SP_Area + SDI_210	**4**	**-508.13**	**0.00**	**0.55**
(1|Plot) + SP_Area + SDI_438	4	-509.26	2.26	0.18
(1|Plot) + SP_Area + SDI_1085	4	-509.40	2.54	0.16
(1|Plot) + SP_Area + SDI_1960	4	-509.75	3.23	0.11

Table B.5. Model selection table for all possible scaup occurrence model subsets (n = 64). The 95% confidence set of models (bolded) was used to calculate model-averaged parameter estimates.

CF_Prop (1085)	WL_Prop (1960)	SDI (210)	SW_Area	WB_Area (210)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	**-0.45**	**NA**	**0.79**	**-0.27**	**NA**	**5**	**-505.46**	**0.00**	**0.37**
NA	**-0.40**	**NA**	**0.77**	**-0.23**	**-0.17**	**6**	**-505.56**	**2.22**	**0.12**
NA	**-0.35**	**NA**	**0.81**	**NA**	**-0.23**	**5**	**-507.00**	**3.09**	**0.08**
NA	**-0.41**	**NA**	**0.86**	**NA**	**NA**	**4**	**-508.04**	**3.14**	**0.08**
-0.10	**-0.49**	**NA**	**0.79**	**-0.28**	**NA**	**6**	**-506.11**	**3.32**	**0.07**
NA	**-0.43**	**0.10**	**0.80**	**-0.25**	**NA**	**6**	**-506.38**	**3.86**	**0.05**
-0.14	**-0.46**	**NA**	**0.76**	**-0.24**	**-0.18**	**7**	**-506.00**	**5.12**	**0.03**
NA	**NA**	**NA**	**0.81**	**NA**	**-0.27**	**4**	**-509.08**	**5.23**	**0.03**
NA	**-0.39**	**0.13**	**0.85**	**NA**	**NA**	**5**	**-508.35**	**5.78**	**0.02**
NA	**NA**	**NA**	**0.78**	**-0.19**	**-0.23**	**5**	**-508.47**	**6.02**	**0.02**
NA	**NA**	**NA**	**0.82**	**-0.24**	**NA**	**4**	**-509.54**	**6.14**	**0.02**
NA	**-0.39**	**0.09**	**0.77**	**-0.21**	**-0.16**	**7**	**-506.60**	**6.32**	**0.02**
NA	**-0.34**	**0.11**	**0.81**	**NA**	**-0.21**	**6**	**-507.64**	**6.39**	**0.02**
-0.07	**-0.37**	**NA**	**0.80**	**NA**	**-0.24**	**6**	**-507.80**	**6.69**	**0.01**
0.01	**-0.41**	**NA**	**0.86**	**NA**	**NA**	**5**	**-508.95**	**6.98**	**0.01**
-0.10	-0.48	0.10	0.79	-0.26	NA	7	-507.01	7.15	0.01
NA	NA	NA	0.87	NA	NA	3	-511.36	7.78	0.01
NA	NA	0.12	0.81	NA	-0.25	5	-509.56	8.20	0.01
0.10	NA	NA	0.82	NA	-0.25	5	-509.93	8.93	0.00
-0.15	-0.45	0.09	0.76	-0.23	-0.18	8	-507.03	9.21	0.00
NA	NA	0.12	0.82	-0.22	NA	5	-510.09	9.26	0.00
0.14	NA	NA	0.82	-0.23	NA	5	-510.15	9.39	0.00
-0.01	-0.40	0.13	0.85	NA	NA	6	-509.25	9.59	0.00
NA	NA	0.10	0.78	-0.18	-0.22	6	-509.29	9.68	0.00
NA	NA	0.15	0.87	NA	NA	4	-511.32	9.71	0.00
0.07	NA	NA	0.78	-0.19	-0.22	6	-509.40	9.89	0.00
-0.07	-0.37	0.12	0.80	NA	-0.22	7	-508.41	9.93	0.00
0.19	NA	NA	0.88	NA	NA	4	-511.58	10.23	0.00
0.09	NA	0.12	0.81	NA	-0.24	6	-510.44	11.98	0.00
0.17	NA	0.14	0.87	NA	NA	5	-511.72	12.52	0.00
0.13	NA	0.11	0.82	-0.21	NA	6	-510.78	12.66	0.00
0.07	NA	0.10	0.78	-0.17	-0.21	7	-510.23	13.58	0.00
NA	-0.41	NA	NA	-0.29	-0.27	5	-530.06	49.20	0.00
-0.22	-0.50	NA	NA	-0.32	-0.29	6	-529.96	51.01	0.00
NA	-0.49	NA	NA	-0.36	NA	4	-532.04	51.15	0.00
NA	NA	NA	NA	-0.26	-0.33	4	-533.25	53.57	0.00
-0.15	-0.55	NA	NA	-0.38	NA	5	-532.41	53.90	0.00
NA	-0.40	0.05	NA	-0.29	-0.26	6	-531.49	54.07	0.00
NA	-0.35	NA	NA	NA	-0.35	4	-533.87	54.81	0.00
NA	-0.48	0.06	NA	-0.35	NA	5	-533.36	55.81	0.00
-0.22	-0.49	0.05	NA	-0.31	-0.28	7	-531.38	55.88	0.00

CF_Prop (1085)	WL_Prop (1960)	SDI (210)	SW_Area	WB_Area (210)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	NA	NA	NA	NA	-0.39	3	-536.03	57.10	0.00
0.02	NA	NA	NA	-0.26	-0.33	5	-534.26	57.61	0.00
-0.12	-0.40	NA	NA	NA	-0.36	5	-534.45	57.98	0.00
NA	NA	0.06	NA	-0.25	-0.32	5	-534.54	58.16	0.00
-0.16	-0.55	0.06	NA	-0.37	NA	6	-533.72	58.53	0.00
NA	-0.34	0.08	NA	NA	-0.34	5	-534.93	58.95	0.00
NA	NA	NA	NA	-0.34	NA	3	-537.26	59.58	0.00
NA	NA	0.09	NA	NA	-0.38	4	-536.95	60.97	0.00
0.06	NA	NA	NA	NA	-0.38	4	-537.00	61.07	0.00
-0.13	-0.39	0.09	NA	NA	-0.35	6	-535.48	62.05	0.00
NA	-0.44	NA	NA	NA	NA	3	-538.55	62.14	0.00
0.02	NA	0.06	NA	-0.25	-0.32	6	-535.55	62.20	0.00
0.13	NA	NA	NA	-0.33	NA	4	-537.99	63.05	0.00
NA	NA	0.08	NA	-0.33	NA	4	-538.32	63.71	0.00
0.05	NA	0.09	NA	NA	-0.37	5	-537.94	64.97	0.00
NA	-0.43	0.11	NA	NA	NA	4	-539.24	65.54	0.00
-0.01	-0.45	NA	NA	NA	NA	4	-539.46	65.98	0.00
0.12	NA	0.08	NA	-0.32	NA	5	-539.09	67.26	0.00
NA	NA	NA	NA	NA	NA	2	-542.80	68.65	0.00
-0.02	-0.44	0.11	NA	NA	NA	5	-540.13	69.35	0.00
0.20	NA	NA	NA	NA	NA	3	-543.00	71.05	0.00
NA	NA	0.13	NA	NA	NA	3	-543.18	71.41	0.00
0.18	NA	0.12	NA	NA	NA	4	-543.52	74.11	0.00

Table B.6. Model selection table for all possible scoter abundance model subsets (n = 64). The 95% confidence set of models (bolded) was used to calculate model-averaged parameter estimates.

CF_Prop (210)	WL_Prop (1085)	SDI (1085)	SP_Area	SP_Area^2	WB_Area (1960)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	**NA**	**-0.49**	**0.70**	**-0.02**	**0.58**	**-0.93**	**8**	**-165.93**	**0.00**	**0.27**
NA	**NA**	**NA**	**0.74**	**-0.02**	**0.62**	**-0.92**	**7**	**-167.26**	**0.63**	**0.20**
NA	**-0.05**	**-0.48**	**0.71**	**-0.02**	**0.56**	**-0.91**	**9**	**-166.11**	**2.38**	**0.08**
NA	**-0.03**	**NA**	**0.74**	**-0.02**	**0.60**	**-0.91**	**8**	**-167.43**	**2.99**	**0.06**
0.11	**NA**	**-0.46**	**0.71**	**-0.02**	**0.58**	**-0.86**	**9**	**-166.42**	**3.00**	**0.06**
0.17	**NA**	**NA**	**0.75**	**-0.02**	**0.61**	**-0.83**	**8**	**-167.58**	**3.29**	**0.05**
NA	**NA**	**-0.54**	**0.77**	**-0.02**	**NA**	**-0.71**	**7**	**-168.67**	**3.46**	**0.05**
NA	**-0.39**	**-0.54**	**0.77**	**-0.02**	**NA**	**-0.65**	**8**	**-167.98**	**4.09**	**0.04**
NA	**NA**	**NA**	**0.81**	**-0.03**	**NA**	**-0.70**	**6**	**-170.41**	**4.90**	**0.02**
0.13	**0.04**	**-0.45**	**0.72**	**-0.02**	**0.59**	**-0.87**	**10**	**-166.47**	**5.14**	**0.02**
0.21	**0.11**	**NA**	**0.75**	**-0.02**	**0.65**	**-0.85**	**9**	**-167.61**	**5.39**	**0.02**
NA	**-0.38**	**NA**	**0.81**	**-0.03**	**NA**	**-0.64**	**7**	**-169.74**	**5.59**	**0.02**
NA	**-0.56**	**-0.57**	**0.82**	**-0.03**	**NA**	**NA**	**7**	**-169.96**	**6.02**	**0.01**
0.12	**NA**	**-0.52**	**0.78**	**-0.03**	**NA**	**-0.65**	**8**	**-169.14**	**6.41**	**0.01**
NA	**NA**	**-0.57**	**0.82**	**-0.03**	**NA**	**NA**	**6**	**-171.42**	**6.93**	**0.01**
NA	**NA**	**-0.53**	**0.80**	**-0.03**	**0.39**	**NA**	**7**	**-170.45**	**7.01**	**0.01**
-0.01	**-0.40**	**-0.54**	**0.77**	**-0.02**	**NA**	**-0.65**	**9**	**-168.43**	**7.03**	**0.01**
NA	**-0.56**	**NA**	**0.86**	**-0.03**	**NA**	**NA**	**6**	**-171.68**	**7.44**	**0.01**
0.17	NA	NA	0.82	-0.03	NA	-0.62	7	-170.72	7.55	0.01
NA	-0.45	-0.54	0.80	-0.03	0.26	NA	8	-169.75	7.63	0.01
NA	NA	NA	0.83	-0.03	0.42	NA	6	-171.83	7.74	0.01
0.34	NA	-0.46	0.82	-0.03	0.42	NA	8	-169.94	8.00	0.00
0.39	NA	NA	0.85	-0.03	0.46	NA	7	-170.96	8.03	0.00
NA	NA	NA	0.86	-0.03	NA	NA	5	-173.12	8.31	0.00
0.30	NA	-0.52	0.85	-0.03	NA	NA	7	-171.18	8.46	0.00
NA	-0.43	NA	0.83	-0.03	0.31	NA	7	-171.19	8.48	0.00
0.07	-0.34	NA	0.81	-0.03	NA	-0.61	8	-170.21	8.56	0.00
0.15	-0.45	-0.54	0.83	-0.03	NA	NA	8	-170.34	8.81	0.00
0.34	NA	NA	0.89	-0.03	NA	NA	6	-172.59	9.26	0.00

CF_Prop (210)	WL_Prop (1085)	SDI (1085)	SP_Area	SP_Area^2	WB_Area (1960)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
0.27	-0.21	-0.48	0.82	-0.03	0.35	NA	9	-169.75	9.67	0.00
0.34	-0.13	NA	0.85	-0.03	0.42	NA	8	-170.88	9.89	0.00
0.22	-0.40	NA	0.87	-0.03	NA	NA	7	-171.91	9.93	0.00
NA	NA	-0.58	NA	NA	0.83	-1.17	6	-195.13	54.35	0.00
NA	-0.02	-0.59	NA	NA	0.82	-1.16	7	-195.48	57.08	0.00
NA	NA	NA	NA	NA	0.92	-1.19	5	-197.85	57.76	0.00
-0.01	NA	-0.59	NA	NA	0.83	-1.17	7	-195.84	57.80	0.00
-0.03	-0.04	-0.59	NA	NA	0.82	-1.17	8	-196.07	60.26	0.00
NA	0.01	NA	NA	NA	0.92	-1.19	6	-198.16	60.40	0.00
0.03	NA	NA	NA	NA	0.92	-1.18	6	-198.50	61.08	0.00
0.04	0.04	NA	NA	NA	0.93	-1.18	7	-198.69	63.49	0.00
NA	NA	-0.64	NA	NA	NA	-0.90	5	-201.77	65.60	0.00
NA	-0.40	-0.64	NA	NA	NA	-0.84	6	-201.00	66.10	0.00
-0.21	-0.51	-0.65	NA	NA	NA	-0.89	7	-201.05	68.22	0.00
-0.05	NA	-0.63	NA	NA	NA	-0.92	6	-202.31	68.70	0.00
NA	NA	NA	NA	NA	NA	-0.90	4	-204.56	69.16	0.00
NA	-0.38	NA	NA	NA	NA	-0.85	5	-203.92	69.91	0.00
-0.06	NA	NA	NA	NA	NA	-0.92	5	-205.07	72.20	0.00
-0.18	-0.47	NA	NA	NA	NA	-0.89	6	-204.08	72.25	0.00
NA	NA	-0.63	NA	NA	0.55	NA	5	-205.87	73.81	0.00
NA	-0.45	-0.63	NA	NA	0.43	NA	6	-204.98	74.05	0.00
NA	-0.59	-0.65	NA	NA	NA	NA	5	-206.12	74.30	0.00
0.24	NA	-0.61	NA	NA	0.58	NA	6	-205.90	75.89	0.00
NA	NA	-0.66	NA	NA	NA	NA	4	-208.02	76.09	0.00
NA	NA	NA	NA	NA	0.59	NA	4	-208.24	76.53	0.00
NA	-0.46	NA	NA	NA	0.48	NA	5	-207.39	76.84	0.00
0.11	-0.38	-0.61	NA	NA	0.46	NA	7	-205.41	76.92	0.00
-0.04	-0.62	-0.65	NA	NA	NA	NA	6	-206.61	77.30	0.00
NA	-0.61	NA	NA	NA	NA	NA	4	-208.88	77.82	0.00
0.26	NA	NA	NA	NA	0.63	NA	5	-208.17	78.40	0.00
0.15	NA	-0.65	NA	NA	NA	NA	5	-208.42	78.90	0.00

CF_Prop (210)	WL_Prop (1085)	SDI (1085)	SP_Area	SP_Area^2	WB_Area (1960)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	NA	NA	NA	NA	NA	NA	3	-210.74	79.51	0.00
0.15	-0.36	NA	NA	NA	0.53	NA	6	-207.72	79.53	0.00
-0.01	-0.62	NA	NA	NA	NA	NA	5	-209.40	80.87	0.00
0.16	NA	NA	NA	NA	NA	NA	4	-211.13	82.30	0.00

Note: I do not present the results of the scale optimization phase of the scoter abundance modeling process because the optimal scales were identical to those identified during the scoter occurrence modeling process.

Table B.7. Importance values and standardized model-averaged parameter estimates for covariates included in all-subsets candidate scoter abundance model set.

Parameter	Estimate (95% CI)	Importance
Intercept	-3.75 (-4.56, -2.94)	-
SP_Area	0.73 (0.54, 0.92)	100%
SP_Area^2	-0.02 (-0.03, -0.01)	100%
WB_Count_438	-0.87 (-1.54, -0.20)	92%
WB_Area_1960	0.59 (0.12, 1.06)	80%
SDI_1085	-0.50 (-1.06, 0.06)	59%
WL_Prop_1085	-0.14 (-0.95, 0.66)	29%
CF_Prop_210	0.14 (-0.33, 0.61)	21%

Note: The estimates and associated 95% confidence intervals were calculated from models in the 95% confidence set of the all-subsets set (Table B.6).

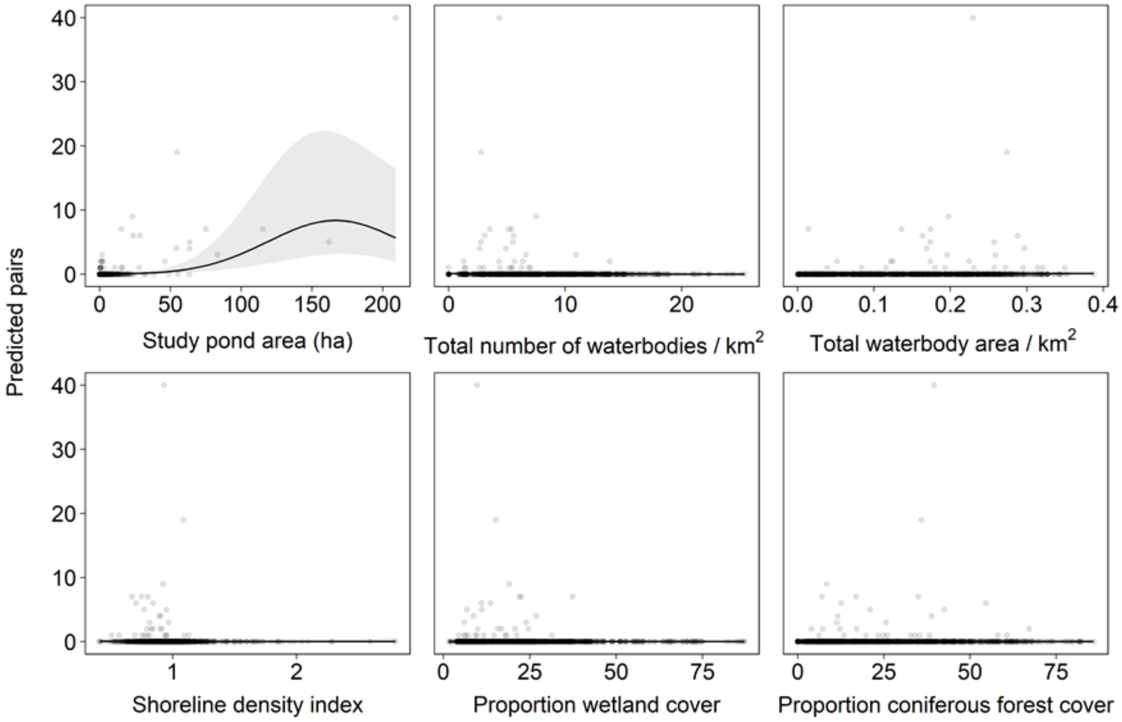

Figure B.1. Relationships between predicted scoter abundance on ponds and pond size and landscape composition covariates.

Table B.8. Model selection table for all possible scaup abundance model subsets (n = 64). The 95% confidence set of models (bolded) was used to calculate model-averaged parameter estimates.

CF_Prop (1085)	WL_Prop (1960)	SDI (210)	SP_Area	SP_Area^2	WB_Area (210)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
NA	**-0.45**	**NA**	**0.51**	**-0.02**	**-0.25**	**NA**	**7**	**-843.82**	**0.00**	**0.38**
NA	**-0.40**	**NA**	**0.49**	**-0.02**	**-0.21**	**-0.17**	**8**	**-843.64**	**1.66**	**0.17**
NA	**-0.42**	**0.11**	**0.52**	**-0.02**	**-0.23**	**NA**	**8**	**-844.24**	**2.85**	**0.09**
NA	**-0.36**	**NA**	**0.51**	**-0.02**	**NA**	**-0.23**	**7**	**-845.57**	**3.50**	**0.07**
-0.07	**-0.48**	**NA**	**0.51**	**-0.02**	**-0.26**	**NA**	**8**	**-844.65**	**3.68**	**0.06**
NA	**-0.42**	**NA**	**0.54**	**-0.02**	**NA**	**NA**	**6**	**-847.19**	**4.72**	**0.04**
-0.12	**-0.45**	**NA**	**0.48**	**-0.02**	**-0.23**	**-0.19**	**9**	**-844.25**	**4.91**	**0.03**
NA	**-0.38**	**0.10**	**0.50**	**-0.02**	**-0.20**	**-0.16**	**9**	**-844.32**	**5.06**	**0.03**
NA	**-0.39**	**0.15**	**0.56**	**-0.02**	**NA**	**NA**	**7**	**-846.58**	**5.52**	**0.02**
NA	**-0.34**	**0.13**	**0.52**	**-0.02**	**NA**	**-0.21**	**8**	**-845.58**	**5.54**	**0.02**
-0.07	**-0.45**	**0.11**	**0.52**	**-0.02**	**-0.24**	**NA**	**9**	**-845.07**	**6.56**	**0.01**
-0.04	**-0.37**	**NA**	**0.50**	**-0.02**	**NA**	**-0.24**	**8**	**-846.54**	**7.46**	**0.01**
NA	**NA**	**NA**	**0.50**	**-0.02**	**NA**	**-0.28**	**6**	**-848.59**	**7.52**	**0.01**
NA	**NA**	**NA**	**0.48**	**-0.02**	**-0.18**	**-0.23**	**7**	**-847.69**	**7.73**	**0.01**
-0.11	-0.42	0.10	0.49	-0.02	-0.21	-0.17	10	-844.97	8.39	0.01
NA	NA	0.14	0.52	-0.02	NA	-0.25	7	-848.17	8.69	0.00
0.04	-0.41	NA	0.54	-0.02	NA	NA	7	-848.21	8.78	0.00
NA	NA	NA	0.51	-0.02	-0.24	NA	6	-849.36	9.06	0.00
-0.04	-0.35	0.13	0.52	-0.02	NA	-0.21	9	-846.53	9.47	0.00
0.02	-0.38	0.15	0.56	-0.02	NA	NA	8	-847.61	9.60	0.00
NA	NA	0.12	0.50	-0.02	-0.16	-0.21	8	-847.82	10.03	0.00
NA	NA	0.15	0.53	-0.02	-0.21	NA	7	-848.94	10.24	0.00
0.12	NA	NA	0.51	-0.02	NA	-0.26	7	-849.40	11.16	0.00
NA	NA	0.17	0.56	-0.02	NA	NA	6	-850.44	11.21	0.00
0.09	NA	NA	0.49	-0.02	-0.18	-0.22	8	-848.64	11.67	0.00
NA	NA	NA	0.54	-0.02	NA	NA	5	-851.82	11.95	0.00
0.16	NA	NA	0.52	-0.02	-0.22	NA	7	-849.86	12.07	0.00
0.11	NA	0.14	0.52	-0.02	NA	-0.23	8	-849.03	12.45	0.00
0.15	NA	0.14	0.54	-0.02	-0.19	NA	8	-849.54	13.47	0.00

CF_Prop (1085)	WL_Prop (1960)	SDI (210)	SP_Area	SP_Area^2	WB_Area (210)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
0.19	NA	0.17	0.56	-0.02	NA	NA	7	-850.63	13.63	0.00
0.22	NA	NA	0.55	-0.02	NA	NA	6	-851.75	13.83	0.00
0.09	NA	0.12	0.50	-0.02	-0.16	-0.20	9	-848.80	14.01	0.00
NA	-0.37	NA	NA	NA	-0.26	-0.26	6	-871.04	52.41	0.00
-0.19	-0.45	NA	NA	NA	-0.28	-0.28	7	-871.06	54.47	0.00
NA	-0.45	NA	NA	NA	-0.33	NA	5	-873.53	55.37	0.00
NA	NA	NA	NA	NA	-0.24	-0.31	5	-874.52	57.36	0.00
NA	-0.36	0.05	NA	NA	-0.26	-0.26	7	-872.53	57.42	0.00
-0.13	-0.50	NA	NA	NA	-0.34	NA	6	-874.07	58.48	0.00
NA	-0.32	NA	NA	NA	NA	-0.33	5	-875.13	58.57	0.00
-0.19	-0.44	0.05	NA	NA	-0.27	-0.27	8	-872.58	59.54	0.00
NA	-0.43	0.06	NA	NA	-0.32	NA	6	-874.87	60.07	0.00
NA	NA	NA	NA	NA	NA	-0.37	4	-877.47	61.25	0.00
0.03	NA	NA	NA	NA	-0.24	-0.31	6	-875.65	61.65	0.00
NA	NA	0.07	NA	NA	-0.23	-0.31	6	-875.77	61.88	0.00
-0.10	-0.36	NA	NA	NA	NA	-0.34	6	-875.89	62.12	0.00
NA	-0.31	0.09	NA	NA	NA	-0.32	6	-876.08	62.51	0.00
-0.13	-0.49	0.06	NA	NA	-0.33	NA	7	-875.41	63.19	0.00
NA	NA	NA	NA	NA	-0.31	NA	4	-879.15	64.60	0.00
NA	NA	0.10	NA	NA	NA	-0.36	5	-878.21	64.75	0.00
0.07	NA	NA	NA	NA	NA	-0.36	5	-878.54	65.40	0.00
-0.10	-0.35	0.09	NA	NA	NA	-0.33	7	-876.83	66.01	0.00
0.02	NA	0.07	NA	NA	-0.23	-0.30	7	-876.91	66.17	0.00
NA	-0.41	NA	NA	NA	NA	NA	4	-880.54	67.38	0.00
0.13	NA	NA	NA	NA	-0.30	NA	5	-879.92	68.16	0.00
NA	NA	0.09	NA	NA	-0.30	NA	5	-880.08	68.48	0.00
0.06	NA	0.10	NA	NA	NA	-0.35	6	-879.30	68.93	0.00
NA	-0.39	0.11	NA	NA	NA	NA	5	-881.03	70.38	0.00
0.01	-0.40	NA	NA	NA	NA	NA	5	-881.58	71.48	0.00
0.12	NA	0.09	NA	NA	-0.29	NA	6	-880.90	72.13	0.00
NA	NA	NA	NA	NA	NA	NA	3	-885.05	74.39	0.00

CF_Prop (1085)	WL_Prop (1960)	SDI (210)	SP_Area	SP_Area^2	WB_Area (210)	WB_Count (438)	k	logLik	Δ AICc	ω*i*
0.00	-0.39	0.11	NA	NA	NA	NA	6	-882.07	74.47	0.00
NA	NA	0.13	NA	NA	NA	NA	4	-885.12	76.55	0.00
0.20	NA	NA	NA	NA	NA	NA	4	-885.19	76.68	0.00
0.18	NA	0.12	NA	NA	NA	NA	5	-885.43	79.17	0.00

Note: I do not present the results of the scale optimization phase of the scaup abundance modeling process because the optimal scales were identical to those identified during the scaup occurrence modeling process.

Table B.9. Importance values and standardized model-averaged parameter estimates for covariates included in all-subsets scaup abundance candidate model set.

Parameter	Estimate (95% CI)	Importance
Intercept	-1.36 (-1.88, -0.83)	-
SP_Area	0.51 (0.39, 0.62)	100%
SP_Area^2	-0.02 (-0.02, -0.01)	100%
WL_Prop_1960	-0.43 (-0.70, -0.16)	96%
WB_Area_210	-0.24 (-0.42, -0.07)	81%
WB_Count_438	-0.19 (-0.38, 0.00)	37%
SDI_210	0.12 (-0.02, 0.25)	21%
CF_Prop_1085	-0.08 (-0.38, 0.22)	14%

Note: The estimates and associated 95% confidence intervals were calculated from models in the 95% confidence set of the all-subsets set (Table B.8).

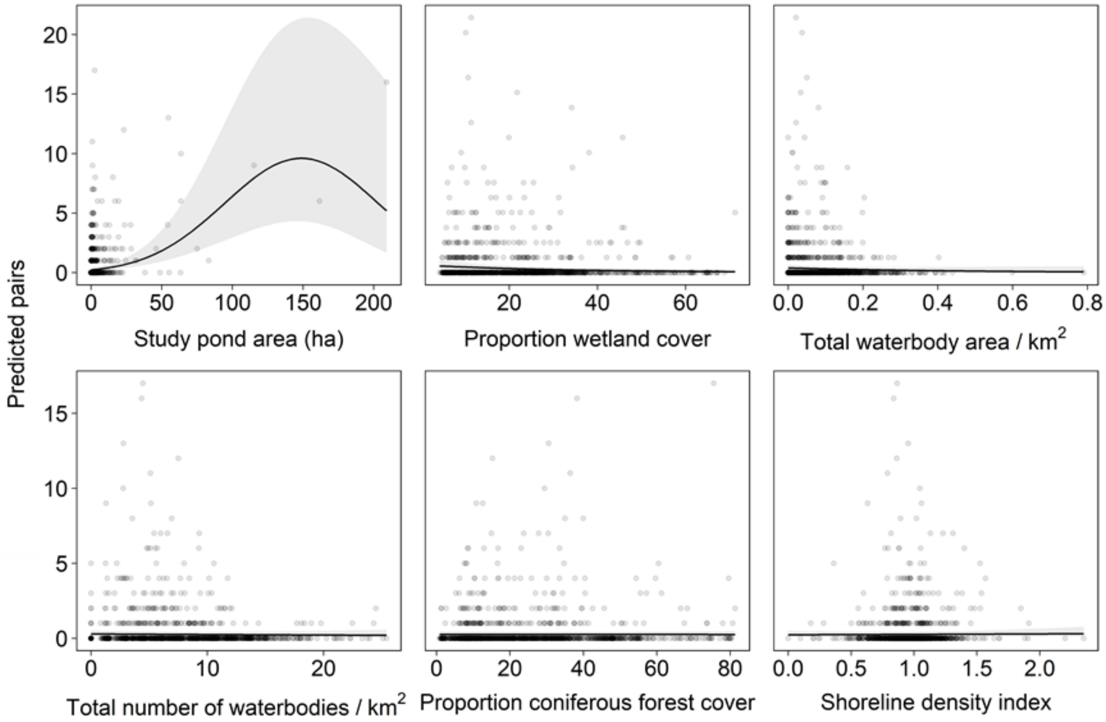

Figure B.2. Relationships between predicted scaup abundance on ponds and pond size and landscape composition covariates.

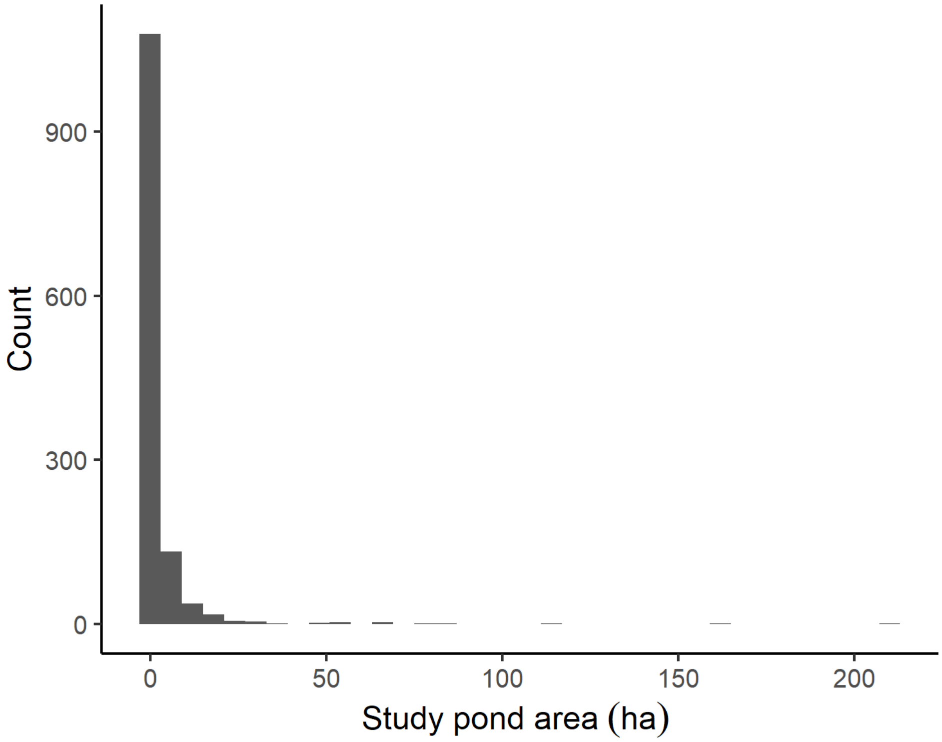

Figure B.3. Histogram of the distribution of study pond sizes in the Ramparts River wetlands study area (mean = 2.7, SD = 10.2, range = 0.02–209.0).