MULTI-SCALE PATTERNS OF BREEDING HABITAT SELECTION IN SANDHILL CRANES ACROSS CANADA'S EASTERN BOREAL FOREST

by

Kiaunna Jessica Lee

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Author's Declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Statement of Contributions

This research was conducted at the University of Waterloo by Kiaunna Lee under the supervision of Dr. Brad Fedy, and in collaboration with co-authors Kelly McLean, Christopher Sharp, and Christine Lepage. This thesis consists of two manuscripts (Chapters 2 and 3) formatted for submission to peer-reviewed journals. Conceptualisation and formulation of the research questions were collaborative efforts among all authors. Data collection was also conducted by all co-authors. Kiaunna Lee was responsible for data analysis, writing, and preparation for submission. All co-authors provided guidance throughout the research process and offered feedback and edits on the contents of both manuscripts. The introduction and conclusion chapters of this thesis (Chapters 1 and 4) are of my original work, with comments and suggestions provided by Kelly McLean.

To reflect the collaborative nature of the research, I use the pronoun ‘we’ in the following chapters to acknowledge the contributions and efforts of all co-authors involved in this project.

Abstract

The boreal forest of Canada serves as a critical breeding ground for numerous waterbird species, including sandhill cranes (*Antigone canadensis*). As sandhill cranes continue to expand their range in the boreal forest, it becomes increasingly important to identify habitat characteristics essential for breeding sandhill cranes for effective conservation and management. Limited research exists regarding the habitat dynamics of breeding sandhill cranes across this vast and remote landscape, necessitating research to understand spatial drivers of territory selection and habitat use in the boreal forest. Using high-resolution satellite telemetry data, we quantified the effects of land cover and land use on breeding habitat selection of sandhill cranes in the boreal forest of Ontario and Quebec, Canada across different scales: the landscape level (i.e., second order selection, which considers the overall landscape within which territories are established) and within the breeding range (i.e., third order selection, which focuses on specific habitat features selected within these territories). At the second order, or landscape level, sandhill cranes established breeding territories containing greater proportions of cropland, recently disturbed areas (e.g., forest cutblocks and burned areas), and wetlands. Sandhill cranes also selected territories with lower proportions of forest, open habitat, and water. At third order, or within their breeding ranges, sandhill cranes selected cropland, wetlands, recently disturbed areas, open habitat, and water, while avoiding forests and urban areas. Our findings suggest that current levels of anthropogenic disturbance do not negatively affect sandhill crane habitat selection, and that wetlands continue to play a crucial role in breeding habitat selection in the boreal forest. However, further research is required to explore the detailed impacts of forestry operations and the selection of recently disturbed areas on breeding behaviour and nest success in sandhill cranes. Our findings highlight the importance of using multi-scale approaches in habitat selection analyses that consider both broad ecological scales and the specific habitat requirements of individuals at the local scale. By comparing habitat use across both landscape and local scales, we demonstrate how sandhill cranes adapt their breeding habitat selection based on the availability and quality of different habitat types, allowing for robust inferences on the mechanisms that drive patterns of habitat selection both within their breeding territories and across the broader landscape. Collectively, this research contributes to the growing body of literature on breeding habitat selection of sandhill cranes, addressing important questions concerning patterns of habitat selection in response to a gradient of land cover and land uses classes in the boreal forest. Findings from this research can be applied to land management practices and assist managers when making inferences about sandhill crane habitat use in the boreal forest. Overall, this empirical approach can also be applied to a variety of species across diverse landscapes to assess how ecological processes differentiate across spatial scales and can support large-scale conservation efforts that ultimately benefits sandhill crane populations and biodiversity conservation in the boreal forest and beyond.

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Chapter 1: Literature Review

1.1 Ecology

Ecology is the scientific study of the relationships between living organisms and the environment (Taylor 1936). It aims to understand the abundance and distribution of living organisms in relation to the abiotic and biotic components of their environment (Hutchinson 1957). By examining the interdependence and interactions between organisms and their surroundings, ecologists are able to elucidate the mechanistic drivers that affect species behaviour and overall fitness (Fretwell and Lucas 1969). Ecological research provides important insights into the principles that govern the structure and function of ecosystems, addressing fundamental questions related to species assemblage and selection of habitat across multiple spatial scales (Rettie and Messier 2000, McLoughlin et al. 2004, Donnelly et al. 2021). Animal habitat selection is a central component of ecological research, driving an array of ecological and evolutionary processes that shape the underlying distribution and abundance of species within ecosystems (Northrup et al. 2022). Understanding the ecological drivers of habitat selection is essential for developing effective land management strategies aimed at conserving critical habitats and preserving wildlife diversity. Prior to developing habitat selection models and formulating probability-based predictions of habitat use, it is important to first understand how habitat use relates to species fitness, as explained by ecological niche theory.

1.2 Ecological niche theory

Ecological niche theory explores how species interact with their environment, linking individual fitness of an animal to their surroundings, and provides researchers with a foundational understanding for how evolutionary processes, competition dynamics, and predator-prey relationships shape habitat selection processes (Hirzel and Le Lay 2008).

Ecological niche can broadly be defined as two distinct concepts: (1) the Grinellian niche; and (2) the Eltonian niche. The Grinnellian niche refers to a range of non-interactive variables and environmental conditions that define a species' habitat in the absence of inter-species interactions (Grinnell 1917, Soberón 2007). It focuses on the ecological components and requirements that condition the presence of a species within a given location (Grinnell 1917), by assessing the species' distribution across habitats of varying environmental gradients (Junker et al. 2019). The Eltonian niche concept relates species existence to biological interactions and resource–consumer dynamics at local scales (Elton 1927, Junker et al. 2019). Presenting as an interaction framework, such as a community or ecosystem (Vandermeer 1972), the Eltonian niche defines the existence of a particular niche in relation to community interactions within a given ecosystem (Junker et al. 2019). Both the Grinnellian and Eltonian niche definitions describe the interactions between organisms within and across trophic levels (Junker et al. 2019) with Grinnellian niches identifying the environmental requirements for a species, while Eltonian niches examines the functional role and impact a species has on their environment (Junker et al. 2019). Linking niche concepts defined by Grinnell and Elton provides researchers with a broad understanding of species interaction, diversity, and community composition and the complex interplay between organisms and system components (Soberón 2007, Junker et al. 2019).

The exploration of ecological niches encompasses not only the Grinnellian and Eltonian concepts but also extends to other principles of ecological niche theory such as Gause's competitive exclusion principle, which explains the dynamics of species interactions within community assemblages (Pocheville 2015). This principle asserts that no two species can occupy the same ecological niche indefinitely (Gause 1934). If two species of the same niche were to coexist, it would either lead to the extinction of the weaker species or a behavioural shift towards a different ecological niche (Gause 1934). Gause's competitive exclusion principle focuses on the importance of resource partitioning and competition in shaping the structure and dynamics of ecological communities, underscoring the balance and competitive pressures that govern species interactions within ecosystems, and thus highlights the importance of niche dynamics and community assemblage processes.

Aspects of Grinnellian and Eltonian niches and the competitive exclusion principle can further be conceptualized and combined into the Hutchinsonian niche (Pocheville 2015). The Hutchinsonian niche provides a conceptual basis for understanding the necessary set of abiotic and biotic conditions required for a species to persist and reproduce within a closed habitat (Hutchinson 1957). By incorporating a species' ecological tolerance to environmental variability, Hutchinsonian niches can be defined as an n-dimensional hypervolume of environmental variables in which a species can persist indefinitely (Hutchinson 1957, Vandermeer 1972). Hutchinson classifies the n-dimension as the fundamental niche, which includes the complete range of physical and biological conditions in which a species could survive and reproduce in the absence of all biotic interactions (e.g., predation, competition, and symbiosis) (Hutchinson 1957). The realized niche represents a portion of the fundamental niche and is shaped by limiting factors imposed by other biotic interactions within the ecosystem (Hutchinson 1957). The fundamental niche is similar in theory to the Grinnellian niche, while the realized niche is consistent with Elton’s niche concept (Vandermeer 1972). However, unlike Hutchinson who attributed niches to species, Grinnell (1917) and Elton (1927) relates niches to environment (Colwell and Rangel 2009). The Hutchinsonian niche, which formalizes the terms fundamental and realized niche, presents a conceptual framework for ecological niche theory, and serves as the foundation for research related to habitat selection.

1.3 Linking ecological niche theory to habitat selection

Ecological niche theory describes the role and position of a species within its community, including all biotic and abiotic factors that influence species survival and reproduction (Vandermeer 1972). The concept of ecological niche can be quantified as a function that links the fitness of an individual to their environment, allowing researchers to study a variety of ecologically related concepts including evolutionary processes, species-interactions, and predation dynamics (Hirzel and Le Lay 2008). The theory of habitat selection builds upon ecological niche concepts by suggesting that species occupy habitat based on trade-offs between resource availability, predation risks, and competition (Rosenzweig 1981). Habitat selection models aim to predict the likelihood of species occurrence across heterogeneous landscapes as a function of the relative profitability within different habitat patches or ranges (Northrup et al. 2022). Thus, habitat selection models can be seen as practical implementations of ecological niche theory, as habitat selection analyses use environmental variables to predict patterns of habitat use and distribution across the range of a species (Hirzel and Le Lay 2008, Northrup et al. 2022).

1.4 Habitat selection

1.4.1 Defining habitat

It is important to first define what habitat and habitat use are before differentiating between habitat preference and habitat selection. Habitat is a point in environmental space, defined by the sum of all resources, conditions, and risks that influence the occupancy, reproduction, and survival of a species (Krausman 1999, Northrup et al. 2022). These resources represent all abiotic and biotic components that impact the abundance, distribution, and individual fitness of a species (Jones, 2001). Habitat use refers to the proportion of time an individual spends within a habitat (Jones, 2001; Krausman, 1999). This can be used to describe the distribution of a species across the landscape with respect to resource use

(Krausman 1999). Habitat preference measures the likelihood of selection and is conditioned on all habitats being equally accessible and available to the individual (Johnson 1980, Manly et al. 2002, Beyer et al. 2010, Lele et al. 2013). Habitat selection is a hierarchical process where an animal will select and use habitat relative to its availability and occurs across different scales of the environment (Johnson 1980, Krausman 1999, Boyce et al. 2002, Lele et al. 2013, Northrup et al. 2022).

1.4.2 Habitat selection and scale

Habitat selection is a central focus of ecological and evolutionary research (Boyce and McDonald 1999, Shafer et al. 2012). The study of habitat selection is important for understanding how environmental variables influence the abundance and distribution of species at both an individual and population-level, across heterogeneous landscapes (Matthiopoulos et al. 2015, Leclerc et al. 2016). Habitat selection also provides important insight into ecosystem functioning by focusing on underlying ecological processes such as trophic structuring, species interactions, and spatial distribution patterns across domains (Lipsey et al. 2017, Northrup et al. 2022). By understanding the factors that influence habitat selection, researchers can also predict the effects of changing environmental conditions, such as climate and land-use (Northrup et al. 2022). Thus, the study of habitat selection allows researchers to assess how ecological processes differentiate across spatial scales, thereby improving our knowledge of animal ecology and evolution, and can help guide conservation decisions and management efforts of species.

Habitat selection is a hierarchical process that occurs across multiple spatial scales (Wiens 1973, Johnson 1980, McLoughlin et al. 2004, McGarigal et al. 2016). Johnson (1980) proposed a four-level framework for studying habitat selection where: first order represents a selection of geographic space, which encompasses the entire range of a species; second order represents the home range of an individual within the species' geographic range; third order relates habitat selection to habitat components within the individual’s home range; and fourth order relates habitat selection to use of resource components within a foraging habitat.

The hierarchical nature of habitat selection (Johnson 1980) allows researchers to conduct selection analyses across different orders and scales (McGarigal et al. 2016, Northrup et al. 2022). However, the order and spatiotemporal scale at which a study is conducted at can impact our understanding of the underlying processes that influence patterns of habitat selection (Orians and Wittenberger 1991, Herfindal et al. 2009). The decision-making processes that animals use when selecting a habitat occur in a hierarchical manner across different spatiotemporal dimensions (Northrup et al. 2022). For example, when studying selection at broader scales, researchers measure habitat selection across the entire species extent, making inferences about species selection at the population level (Krausman 1999, Manly et al. 2002). At finer scales, researchers sample use for each animal, measuring patterns of habitat selection at an individual level (Manly et al. 2002, Ciarniello et al. 2007). Therefore, it is important to assess habitat selection across all relevant hierarchal levels and scales to understand the complex interplay between environmental factors and individual fitness.

1.4.3 Modelling habitat selection

The advancement and development of new remote sensing technologies (e.g., Global Positioning System (GPS) transmitters) has made it possible to integrate the study of animal movement with environmental data at fine spatial and temporal scales (Neumann et al. 2015, Signer and Fieberg 2021), allowing researchers to develop novel modelling techniques that establish links between animal movement decisions and habitat characteristics (Holbrook et al. 2017). Common approaches for analysing patterns of habitat selection from telemetry and environmental data include resource selection functions (RSFs) (Boyce and McDonald 1999).

RSFs provide a robust framework for modelling habitat selection by estimating the apparent effect of a spatial covariate on the distribution of a species (Northrup et al. 2013). RSFs are typically conducted under a use-availability design, comparing the proportion of resource units that are used by an animal, to those that are available, across a defined habitat (Boyce and McDonald 1999, Fieberg et al. 2021). Habitat is defined as a set of environmental covariates located within the area of where an animal was observed, while available habitat is quantified as the distribution of resources that are available and accessible to the animal (Boyce et al. 2002, Northrup et al. 2013). Available habitat is often represented by set of randomly distributed points placed within the study region, from which species data is missing (Pearce and Boyce 2006). These points are assumed to represent true absences, denoting areas where a species is not known to occur (Boyce et al. 2002). However, since continuous 24-hour monitoring of animals is impossible, areas assigned as available may include undetected points used by the animal (Graham et al. 2004). Habitat selection is assessed by fitting a logistic regression model that evaluates the probability of a species using a specific environmental covariate relative to proportion of habitat that is available to be selected (Fieberg et al. 2021, Northrup et al. 2022). Habitat is considered selected when it is used in excess of its availability (Boyce et al. 2002). Model results can then be used to develop spatial maps predicting relative probability of habitat selection across the landscape (DeCesare et al. 2012, Hebblewhite et al. 2014, Holbrook et al. 2017).

1.4.4 Limitations of resource selection functions

RSFs are limited by how availability is defined. The choice of criteria used to define availability can impact the results of resource selection analyses, making it difficult to correctly align availability with the perception of habitat that is truly available to an animal or population (Beyer et al. 2010, Northrup et al. 2013). The chosen availability domain can also affect the estimated habitat selection parameter (Beyer et al. 2010), which may lead to inaccurate inferences about the importance of a resource based on the strength of selection or avoidance. This has important implications for guiding conservation management research as the results of a resource selection analysis may not accurately reflect the true habitat use of the animal or population (Rettie and Messier 2000, Beyer et al. 2010, Northrup et al. 2013, Holbrook et al. 2017). This is a particular concern when evaluating habitat selection across different hierarchical orders (e.g., only assessing habitat selection at third order compared to second order) (Levin 1992, Rettie and Messier 2000). For example, assessing habitat selection at higher orders may create an overabundance of available resources that may appear to be irrelevant at lower levels of selection (Johnson 1980, Levin 1992, Anderson et al. 2012, Holbrook et al. 2017). To address this limitation, researchers may instead choose to evaluate habitat use and availability across multiple scales to provide a more comprehensive and holistic understanding of the complex relationships between habitat and species (e.g., Ciarniello et al. 2007, DeCesare et al. 2012, Holbrook et al. 2017). By doing so, researchers may be better able to align availability with the perception of an animal or population and avoid the potential biases that can arise when defining availability across scales.

1.5 Habitat selection in avian ecology

In the early stages of habitat selection theory, avian research centred around community ecology and species assemblage (Kendeigh 1945, Hildén 1965), and correlative models were a common approach to describe the relationship between species abundance and habitat characteristics (Jones 2001). In the 1970s and 1980s, researchers began to develop more complex models involving density dependence such as the ideal free distribution model (Fretwell and Lucas 1969). The ideal free distribution model predicts how individuals will distribute themselves among available habitat relative to resources to maximize fitness and reduce resource competition (Fretwell and Lucas 1969). Advancement in technological and statistical techniques during the 1990s and 2000s allowed researchers to develop more complex models for habitat selection analyses (Boyce et al. 2002, Manly et al. 2002, Thurfjell et al. 2014, Avgar et al. 2016). Common approaches to studying habitat selection today in avian research include fixed order selection (Beatty et al. 2014, Miller and Barzen 2016, Dyson et al. 2019) and hierarchical selection (Johnson 1980, Rolstad et al. 2000, Ciarniello et al. 2007, Lipsey et al. 2017).

Management of avian species can occur across multiple scales and over large landscapes, especially for migratory species. The annual cycle of migratory birds is characterized by long-distance movements across diverse geographic landscapes (Fronczak et al. 2017, Stanley et al. 2021, Sorais et al. 2023). Migratory behaviour also varies throughout a species' annual cycle which affects individual settlement decisions and habitat selection processes (Davis 2001, Su 2003, Miller and Barzen 2016, Fronczak et al. 2017, Kruse et al. 2017, Collins et al. 2023). Therefore, mechanisms for assessing habitat selection throughout an individual's annual cycle is dependent on the chosen order and temporal scale of habitat selection theory (Wiens 1973, Johnson 1980). For example, at selection at higher orders can differ based on the type of home range the individual is selecting (e.g., breeding versus non-breeding ranges, stopover sites, wintering ranges), while at finer scales, selection within the home range is linked to factors that influence habitat use (e.g., food versus nesting availability, nest predation risk) (Legagneux et al. 2009, Aborn 2010, Kruse et al. 2017, Dyson et al. 2019, Donnelly et al. 2021, Séchaud et al. 2021, Stanley et al. 2021, Casabona I Amat et al. 2022). Evaluating how decision-making processes vary across temporal scales is also important. For example, seasonal decisions may vary across an annual cycle (e.g., breeding versus migration versus wintering seasons) based on the habitat needs of the individual (Iverson et al. 1987, Beatty et al. 2014, Miller and Barzen 2016, Pearse et al. 2017, David M. Baasch et al. 2019, Stanley et al. 2021). Therefore, it is important to understand how habitat selection processes occur at various spatial and temporal scales throughout the annual cycle of migratory bird species to fully understand the complex relationship between avian species and their habitat.

1.6 Sandhill crane ecology

Sandhill cranes (*Antigone canadensis*) provide a unique opportunity to study habitat selection at multiple spatial scales due to their complex migratory behaviour, expansive geographic range, and socio-economic relevance. The Eastern Population (EP) of sandhill cranes (hereafter, “cranes”) were nearly extirpated in the 1900’s due to overharvesting, anthropogenic disturbance, and habitat loss (Walkinshaw 1949, Walkinshaw and Wing 1955, Lumsden 1971, Gerber et al. 2014). However, the development of conservation efforts over the last century, such as hunting regulations, habitat protection, and restoration, has resulted in the population recovery and range expansion of sandhill cranes (Lumsden 1971, Meine and Archibald 1996, Sutherland and Crins 2007, Van Horn et al. 2010, Gerber et al. 2014, Fronczak et al. 2017, Lepage 2019, Casabona I Amat et al. 2022). The success of crane conservation is of social importance, providing economic benefits through ecotourism and harvest (Van Horn et al. 2010, Fronczak et al. 2017). Despite the positive outcomes of crane conservation efforts, there have also been an increase in the number of conflicts between humans and cranes (Van Horn et al. 2010, Hemminger et al. 2022). Sandhill cranes are known to forage on crops such as corn, soybeans, and wheat, causing excessive damage to agricultural lands (Reinecke and Krapu 1986, Sudgen et al. 1988, Barzen et al. 2021), resulting in crop loss incurred by agricultural producers (Van Horn et al. 2010, Austin 2012, Hemminger et al. 2022). Furthermore, as a migratory game species, the management of cranes requires multilateral agreement across system levels. This includes cooperation across international, federal, and provincial borders as well as coordination between government bodies and various stakeholders. Such efforts are necessary to ensure sustainable harvest rates and the protection of critical habitats are met across borders and demonstrates the importance of linking local and regional-scale habitat management actions to continental-scale conservation and management.

Cranes serve as a unique focal species for studying habitat selection across multiple scales. The geographic range of cranes extends from Ontario to Florida, with migration routes encompassing the Atlantic and Mississippi flyway states (Van Horn et al. 2010, Amundson and Johnson 2011, Fronczak et al. 2017). Wintering grounds extend from Indiana to Florida while summer areas are distributed throughout Minnesota, Wisconsin, Michigan, and the Great Lakes region (Van Horn et al. 2010, Amundson and Johnson 2011, Lacy et al. 2015, Fronczak et al. 2017, Casabona I Amat et al. 2022). Recent conservation efforts have also led to further range expansions and suspected re-occupation of historical breeding ranges in Canada’s boreal forests (Van Horn et al. 2010, Gerber et al. 2014, Casabona I Amat et al. 2022). Given their large geographic extent, management of cranes and their habitat requires a multi-scale systems approach to describe patterns of habitat selection across different spatial scales.

As cranes migrate from breeding to stopover to wintering sites, their habitat requirements will vary depending on the life stage and annual cycle of the individual (Aborn 2010, Gerber et al. 2014, Donnelly et al. 2021). Previous studies have investigated habitat selection in cranes throughout the non-breeding season (Amundson and Johnson 2011, Gerber et al. 2014, Fronczak et al. 2017) However, there is considerably less knowledge about breeding habitat selection and breeding phenology of cranes (Casabona I Amat et al. 2022). Breeding habitat is a key resource for cranes and nest success is vital for regulating crane abundance and population persistence (Jiménez-Franco et al. 2018). Anthropogenic disturbances throughout this critical life-history stage may lead to declines in population size, survivorship, and nest viability through nest abandonment, intraspecific competition, and nest predation (Toland 1999, Barwisch et al. 2022). Given their recent range expansion (Lumsden

1971, Van Horn et al. 2010, Amundson and Johnson 2011, Gerber et al. 2014, Casabona I Amat et al. 2022), our knowledge of breeding ecology remains limited, and research is required to understand spatial and temporal drivers of breeding territory selection for effective conservation planning and management.

1.7 Research objectives and thesis outline

Between 2019-2022, we deployed GPS-GSM transmitters on 122 adult cranes across Eastern Canada to estimate the population distribution and quantify patterns of habitat use. These efforts provide a unique opportunity to investigate drivers of habitat use across multiple spatial scales.

Leveraging this unique dataset, this thesis aims to understand how land cover and land use effects breeding habitat selection of cranes in Eastern Canada's boreal forest across multiple orders by answering the following questions:

1. What land cover and land use variables influence the establishment, distribution, and selection of breeding territories of cranes?
2. What land cover and land use variables effect patterns of habitat selection within the home ranges of breeding cranes?

Chapter 2 addresses the first research objective by quantifying the effects of land cover and land use variables on second order selection (Johnson 1980) and predicting the probability of crane breeding territory selection across the boreal landscape. Chapter 3 addresses the second research objective to quantify patterns of crane breeding habitat selection at the third order (Johnson 1980). Chapter 4 provides a general summary of findings, management implications, and conclusions and contextualizes the importance of using multi-scale approaches when conducting habitat selection analyses. Overall, this research provides important insight into crane ecology, particularly how land use and land cover drive breeding territory and breeding habitat selection within the boreal forest. Findings from this research can be used to guide land management practices that prioritize the conservation of breeding habitats, which is especially important as cranes continue to expand their breeding ranges into the boreal forest.

1.8 Study system

Canada's boreal forest is a vast and diverse ecosystem that covers almost 30% of North America’s land mass, making it one of the largest intact forest regions in the world (Brandt 2009). The boreal forest plays a major role in social, cultural, and economic wealth of Canada, while also supporting a large diversity of wildlife populations (Venier et al. 2014, Chen et al. 2016). Interactions and feedbacks that maintain forest resiliency, ecosystem function, and wildlife biodiversity are sensitive to external and internal pressures such as human activity and industrial development (Venier et al. 2014, Cumming and Allen 2017). Over the past century, the boreal forest has experienced an increase in anthropogenic disturbance, primarily in the form of intensive logging practices and development of linear features such as roads (Brodeur et al. 2008, Wells 2011, Hermosilla et al. 2016, St-Pierre et al. 2022). These anthropogenic activities are a substantial driver in shaping the boreal landscape and can influence overall patterns of habitat use in wildlife species (Lemelin et al. 2007, Dyson et al. 2019, St-Pierre et al. 2022, Tattersall et al. 2023). However, the extent to which these activities affect wildlife diversity, habitat quality, and the integrity of the boreal forest ecosystem remains complex and unclear (Lemelin et al. 2007, Brandt 2009, Houle et al. 2010, Wells 2011, Jones et al. 2015, Fryxell et al. 2020, Wilson et al. 2020, Johnstone et al. 2023)

Our study area was located in the Northern Forest Ecoregion (hereafter, “boreal forest”; US EPA 1997), of Ontario and Quebec, Canada. The boreal landscape is dominated by coniferous, broadleaf, and mixedwood forests. Common tree species found within the study extent include black and white spruce (*Picea mariana, Picea glauca*), balsam fir (*Abies* *balsamea*), eastern white cedar (*Thuja occidentalis*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) (Bergeron et al. 2014, Baret et al. 2017). Hydrological features such as wetlands, rivers, and lakes are also interspersed across the landscape, along with barren, shrubland, and grassland habitats. Land cover composition across the boreal forest has also been influenced by natural disturbance events (e.g., wildfires) and anthropogenic development (e.g., urban centres, cities, agricultural land, forestry cutblocks, and linear road networks) (Latham et al. 2011, Bergeron et al. 2014, Pickell et al. 2015, Hermosilla et al. 2016).

Chapter 2: Breeding territory selection of sandhill cranes across the boreal forest

2.1 Abstract

Understanding the spatial distribution and individual selection of breeding habitat is important for effective conservation and management of wildlife species. Advancement in GPS-tracking technology allows for the collection of high-resolution location data and analysis of habitat selection in remote areas. Here, we investigated territory selection of breeding sandhill cranes (*Antigone canadensis*) in the boreal forests of Ontario and Quebec, Canada, using high-resolution GPS tracking data across a gradient of land cover and land use classes. We quantified breeding territory selection across a large geographic extent using resource selection functions and developed spatial maps to predict the distribution of breeding territories across the boreal forest landscape. Sandhill cranes (n=49) arrived at their breeding territories in late April and departed in late August, remaining on breeding grounds for approximately 4 months. The size of breeding territories varied considerably among individuals, with an average size of 14.1 ± 21.7 km^2. Our resource selection models revealed selection for habitats containing greater proportions of cropland, forest disturbance, and wetland. Management efforts should focus on enhancing the quality and connectivity of selected habitats, particularly wetlands, to support sandhill crane management in the boreal forest. These findings underscore the importance of integrating landscape-level analyses with detailed patterns of habitat selection to inform the development of effective management strategies that support the long-term conservation of breeding sandhill cranes in the boreal forest.

2.2 Introduction

Habitat selection is a central focus of ecological research in wildlife species, providing ecologists and managers with important information on how animals select and use resources across the landscape and life stages. Understanding interactions between species and their habitats provides researchers with fundamental insights into factors that affect distribution and habitat selection at both individual and population levels (Fretwell and Lucas 1969, Hirzel and Le Lay 2008, Matthiopoulos et al. 2015). The incorporation of spatially-explicit covariates into habitat selection analyses allows researchers to also spatially project models predicting the relative probability of use across landscapes (Boyce et al. 2002, Morris et al. 2016, Holbrook et al. 2017). These spatial predictions can guide land use practices that aid in the conservation and management of species.

Habitat selection is a hierarchical process across multiple spatial scales (Rettie and Messier 2000, McLoughlin et al. 2004, Ciarniello et al. 2007). Johnson (1980) characterized selection across four orders: first order, which encompasses the geographic range of a species; second order, which represents home range selection; third order, which describes habitat use within the home range; and fourth order, which identifies the selection of particular resource components. Because habitat selection is scale dependent, inferences about habitat use can vary depending on the scale or level at which it is studied (Orians and Wittenberger 1991, Herfindal et al. 2009, Paton and Matthiopoulos 2016, Holbrook et al. 2017). Studies, particularly in avian species, commonly assess habitat selection at the third and fourth orders (Nesbitt 1988, Davis 2001, Maxson et al. 2008, Batbayar et al. 2014) with research of habitat selection at the second order being less common. By studying habitat selection at the second order, researchers can analyse patterns of habitat use across the landscape, allowing for a more comprehensive understanding of how species interact with their environment and select home ranges (Meyer and Thuiller 2006).

Quantifying habitat selection for species in remote habitats is particularly difficult due to the challenges of access and monitoring (Davis et al. 2014). For wide-ranging species, difficulties are further compounded by the researcher’s limitations in capturing complex ecological processes over large spatial extents. The development of high-resolution GPS tracking technology has revolutionized the ability for researchers to monitor habitat use through the remote collection of location data from individuals across large spatial scales and over multiple life stages (Martin et al. 2009, Hebblewhite and Haydon 2010). Habitat selection studies that do not use GPS technology often requires the researcher to define the study extent *a priori*, typically based on access. However, constraining the extent of a study to a pre-defined study area boundary fundamentally influences research findings and conclusions and thus, interpretations of habitat-animal relationships in habitat selection studies (Doherty et al. 2016). One of the unique advantages of using GPS technology is that the study extent is defined based on the animal movements rather than a researcher's access to a particular study area, thereby improving the accuracy, external validity, and robustness of habitat selection findings.

Sandhill cranes (*Antigone canadensis)* are a large, migratory, waterbird with a wide geographic distribution across North America (Krapu et al. 2011, Fronczak et al. 2017). In the 20th century, the Eastern Population of sandhill cranes (hereafter "*cranes*"), faced near extirpation due to unregulated hunting, anthropogenic disturbance, and loss of wetland habitats (Walkinshaw 1949, Walkinshaw and Wing 1955, Lumsden 1971). Recent conservation efforts and development of management policies have facilitated the population recovery and expansion of ranges, including the re-colonization of suspected historical breeding ranges in Ontario and Quebec, Canada (Lumsden 1971, Meine and Archibald 1996, Sutherland and Crins 2007, Van Horn et al. 2010, Fronczak et al. 2017, Lepage 2019, Casabona I Amat et al. 2022). Breeding habitat is an essential resource for cranes and plays an important role in regulating population persistence throughout their annual life cycle (Toland 1999, Gerber et al. 2015, Jiménez-Franco et al. 2018, Swift et al. 2023). Therefore, understanding the spatial distribution and patterns of breeding habitat selection is important for the successful conservation and management of crane populations.

While previous studies have investigated habitat selection of sandhill cranes throughout the breeding season (Baker et al. 1995, Maxson et al. 2008, Miller and Barzen 2016, Kruse et al. 2017), there is considerably less knowledge about the spatial distribution of breeding ranges, especially within the boreal region (Casabona I Amat et al. 2022). The remote and inaccessible nature of the boreal forest in Ontario and Quebec presents barriers for conducting breeding habitat selection studies within this region (Andrew et al. 2012). GPS technology facilitates a more accurate analysis of breeding habitat selection for cranes in the region by allowing for the remote collection of animal location data over broad extents. Thus, the study extent is defined by movement of the cranes themselves rather than researcher-imposed limits, allowing for a more species-driven approach to modelling habitat selection. Allowing the species to define the study extent not only improves the precision of habitat selection studies and relevance of the findings, but can also lead to more targeted conservation and management strategies that address the specific habitat requirements of cranes in the boreal forest ecosystem.

To understand patterns of breeding habitat selection at the second order (i.e., territory selection), we address the following research objectives: (1) identify the distribution of home ranges (hereafter, breeding territories) used by cranes throughout the breeding season in the boreal forest of Ontario and Quebec, Canada; (2) evaluate how land cover and land use influence breeding territory selection of cranes at the landscape level (i.e., second order selection) in the boreal forest; and (3) spatially project our models across our study extent and develop habitat maps predicting the probability of breeding territory selection in order to help inform and guide conservation and management decisions related to the breeding habitat of cranes in the boreal forest.

2.3 Methods

2.3.1 Study area

Our study area, which encompassed the breeding grounds of cranes determined using the GPS locations of our tagged cranes (n=144), was located in the Northern Forests Ecoregion (hereafter boreal forest, US EPA 1997), across Ontario and Quebec, Canada (Figure 2.1). We excluded 14 transmittered cranes that bred in the Taiga and Hudson Plain Ecoregions because the availability of land cover variables located outside the boreal forest were limited across the remainder of our study extent. The boreal forest is dominated by coniferous, hardwood, and mixedwood trees (Bergeron et al. 2014), with lakes, rivers, and wetland habitats interspersed across the landscape (Pelster et al. 2008) along with occasional human settlements, agricultural lands, and industrial development complexes (Farrell et al. 2017, Casabona I Amat et al. 2022). Over the past decades, land cover composition and ecosystem dynamics have been influenced by both natural disturbance events (e.g., wildfires) and forestry practices (Bergeron et al. 2014). Recreational access and industrial features have also altered the composition of natural landscapes through the development of linear networks, such as roads, and polygonal features, such as forestry cutblocks (Latham et al. 2011, Pickell et al. 2015).

2.3.2 Capture and handling

All procedures were approved by the Environment and Climate Change Canada Animal Care Committee (permit 19CS02, 20CS02, 21CS02, and 22CS02) and the University of Waterloo Animal Care Committee (AUPP #43725). Capture and handling of cranes were permitted under the Environment and Climate Change Canada banding permits (#10847 and #10546G).

2.3.2.1 Site selection

We identified major staging areas in Ontario and Quebec, where large gatherings of cranes were observed, to ensure we obtained a sample that was representative of the Eastern Population of cranes in Ontario and Quebec (McLean et al. *in prep*). We used eBird observations (eBird 2019) and reports from agricultural producers who had experienced conflicts with cranes to estimate the approximate arrival dates to agricultural fields throughout the fall season. Within Quebec, we also incorporated data from the Second Atlas of the Breeding Birds of Southern Quebec (Lepage 2019) to identify other potential staging areas. Additionally, a separate pilot Eastern Population crane survey was conducted in Ontario during the fall of 2012-2016 (Sharp et al. 2016, unpublished data) to determine further areas of interest within Ontario. Once potential capture locations were identified, we travelled to these areas to identify capture sites based on the preferred habitat of cranes, which included agricultural fields and grasslands, and repeated observations of cranes.

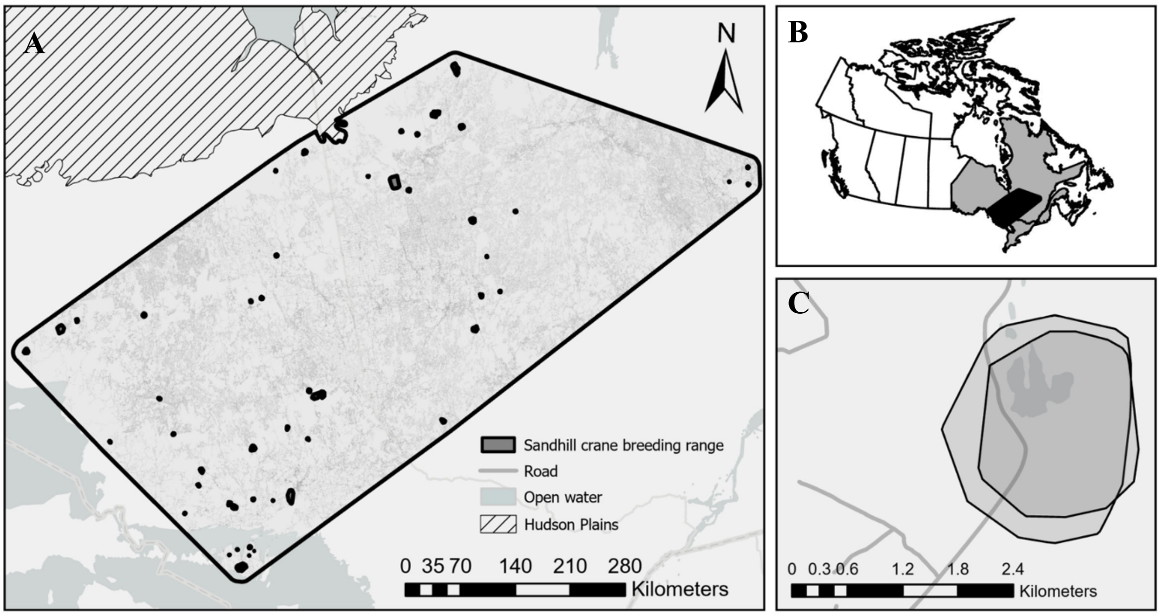

Figure 2.1. Location of sandhill crane breeding ranges across the boreal forest of Ontario and Quebec, Canada during 2020-2023 breeding season. Figure A represents the map of the study area and distribution of home ranges (n=90) of breeding sandhill cranes (n=49). Study area was clipped to the Northern Forest Ecoregion and any areas located outside of the zone were removed[a]. Figure B shows the geographic location of the study area in Ontario and Quebec, relative to Canada. Figure C is a fine-scale example depicting the spatial overlap of an individual crane's breeding territory between 2 successive breeding years.

[a] Note: Some breeding territories were located north of the study area (n=14 breeding territories). These individuals were excluded from our analysis as our study was focused on breeding territory selection within the boreal forest (see Study Area section in the Methods).

2.3.2.2 Capture and deployment

Trapping and capture of cranes occurred from September to October 2019-2022, using an 18.3 x 12.2-meter rocket Ontario or canon Quebec propelled net assembly, in accordance with protocols developed by Krapu et al. (2011) and Fronczak et al. (2017). Net set-up occurred either the night prior or early in the morning prior to the expected arrival of cranes to the field. Nets were placed in previously identified areas hosting high concentrations of cranes. Crane decoys and a remote-controlled speaker (FoxProXL, Lewistown, PA, USA) were placed around some of the trapping areas. We also lightly baited the field with corn or barley (depending on the field type), placing bait around the trapping area and within the capture zone. The safety zone within the capture area was marked using natural materials and the net was deployed once all target cranes were within the safety zone. Following net deployment, cranes were immediately removed from the net and placed in modified holding bags.

We focused our tagging efforts on adult females as they were more likely to return to breeding territories located in Ontario and Quebec the following years, compared to juveniles, sub-adults, and adult males (Walkinshaw 1949, Drewien 1973, Wolfson et al. 2020). Minimal morphological differentiation exists between males and females, making it difficult to reliably sex cranes by plumage in the field (Tacha et al. 1994). The only univocal method of reliably sexing cranes involves collecting blood samples and conducing post-capture genetic analysis.

In the field, presumed female cranes were identified and targeted by differences in behavioural characteristics, size, and weight. Males are more likely to display vigilant and agonistic behaviours towards conspecifics, while females and juveniles spend more time foraging (Tacha 1988). Females are also generally smaller than males (Lockman et al. 1987). Following capture, cranes were weighed and cranes $\leq$ 5000g were assumed to be female (Lockman et al. 1987). Transmitter deployment on presumed females also reduced the probability of targeting pair bonds when $\geq$2 cranes were captured. Because cranes are perennially monogamous, duplicate data may occur between pairs as cranes will only re-remate after death or, in certain cases, when breeding attempts fail (Tacha et al. 1994). In cases where we captured >1 pair, and the majority of captured cranes were male, transmitters were placed on adult male cranes instead of females, allowing us to maximize the number of transmitters deployed per catch. We differentiated adults and sub-adults (>1 years) from juveniles ($\leq$1 years) by head and eye colour (Pyle 2008).

All captured cranes received a single aluminium butt-end size-8 band. For cranes that were selected to receive a transmitter, we attached the transmitter to the leg opposite of the band. Both the band and the transmitter were placed above the tibio-tarsus joint. Transmitters weighed approximately 65g and were 20cm in length, encased within a 3D printed plastic case with a removable sliding door that allowed transmitters to be affixed onto the leg of the crane. The top of the transmitter was equipped with 3 solar panels while the bottom had a narrow 10cm band to prevent the transmitter from touching the tibio-tarsus joint, allowing cranes to have full leg mobility (D. Brandt, United States Geological Survey, *personal communication*).

Upon placing the transmitter onto the crane, we secured the door with 5-minute epoxy. Throughout 2020 – 2022, transmitters included a locking mechanism that automatically locked once the transmitter doors were fully inserted. During 2020-2021, as a precautionary measure, we continued to apply 5-minute epoxy to these transmitters. For each transmittered crane, 2ml of blood was collected from the metatarsus vein below the tibio-tarsus. Sex was genetically determined for the 2019 transmittered cranes using the collected blood samples, which were then analysed by the Natural Resources DNA Profiling and Forensics Centre at Trent University, Ontario. Genetic sampling was not conducted for the 2020-2022 transmittered cranes. Cranes were released immediately once the band and/or transmitter was successfully mounted, unless it was a juvenile (<1 year) in which case they were held until we were able to release it with an adult.

Global Positioning System-Global Systems for Mobile Communications (GPS-GSM) transmitters were used to monitor crane movements between 2020-2023, with locations uploaded via the cellular network. We deployed Cellular Tracking Technologies (CTT; New Jersey, USA) transmitters between 2019-2021 as well as Ornitela (Vilnius, Lithuania) transmitters from 2021-2022. Both transmitters had an estimated lifespan of 3-years. CTT and Ornitela transmitters collected locations every 30 minutes and 15 minutes, respectively, with locations uploaded once daily. If locations were collected outside the cellular network coverage zone, the locations were stored on the local device until the crane returned to an area with coverage.

2.3.3 Analysis

2.3.3.1 Data management

Location data was stored on the online repository Movebank (study name “EP SACR Transmitters (ON & QC)”, study ID 1058462512). We filtered out locations with > 40m accuracy (horizontal dilution of precision > 4) (Askren et al. 2022) and removed duplicate locations using individual ID and timestamp. To account for differences in the sampling time intervals between our CTT and Ornitela transmitters, we resampled locations at 30-minute intervals across all individuals to align with the median sampling rate between successive locations (Signer et al. 2019). We also filtered our final dataset to only include the location data of individuals that bred in the boreal forest throughout the breeding season. To accomplish this, we removed individuals if there were >20d of missing locations throughout the breeding period (n=4) (Frair et al. 2004, Nielson et al. 2009) or if breeding territories were located outside the boreal forest (n=14). Individuals were also removed from our analysis if transmitter failure or mortality occurred throughout the breeding season (n=65). While we could not definitively distinguish between transmitter failures and mortality events, observed rates of transmitter success and failure between deployment years suggest that most events were likely due to transmitter issues rather than mortality (McLean et al. *in prep*). Because we also had a potential breeding pair in our dataset, we removed the location data from the breeding male to avoid pseudo-replication in our analysis.

2.3.3.2 Estimation of breeding territory arrival and departure dates

To estimate breeding territory arrival and departure dates, we conducted a change point analysis (CPA) of net-squared displacement (NSD) using the At Most One Change (AMOC) algorithm in the *changepoint* package (Killick and Eckley 2014) in R (R Core Team 2023). These changepoints represented significant changes in movements patterns, which we assumed represented the beginning or end of breeding territory establishment. We visually inspected NSD graphs for each individual crane and respective breeding season and trimmed the NSD plot using CPA until the graph resembled a horizontal plateau. If the horizontal plateau occurred for at least 3 months, anytime between March and October (Fronczak et al. 2017), we assumed it was a breeding territory (Figure 2.2). For individuals that did not have a defined plateau, we used the mean arrival and mean departure dates calculated for all cranes with a clear plateau for each year.

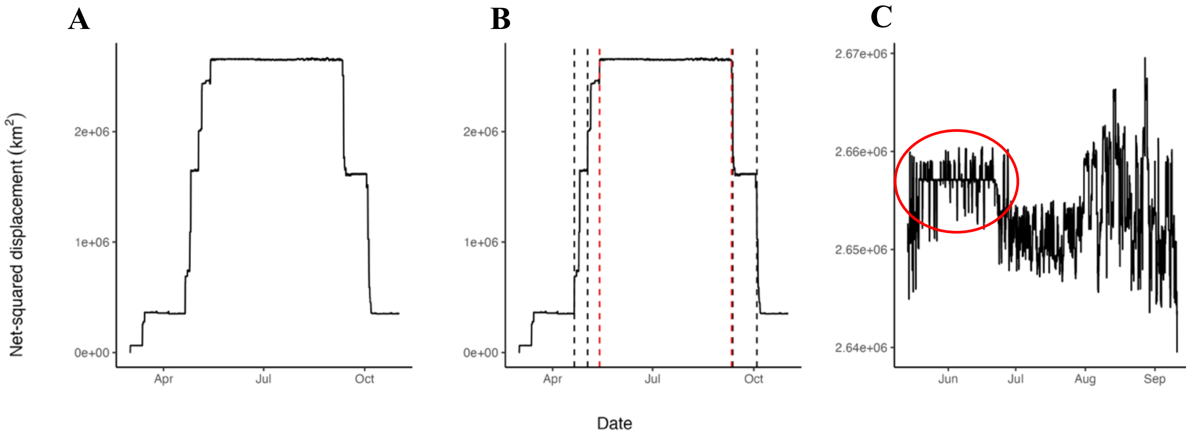

Figure 2.2. Changepoint analysis of the net-squared displacement of a single crane used to determine breeding territory arrival and departure dates and identify successfully breeding individuals in the boreal forest of Ontario and Quebec, Canada throughout the 2020-2023 breeding season. Figure A represents the complete net-squared displacement segment of an individual crane from the beginning of March to the end of October. Figure B identifies the occurrence of significant changes in the net-squared displacement for the same individual using changepoint analysis (indicated by the dotted lines). The third and fourth changepoints (highlighted by the red dotted lines) denote the arrival and departure dates to and from the breeding territory. All data preceding the third changepoint (i.e., arrival date) and following the fourth changepoint (i.e., departure date) were removed from subsequent analysis. Figure C represents the clipped net-squared displacement segment of the individual throughout the breeding season. The 30-day linear plateau that occurs around mid-May to late-June (circled in red) suggests that the individual successfully bred.

To focus our analysis on successfully breeding individuals, we applied an exclusion criterion, using NSD plots, to remove cranes that did not establish a territory or breeding home range. Cranes are central place foragers and often select foraging sites close to roosts (Ivey et al. 2015, Nilsson et al. 2020), which restricts overall activity to small, localized areas. Breeding behaviour, such as incubation, territory defence, and parental care of pre-fledged young, also impose spatial constraints on general movement patterns as adult breeding cranes return to nest sites. This allowed us to use NSD plots to visualise individual movements and identify nesting periods within the breeding territory. After visually inspecting NSD plots for every individual, we chose to retain cranes if there was a linear 30-day plateau, where movement was restricted to ±2.5 km from the plateau (Figure 2.2). We assumed that this 30-day plateau represented the incubation period of cranes. Because cranes begin to migrate around mid-September (McLean et al. *in prep*), the 30-day plateau had to occur any time before mid-June as juveniles fledge 7-weeks after hatching and cranes incubate eggs for 30 days (Gerber et al. 2020).

2.3.3.3 Spatial analysis

We quantified habitat selection of breeding territories at the second order by calculating annual 95% minimum convex polygons (MCPs) for every individual (Holbrook et al. 2017) using the *amt* package (Signer and Fieberg 2021) in R (R Core Team 2023). We then determined if cranes were using habitats in excess of their availability by comparing used to available territories within a resource selection framework. To calculate our availability domain, we buffered each individual MCP using the radius of a circle equal to the area of the greatest observed breeding territory in our sample (Johnstone et al. 2023). This ensured we captured both the area of the breeding territory and the surrounding landscape. We then calculated our spatial extent by fitting a 100% MCP around the individually buffered MCPs (Figure 2.1). To sample availability, we generated 9,000 (1:100 used to available; Northrup et al. 2013) random polygons within our spatial extent that were equal in area to the median breeding territory (Holbrook et al. 2017). Because cranes primarily roost and nest in wetlands and shallow water (Lovvorn and Kirkpatrick 1981, Baker et al. 1995) and are not typically found nesting or foraging in large open bodies of water with deep water, such as lakes or the open ocean, we excluded areas predominantly covered by water by removing available ranges that contained a higher proportion of water compared to the used home-ranges. This step ensured that our analysis focused on relevant breeding habitats for cranes.

We characterised our study extent by including several habitat covariates we expected to influence breeding crane resource use and territory selection. General land cover was measured using the North American Land Change Monitoring System raster layer (NALCMS

2020). Due to high degrees of spatial overlap between the urban covariate (i.e., areas where >30% of the land is occupied by structures designed for human use, such as cities, towns, and transportation networks) in the NALCMS dataset and our roads layer, we modified urban features by clipping urban to nearest city (Statistics Canada 2017) and removing any features outside of the city boundary. Any urban features that overlapped with our roads layer within the city boundary were also removed. We also considered forest disturbance events (e.g., wildfires, cutblocks, and forest harvest areas), and other wetland habitat not quantified by NALCMS as additional land cover covariates that may influence breeding territory selection. We quantified forest disturbance and cutblocks using the Canada Landsat Derived Forest Harvest Disturbance 1985-2020 raster layer (Hermosilla et al. 2016) but limited the disturbance period to 2015-2020 to account for changes in tree growth and stand height that could restrict the establishment of breeding territories. Additional wetland habitat for Ontario and Quebec were classified using layers from the Ministry of Natural Resources and Forestry Wetland dataset (MNRF 2020) and the Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs Potential Wetlands dataset (MELCCFP 2019), respectively. To create our land cover map, we used the general land cover layer as our base layer before overlaying it with the forest disturbance and wetland layers.

We quantified land use using roads layers from the Ontario Road Network: Road Net Element (OMNRF 2019), Ontario Ministry of Natural Resources and Forestry Road Segments (MNRF 2019), and Addresses Québec AQréseau+ (AQR 2023). We excluded non-road features such as railways and virtual roads, as well as winter roads. All road layers were downloaded as a vector which we converted into rasters and calculated as the total length per pixel within a breeding territory.

We grouped similar land cover and land use variables together (Table 2.*1*) to better reflect the ecology of the species, reduce the total number of covariates in our models, and facilitate model convergence. We mapped all land cover and land use variables in ArcGIS and assessed them at a 30-m x 30-m resolution (ArcGIS Pro Desktop V3.1.2; ESRI Inc. 2022) before extracting all covariates in R (R Core Team 2023) using the *terra* package (Hijmans 2023). Land cover and land use covariates were summarised as proportional estimates of land cover and indices (km/km^2), respectively. Due to cranes demonstrating strong annual breeding territory fidelity (Figure 2.*1*), proportional estimates for all covariates were averaged across each crane over all their breeding years to account for non-independence among repeated samples of used breeding territories.

Table 2.1. Description of the land cover and land use covariates that were used to develop resource selection functions and model habitat selection of breeding sandhill cranes in the boreal forest of Ontario and Quebec during the 2020-2023 breeding season. All covariates were analysed at a 30m spatial scale.

Covariate	Description	Units	Range	Reference
Land cover				
Cropland	Agricultural areas used to manage crops including the production of annual crops, such as cereal and pulses; perennial grasses for grazing; and woody crops. >20% crop vegetation cover.	%	0–89.55	NALCMS (2023)
Forest	Includes needleleaf, evergreen, and mixed forest types. Trees typically >3m in height and constituting >5-20% of the total vegetation cover.	%	0–97.28	NALCMS (2023)
Forest Disturbance	Includes disturbances caused by wildfires or anthropogenically-induced harvest activities that occurred between 2015-2020.	%	0–33.79	Hermosilla et al. (2016)
Open habitat	Includes barren, grassland, and shrubland habitat.	%	0–74.46	NALCMS (2023)
City	>30% of landscape is covered by constructed materials intended for human activities, including cities and towns.	%	0–25.34	NALCMS (2023)
Water	Includes large open bodies of water such as lakes, ponds, rivers, and the ocean.	%	0–42.78	NALCMS (2023)

Wetland	Includes marshes, swamps, fens, and bogs. Characterised by areas that are seasonally or permanently inundated by shallow water or where the water table is near the surface.	%	0–100	MELCCFP (2019), MNRF (2020), NALCMS (2023)
Land use				
Roads	Includes municipal roads, provincial highways, and resource and recreational roads, measured as density of roads (km/km^2), within each polygon.	Index	0-33.33	MNRF (2019), OMNRF (2019), AQR (2023)

2.3.3.4 Statistical Analysis

We built a fixed-effect logistic regression-based resource selection function (RSF) to understand patterns of habitat selection at the second order and to develop spatially predictive maps highlighting the distribution of relevant crane breeding habitat across the landscape. RSFs are a robust tool for quantifying patterns of habitat selection by fitting logistic regression models that compare locations where an animal is known to occur (used locations) to a set of random points representing available habitat for the animal (available locations) (Boyce et al. 2002, Manly et al. 2002).

Before fitting our fixed-effect models, we standardised all land cover covariates by subtracting the mean and dividing by the standard deviation. Additionally, we tested for collinearity between covariates to prevent the inclusion of highly correlated variables (Pearson's $r > |0.65|$) within the same model (Dormann et al. 2013). We used weighted binomial logistic regression to identify patterns of breeding territory selection by cranes (Holbrook et al. 2017). Weights were assigned to our available:used observations at a ratio of 0.090:1 to compensate for the difference in sample sizes between the total number of breeding territories that were used and those that were available (Holbrook et al. 2017). We then evaluated all model combinations using Akaike's Information Criterion for small sample sizes (AICc) to rank models in our candidate model set and presented all models that were within Δ2 AICc from the top model (Arnold 2010). To ensure model fit, we visually assessed model residuals by generating a residual versus fitted plot, plotting the predicted values of our top model against Pearson’s residuals. We then developed marginal effects plots for all habitat covariates that appeared in our top model, allowing us to visually assess the relationship between probability of selection and habitat cover. If a quadratic relationship was present or made sense biologically, a quadratic term was added post-hoc and included in our model dataset.

We developed probability maps based off our top model to identify important breeding territories for cranes in the boreal forest across Ontario and Quebec. We first summarised our covariates using moving windows equal in area to the median breeding territory (Johnstone et al. 2023) in ArcGIS (ArcGIS Pro Desktop V3.1.2; ESRI Inc. 2022). After rescaling the RSF values of our top ranked model with the lowest ΔAICc, we then predicted the relative probability of selection across the landscape using the *terra* package (Hijmans 2023) in R (R Core Team 2023). Landscape values that exceeded the range of habitat cover in our used breeding territories were assigned null values in the predictive map (Johnstone et al. 2023) to prevent misinterpretation of our results and stay within the boundaries of our model estimates.

2.4 Results

Between September to October 2019-2022, we captured and deployed transmitters on 122 adult cranes (24 in 2019, 38 in 2020, 42 in 2021, and 18 in 2022). Of the cranes captured in 2019, genetic sex sampling confirmed that transmitters were deployed on 18 (75%) females and 6 (25%) male cranes. Genetic sex sampling did not occur for 2020-2022.

Cranes were monitored year-round between 2020-2023; however, because we were only interested in breeding individuals attending a nest site, we limited our dataset based on multiple criteria. A total of 70 cranes were excluded from our analysis between successive breeding years due to transmitter failure or mortality (n=65; McLean et al. *in prep*) or if there were an insufficient number of GPS locations that were collected throughout the breeding season (n=4). We also removed the location data of the breeding male from a suspected pair bond. In 2019, 1 male and 1 female crane, as confirmed by molecular sexing, were captured on the same day at the same capture location. Subsequent analysis revealed that the male and female occupied the same breeding territory throughout the 2019-2022 breeding season.

Based on our filtering criteria, breeding data of cranes were also removed from our final dataset if cranes failed to establish a breeding territory during the breeding season (n=58) or established a breeding territory outside the boreal forest (n=14). Following the removal of non-breeding individuals, our final sample size consisted of 49 cranes that established a total of 90 breeding territories over 4 breeding seasons.

After filtering the dataset to match the respective breeding territory arrival and departure dates of each successfully breeding individual, we collected 516,669 GPS locations from 49 cranes throughout the 2020-2023 breeding season, averaging 5471 ± 870 locations per individual. The mean breeding territory arrival and departure dates were 20 April ± 8.8 (SD) days and 26 August ± 15.6 days respectively, with cranes remaining on breeding ranges for an average of 127.9 ± 16.8 days (Table A.2.1 and Figure A.2.1). The size of breeding territories varied among individual, with the mean territory size being 14.1 ± 21.7 km^2 (Table A.2.1 and Figure A.2.1).

Cranes with 2 to 4 consecutive breeding events demonstrated strong breeding site fidelity between years. The mean distance between all breeding territories observed across consecutive breeding years for individual cranes was 0.8 + 1.4 km, with distances between consecutive breeding territories ranging from 0.02 km to 4.6 km (Table A.2.2).

The distribution of habitat covariates in breeding territories and potential available territories overlapped substantially for several covariates. However, we observed patterns where cranes used areas containing greater proportions of cropland, forest disturbance, roads, and wetlands (Figure 2.3). Used breeding habitats tended to have lower proportions of forest, open, habitat and water compared to available territories (Figure 2.3). After testing for collinearity, both wetland and forest appeared to be highly correlated (Pearson's r = -0.83) and thus did not appear within the same model. We then evaluated all potential model combinations using the 8 covariates in our dataset, resulting in a total of 192 models in our candidate dataset.

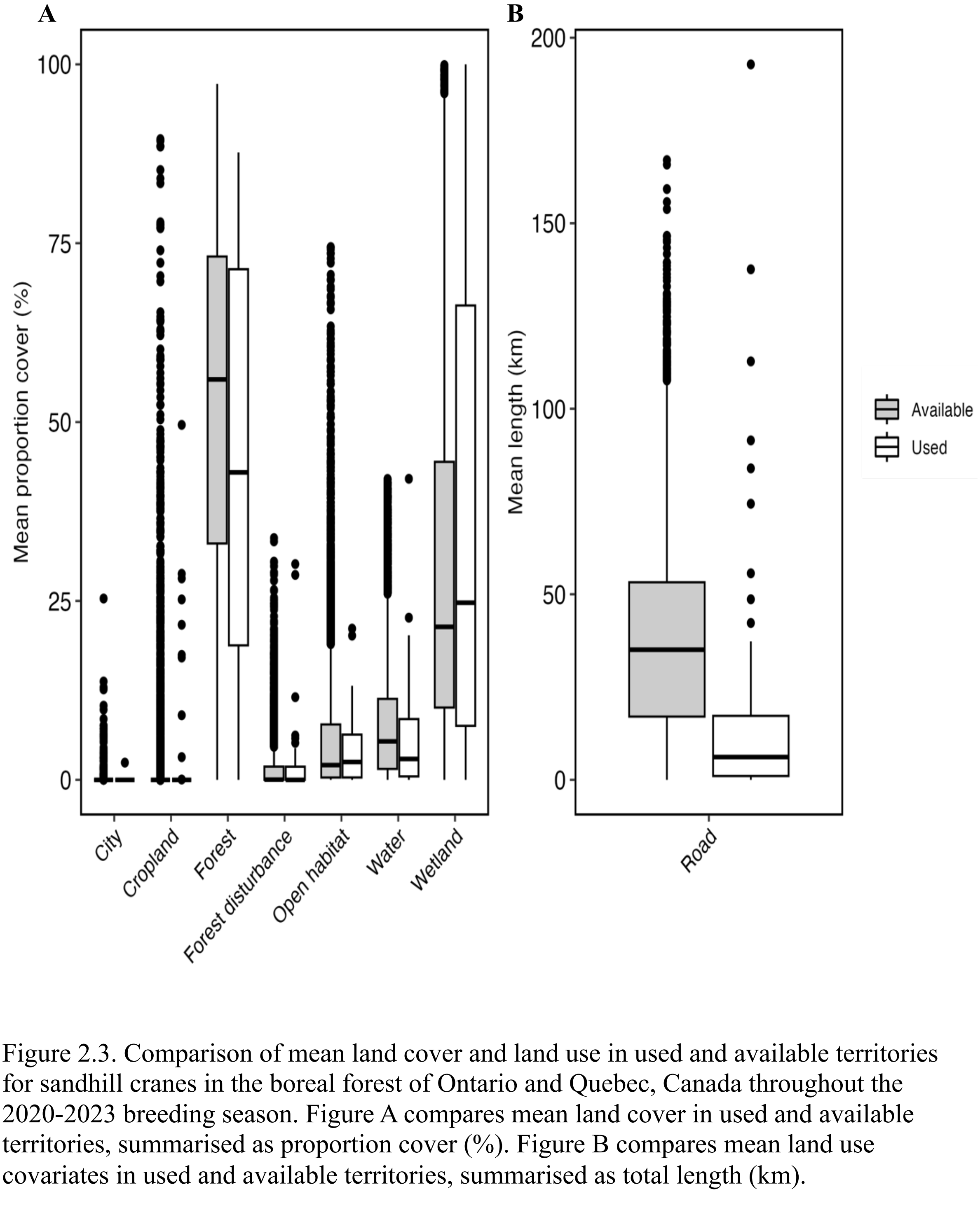

Figure 2.3. Comparison of mean land cover and land use in used and available territories for sandhill cranes in the boreal forest of Ontario and Quebec, Canada throughout the 2020-2023 breeding season. Figure A compares mean land cover in used and available territories, summarised as proportion cover (%). Figure B compares mean land use covariates in used and available territories, summarised as total length (km).

Our top ranked model that best predicted breeding habitat selection across the landscape included cropland (β = 0.3, 95% CI = 0.08 to 0.4), forest disturbance (β = 0.2, 95% CI = -0.03 to 0.4), and wetland (β = 0.4, 95% CI = 0.1 to 0.7). When developing the marginal effects plot for our top model, a quadratic term was included post-hoc for cropland, which improved model fit (based on the lowest AICc value) (Table 2.2 and Figure 2.4). Our candidate dataset consisted of an additional 15 competitive models that were within Δ2 AICc of our top model. Except for 1 model combination, all models in our competitive model dataset contained either the appearance or non-nested combination of our top covariates (Table 2.2). Out of our competitive models, cropland appeared 14 times, wetland appeared 9 times, open habitat appeared 10 times, and forest disturbance appeared 8 times. Overall, breeding territories containing greater proportions of cropland, forest disturbance, and wetland positively influenced the probability of habitat selection by breeding cranes (Figure 2.4).

Spatial predictions of the top model resulted in maps delineating the relative probability of breeding territory use across our study extent at a 30 m pixel size (Figure 2.5). A standard error map was also created from the RSF coefficients of our top model to model the uncertainty in our spatial predictions (Figure 2.5).

Table 2.2. Resource selection functions predicting breeding territory selection of sandhill cranes in the boreal forest of Ontario and Quebec, Canada throughout the 2020-2023 breeding season. We analysed a total of 192 model combinations and present the number of parameters (K), corrected Akaike's Information Criterion values (AICc), log-likelihoods (LL) and model weights (w_i) for all competitive models that were within Δ2 AICc of the top model.

Model	K	LL	AICc	w_i
Cropland + cropland^2 + forest disturbance + wetland[a]	5	-128.85	267.7	-
Cropland + forest disturbance + wetland	4	-131.3	270.6	0.04
Cropland + forest disturbance + road index + wetland	5	-130.4	270.9	0.03
Cropland + forest disturbance + open habitat + wetland	5	-130.5	271.0	0.03
Cropland + wetland	3	-132.6	271.2	0.03
Cropland + forest disturbance + open habitat + road + wetland	6	-129.7	271.4	0.03
Cropland + road index + wetland	4	-131.9	271.7	0.02
Cropland + open habitat + wetland	4	-131.9	271.7	0.02
Cropland + forest + open habitat	4	-132.0	272.0	0.02
Cropland + forest + forest disturbance + open habitat	5	-131.1	272.1	0.02
Cropland + forest + forest disturbance + open habitat	5	-131.1	272.2	0.02
Cropland + open habitat + road index + wetland	5	-131.2	272.3	0.02
Cropland + forest disturbance + water + wetland	5	-131.2	272.4	0.02
City + cropland + forest disturbance + wetland	5	-131.3	272.5	0.01
Forest + open habitat + water	4	-132.3	272.5	0.01
Cropland + forest + open habitat + road index	5	-131.3	272.5	0.01
Cropland + forest + forest disturbance + open habitat + water	6	-130.3	272.5	0.01

[a] Note: This model was developed post hoc after identifying the top model in our model dataset and determining that the inclusion of the quadratic term for cropland was required.

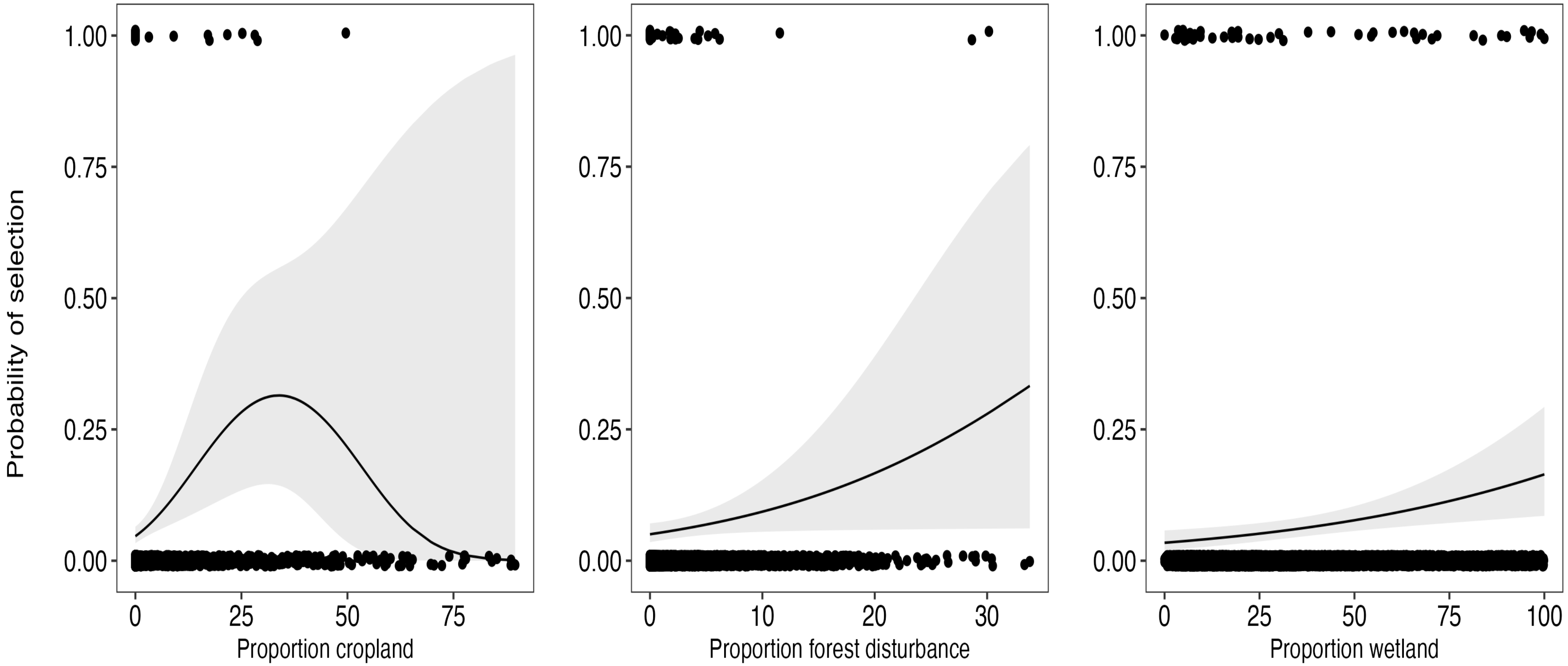

Figure 2.4. Predicted effect plots for all land use covariates that appear in the top resource selection function model for breeding sandhill cranes in the boreal forest of Ontario and Quebec, Canada from 2020-2023, with 95% confidence intervals. Points along the x-axis represent the probability of selection for each used (1) and available (0) territory in our dataset.

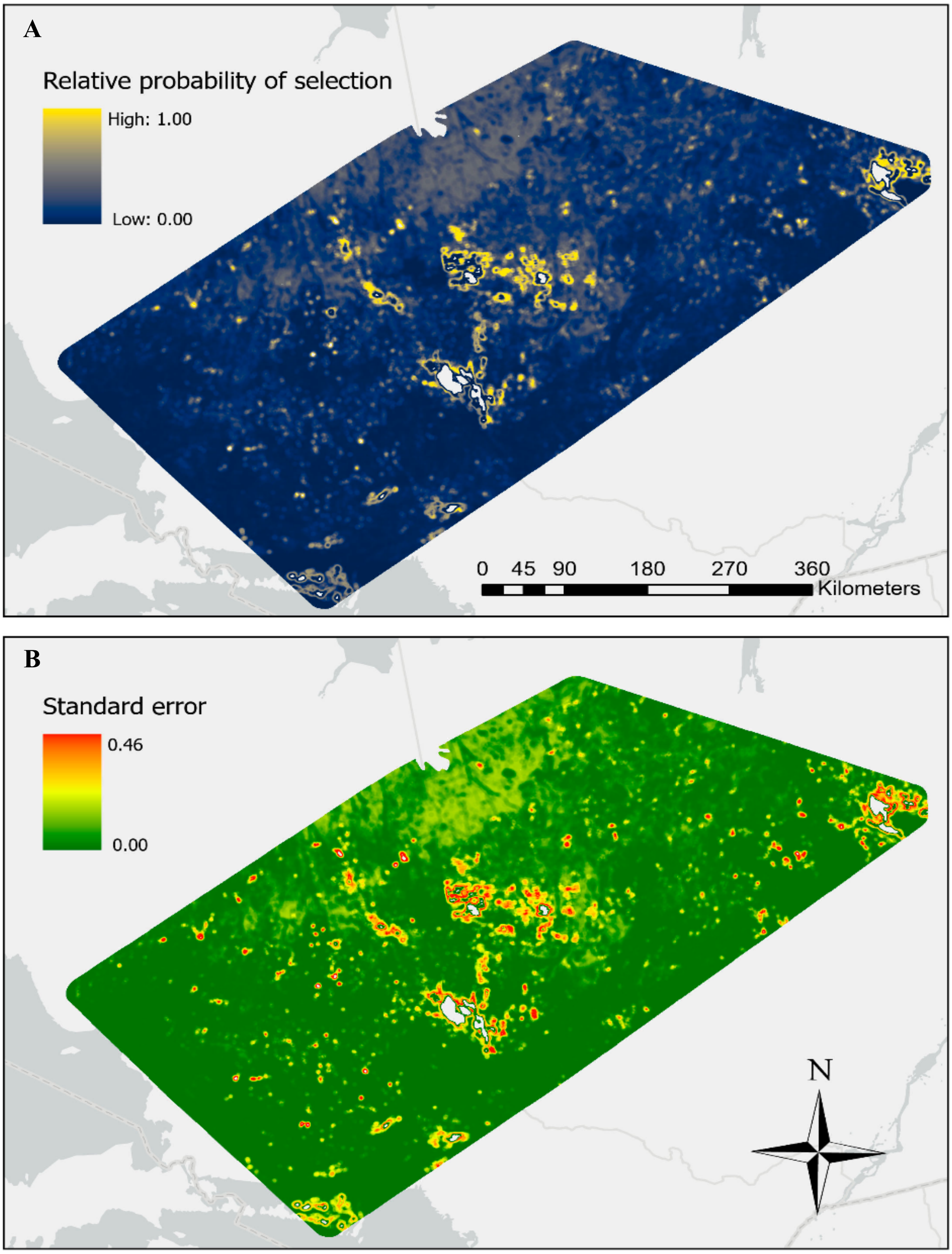

Figure 2.5. Predictive maps describing relative probability of nesting territory habitat use by breeding sandhill cranes in the boreal forest of Ontario and Quebec, Canada from 2020-2023. based on the top resource selection model. Figure A describes probability of breeding territory selection. Figure B depicts the standard error and uncertainty from the spatial predictions of the probability map.

2.5 Discussion

Understanding the distribution of breeding habitat and how species select breeding habitat across the landscape is important for the successful conservation and management of cranes. Here, we quantified the effects of land cover and land use on second order habitat selection of breeding cranes in the boreal forest of Ontario and Quebec and developed maps predicting the spatial distribution of breeding territories across a large area (> 300,000 km^2) of the boreal forest.

Our results suggest that cranes selected breeding territories containing greater proportions cropland, forest disturbance, and wetlands. Our spatial predictive map summarises key findings that can help aid in the management of crane breeding habitats in the boreal forest. Results from our study quantify patterns of habitat selection in remote areas and can help guide the development of species-level conservation initiatives within the boreal forest ecosystem.

2.5.1 Arrival on the breeding grounds and duration of stay

Cranes arrived at their breeding territories around late April and departed around late August, remaining on breeding grounds for approximately 4 months. Average distance between breeding territories across successive breeding years was similar to Fronczak et al. (2017) and Krapu et al. (2011) who reported a mean and median distances of 1.6 km, respectively. The timing and duration of their stay on breeding territories were consistent with observations from the Mid-continental Population of cranes in the East-central Canada-Minnesota area (Krapu et al. 2011). However, they differed from the Eastern Population of cranes observed in the study by Fronczak et al. (2017), who reported a longer length of stay (approximately 6 months) along with an earlier arrival and later departure date (late March and early October, respectively).

Observed differences in the chronology and duration of stay across studies may have to do with the geographic areas of where the breeding grounds were located. Our breeding territories were located across the same longitude as the Mid-continental Population of cranes that bred around the East-central Canada-Minnesota region (Krapu et al. 2011), but at higher latitudes than the Eastern Population of cranes that established summer ranges around the Great Lakes region (Fronczak et al. 2017). Differences in breeding chronology across the latitudinal gradient suggests that cranes in our study likely arrived later and departed earlier due to the longer migration distances travelled from their wintering grounds to breeding areas, which were located further northward, compared to the Eastern Population of cranes observed by Fronczak et al. (2017).

2.5.2 Breeding territory size

The size of breeding territories in our study differed from previous studies that delineated breeding (Miller and Barzen 2016) or summer (Kruse et al. 2017) ranges. The differences in breeding territory size among studies may be due to the ecology of the species or study design. Miller and Barzen (2016) reported much smaller home range sizes (2.83 ± 0.60 km^2) of breeding cranes. Difference in home range sizes may partially be due to differences in sample size or distance between nesting/brooding sites and foraging areas. Our sample size was approximately 4 times larger than the 12 breeding sandhill cranes tracked by Miller and Barzen (2016) and therefore, likely captured a greater range of variability in territory size.

We estimated 90 breeding territories throughout our study from 49 individuals. From our estimated sample size, 17 breeding territories (13 individuals), were smaller than 2.8 km^2, as observed by Miller and Barzen (2016). If we also removed outliers and re-calculated the mean, we would expect to observe a much smaller average territory size in our study (e.g., removing $n = 7$ territories with sizes > 40 km^2 resulted in a mean territory size of 8.8 ± 7.9

km^2). In Miller and Barzen (2016)'s study, the majority of cranes also selected territories where cropland and wetland habitats were located adjacent to each other. Home ranges are defined by the underlying distribution of resource (Brown 1975, Schoener 1983), with Legagneux et al. (2009) observing a decrease in home range size in relation to increased resource availability. Though a direct comparison between studies was not possible, we assume that the locations of nest areas were generally not adjacent to cropland. Kruse et al. (2017) reported larger summer range sizes (64.77 ± 16.38 km^2) compared to our study, which likely resulted from the inclusion of non-breeding individuals in their analysis. Non-breeding individuals typically exhibit more variable movement patterns and often forage further from wetlands compared to breeding individuals (Su 2003, Wolfson et al. 2020).

2.5.3 Breeding territory selection

Overall, cranes selected habitats with greater proportions of wetland, forest disturbance, and cropland. However, there was minimal differentiation in the habitat covariates that were included among our competitive model set. The high number of models within Δ2 AICc of our top model, may be attributed to the abundance of high-quality breeding territories available to cranes within our study extent. Limited human disturbance and high availability of potential nesting territories in the boreal forest could influence the accuracy of our habitat selection models in the region. Overall, our findings are consistent with those of other habitat selection studies conducted in similar habitats.

The influence of wetland and forest were consistent with previous studies with a positive association with wetland habitats and avoidance of forest (Baker et al. 1995, Miller and Barzen 2016, Kruse et al. 2017, Casabona I Amat et al. 2022). The boreal ecoregion is characterised by extensive forest cover, interspersed with a mosaic of wetland habitats. Wetlands are important components of breeding habitats for cranes (Toland 1999, Miller and Barzen 2016, Casabona I Amat et al. 2022), providing the necessary resources and environmental conditions required for reproductive success (McWethy and Austin 2009). Wetlands offer open spaces, shallow water bodies, and dense vegetation that provide ideal nesting sites, food sources, and protection from predators. Conversely, the closed canopy, dense understory, and limited visibility of forests may not provide suitable nesting habitat or protective cover for breeding waterbirds (Holopainen et al. 2015). Water depth (up to ~30 cm) and vegetation composition (e.g., bulrush, cattails, phragmites, and sedge) have been identified as important indicators of nest success in wetland for cranes (Lovvorn and Kirkpatrick 1981, Austin et al. 2007, Maxson et al. 2008). Bennett (1992) also found that cranes preferred marsh over swamps. Previous research on nesting waterbirds have observed variation in selection choices among different types of wetland habitats (Dyson et al. 2022, Johnstone et al. 2023). Unfortunately, the available spatial data for our study did not differentiate among wetland classes. More refined land cover layers, particularly wetland classes, could refine our models.

Our top model indicated selection for breeding territories with greater proportion forest disturbance areas while our competitive models demonstrated avoidance of areas with greater proportions of open habitats. This aligns with previous research demonstrating selection of forest disturbance habitats in ground nesting waterbirds (Lemelin et al. 2007, Dyson et al. 2018). Forest disturbance events in the region take the form of cutblocks and wildfires (Hermosilla et al. 2016). These events promote the rapid succession and regeneration of shrub species and grassland plant communities (MacDonald et al. 2004, Ram et al. 2020), creating early-successional communities reminiscent of open habitat (Kellett et al. 2023). We suspect that snow melt throughout spring causes open habitat and forest disturbance areas to become seasonally flooded, creating wetland-like habitats throughout the early breeding period (Kurkowski et al. 2023).

While both open habitats and forest disturbance areas provide the necessary wetland components required for breeding, forest disturbance areas may provide cranes with additional foraging opportunities while also maintaining protective cover required for nesting and chick-rearing, as with other waterbird species (Dyson et al. 2018). Disturbance events can also modify vegetative cover and soil composition which may facilitate increased availability of insects, seeds, and tubers (Forsman et al. 2010), thereby providing additional foraging opportunities for cranes (Austin 2018). However, while we observed strong selection for forest disturbance, disturbed forest was not the predominant habitat feature within the region, representing only 1.5% of the land cover surface within our study extent. Wetland also had a stronger effect than forest disturbance (Avgar et al. 2017), suggesting that within our study extent, wetlands played a more important role in influencing territory selection compared to disturbed forests. Tree removal and forest harvesting can alter hydrology and streamflow (Wei et al. 2022), thereby impacting wetland composition and availability of these areas as potential breeding habitats for cranes in the boreal forest.

We also observed general avoidance of breeding territories containing greater proportion of water. While we attempted to account for the effect of large water bodies in our analysis by removing available territories that contained greater proportions of water compared to our used territories, deep-water bodies (e.g., large lakes) were still predominant water features within in our study area. Previous research found that cranes prefer habitats with shallow water and emergent vegetation (Lovvorn and Kirkpatrick 1981, McWethy and Austin 2009) and that riverbanks and lake edges can provide suitable habitat for cranes (Iverson et al. 1985, David M Baasch et al. 2019). Because deep waters (e.g., lakes) are unsuitable for nesting, their inclusion likely drove the detected avoidance of open water.

Numerous studies of cranes have investigated the effects of cropland on habitat selection, due to concerns over the increasing rates of crop damage resulting from the recent population expansion (Krapu et al. 1984, Sudgen et al. 1988, Casabona I Amat et al. 2022). Consistent with previous research, we also documented strong selection for areas with greater proportions of cropland (Miller and Barzen 2016) . Cropland is an important foraging habitat for cranes, providing high-energy foods with minimal energetic cost, which allows cranes to easily meet the daily energy requirements for survival (Reinecke and Krapu 1986, Pearse et al. 2017, Nilsson et al. 2020).

Despite our models indicating strong selection for cropland, our predictive models showed large standard errors in cropland selection. This may be due to differences in habitat use between successful and non-successful breeding cranes, and variations in crop availability between different areas within the study extent. Su (2003) observed differences in habitat use between breeding and non-breeding cranes, with non-breeders using greater proportions of cropland. If a crane failed to breed or the chick died during the breeding period, we might expect to observe increased use of cropland throughout the latter part of the breeding season, potentially explaining the strong selection we observed for cropland. Despite the limited availability of cropland within the study area, it was heavily used by cranes when accessible. In breeding territories where cropland was present (n=10), cropland comprised 20.0 ± 14.4% of the habitat composition. However, the low coverage of cropland within the spatial extent (1.3% of total land cover surface) may limit overall availability, which may explain the large variation in cropland use among individuals.

Results from our competitive models revealed weak selection for cities, which contradicts findings previous studies that found that cranes avoided areas with high densities of human structures (Boggie et al. 2018). We presume that selection for city was because the majority of cities were located in close proximity to agricultural areas and were thus incidentally captured in the used breeding territories. Future research using more refined habitat layers at finer orders of selection is required to assess the influence of urban, exurban, and agricultural areas on breeding habitat selection.

2.6 Management implications

Assessing habitat selection at second order provides novel insight into the distribution of breeding habitats and effects of land cover and land use on breeding territory selection for cranes. Our spatial predictive maps can help land managers in developing species-specific conservation plans that prioritise crane breeding habitats in the boreal forest. Given strong fidelity of cranes that migrate from wintering grounds to breeding sites, loss of wetland habitat may negatively impact populations of cranes that return to these breeding areas. Therefore, within the boreal forest, we recommend conservation and management plans that prioritise the protection of areas dominated by wetland habitats. Further research should explore effects of cropland and forest disturbance at finer habitat scales and use more refined wetland classifications to quantify effects of wetland types on breeding habitat selection. In addition to improving our understanding of the breeding ecology of cranes in boreal habitat, our research provides important information for identifying breeding territory selection across the landscape. This is important for future conservation efforts as cranes continue to expand their breeding range into Ontario and Quebec.

Chapter 3: Spatial drivers of breeding habitat selection in sandhill cranes in Canada's eastern boreal forest

3.1 Abstract

Canada’s eastern boreal forest serves as a critical breeding habitat for sandhill cranes (*Antigone canadensis*). However, as these regions experience increased anthropogenic activity, including intensive logging and habitat fragmentation, understanding the spatial drivers of breeding habitat selection is crucial for effective conservation and management. Using high-resolution satellite telemetry data, we developed resource selection functions to assess the influence of land cover and land use on breeding habitat selection of sandhill cranes (n=42) in Ontario and Quebec, Canada. Within the breeding territory, sandhill cranes exhibited strong selection for wetlands, croplands, forest disturbance, and water and avoidance of intact forests and urban areas. These findings underscore the importance of wetlands as a predictor of habitat use and suggest that current anthropogenic disturbances, including forestry practices, do not adversely affect breeding crane habitat selection in the boreal forest. We recommend management actions that prioritise the conservation of wetlands. As anthropogenic activity continues to increase in the future, further research is required explore the impacts of forest disturbance on breeding success in sandhill cranes.

3.2 Introduction

The boreal forest covers approximately 30% of Canada (Brandt 2009) and supports a wide diversity of wildlife (Venier et al. 2014, Holopainen et al. 2015). Wetlands are dominant land cover features in the boreal forest and provide important breeding grounds for many waterfowl species (Holopainen et al. 2015). Canada’s eastern boreal forest has experienced a recent increase in anthropogenic activity, primarily in the form of intensive logging practices including clear-cutting activity (Brodeur et al. 2008, Hermosilla et al. 2016). Anthropogenic disturbance can influence species distributions and population viability by modifying niche space through alterations in ecosystem dynamics and function and changes in habitat structure (Lemelin et al. 2007, Venier et al. 2014, St-Pierre et al. 2022). As anthropogenic activity continues to transform natural landscapes within the boreal forest, research is required to elucidate patterns of habitat selection for wildlife species of conservation interest.

Habitat selection estimates patterns of space use by linking the distribution of species to a set of environmental factors, providing researchers with important insights into the underlying factors that affect animal behaviour. The study of habitat selection is a scale-dependent process, where the distribution and availability of resources vary across spatial scales (Meyer and Thuiller 2006, Northrup et al. 2013). The influence of particular habitat features can differ across scales in terms of the direction and strength of selection (Ciarniello et al. 2007, Holbrook et al. 2017, Dyson et al. 2022, Johnstone et al. 2023). In addition to scale, results and their ecological interpretation are also influenced strongly by how we define and sample "available" habitats (Levin 1992). Therefore, when designing studies, it is important for researchers to correctly match habitat availability to the biologically-relevant spatial scale (Levin 1992).

Sandhill cranes (*Antigone canadensis*) are a long-lived (20-30 years) migratory species that experience slower reproductive rates and lower fecundity than other migratory game birds (Nesbitt 1992, Gerber et al. 2014). Throughout the 20th century, the Eastern Population (EP) of sandhill cranes (hereafter cranes) experienced extensive population declines due to intensive harvest, habitat fragmentation, and loss of wetland habitat (Walkinshaw 1949, Walkinshaw and Wing 1955, Lumsden 1971). The development of conservation initiatives has led to recent range expansion and recolonization of suspected historical breeding ranges into the eastern boreal forest of Ontario and Quebec, Canada (Lumsden 1971, Meine and Archibald 1996, Sutherland and Crins 2007, Van Horn et al. 2010, Fronczak et al. 2017, Lepage 2019, Casabona I Amat et al. 2022). Breeding habitat is critical for population viability and anthropogenic disturbances throughout the breeding period may lead to declines in population abundance through habitat degradation, nest abandonment, and nest predation (Dwyer and Tanner 1992, Austin et al. 2007, Ivey and Dugger 2008, Jaworski et al. 2023). The boreal forest is predicted to become increasingly important for cranes as they continue to expand their breeding range into Ontario and Quebec, Canada (Casabona I Amat et al. 2022).

To characterise the hierarchical nature of habitat selection, Johnson (1980) proposed a four-orders of habitat selection. First and second orders of selection answer broad population-level questions about geographic and home-range selection, while third and fourth orders focus on fine-scale patterns of habitat use within an animals home range (Johnson 1980). Previous research has examined higher orders of selection of cranes within the boreal forest (e.g., second order selection; Casabona I Amat et al. 2022); however, investigations into finer scales of selection (i.e., third order) remains limited. Selection processes at coarse orders (i.e., first and second order) may mask selection choices within the home range (i.e., third and fourth order selection), thereby impacting the accuracy of management strategies aimed at conserving habitat patches important for cranes within the home range. Therefore, investigating habitat selection at third order will fill important knowledge gaps in identifying key habitat components used by breeding cranes within the home range.

We used high-resolution satellite telemetry data to evaluate patterns habitat selection of breeding cranes in the boreal forest of Ontario and Quebec, Canada. We developed resource selection functions (RSFs) to quantify the influence of land cover and anthropogenic disturbance on the habitat selection behaviour of breeding cranes within the home range (i.e., third order; Johnson 1980). Results from our study can be used to develop targeted approaches that conserve important habitat components used by breeding cranes within their home range in Ontario and Quebec, Canada.

3.3 Methods

3.3.1 Study Area

The study was conducted within the breeding range of cranes in the boreal forest of Ontario and Quebec, Canada. Land cover varies across the geographic extent but is primarily dominated by coniferous, broadleaf, and mixedwood forests. Coniferous tree species commonly found in the boreal forest include black and white spruce (*Picea mariana, Picea glauca*), balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*), while deciduous species in the region comprise of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) (Bergeron et al. 2014, Baret et al. 2017). The landscape also features hydrological features such as wetlands, rivers, and lakes, along with barren, shrubland, and grassland habitats. The presence of anthropogenically developed areas is also evident across the extent of our study area and includes urban centres (i.e., cities), agricultural land, forestry cutblocks, and linear road networks.

3.3.2 Transmitter Deployment

All animal handling and capture procedures were approved by the Environment and Climate Change Canada Animal Care Committee (permit CS2019, CS2020, CS2021, and CS2022), Environment and Climate Change Canada banding permits (#10847 and #10546G), and the University of Waterloo Animal Care Committee (AUPP #43725).

Cranes were captured in Ontario and Quebec, Canada, between September to October 2019-2022, using methods described in McLean et al. *in prep*). Tagging efforts were directed towards adult females due to their higher likelihood of returning to breeding territories in Ontario and Quebec in subsequent years (Walkinshaw 1949, Drewien 1973). On the field, we determined sex using morphological and behavioural characteristics, and subsequently confirmed sex through genetic analysis. Because cranes are perennially monogamous, deploying transmitters on presumed females also reduced the probability of collecting duplicate data between pair bonds when more than two cranes were captured (Tacha et al. 1994). If the majority of captured cranes appeared to be male, when more than one pair of cranes were caught, we placed transmitters on adult male cranes rather than females to maximise the number of transmitters deployed per catch.

Captured cranes selected to receive transmitters were fitted with leg-mounted solar-powered GPS-GSM (Global Positioning System-Global System for Mobile Communications) transmitters. Between 2019 and 2021, we deployed Cellular Tracking Technologies (CTT; New Jersey, USA) in addition to Ornitela (Vilnius, Lithuania) transmitters in 2021-2022. Tagged cranes were monitored from 2020-2023. We programmed CTT and Ornitella transmitters to record GPS locations every 30 and 15 minutes, respectively, with locations uploaded once daily using the cellular network. To account for the spatial accuracy of the collected GPS locations, we removed locations with >40m accuracy (horizontal dilution of precision (HDOP) > 4) and poor connections (GPS Satellite Count > 0) (Askren et al. 2022). Finally, we resampled location data to 30-minutes relocation intervals for all individual in our dataset to account for potential differences in sampling rates between CTT and Ornitela transmitters (Signer et al. 2019).

3.3.3 Statistical Analysis

Our final dataset was filtered to only include the location data of breeding individuals in the boreal forest. We removed individuals that experienced transmitter failure or mortality throughout the breeding season, those with >20 days of missing location data during the breeding season (Nielson et al. 2009), or whose breeding range fell outside the spatial coverage of our landcover layer. Location data from the male of a potential breeding pair was also removed from our final dataset to avoid pseudo-replication of habitat use between the pair (the male and female were captured on the same day at the same site. Genetic sexing confirmed the sex of the male and female and subsequent analysis revealed high degrees of spatial overlap in their breeding ranges across multiple breeding years). Lastly, because cranes experienced strong breeding site fidelity between successive breeding years, if we had multi-year breeding data from an individual, only breeding data from one year was selected for inclusion in our final analyses. To address potential variability in climate and associated changes in landscape dynamics between years, we systematically removed individuals based on the maximum number of recorded breeding territories per year. We first identified the breeding year with the most recorded number of breeding territories across individuals and retained the breeding data for those individuals in that year. We subsequently removed all other breeding data from those individuals for all other breeding years. This process was repeated iteratively for each breeding year until we obtained a dataset representative of single-year breeding events for each successfully breeding crane.

3.3.3.1 Breeding territory arrival and departure dates

We estimated the arrival and departure dates of breeding territories by conducting single changepoint (CPA) analyses (Killick and Eckley 2014) to calculate significant changes in the net-squared displacement of an individual in R (R Core Team 2023). These changepoints can detect key movement phases corresponding to the arrival and departure of cranes from their breeding grounds (Patel et al. 2015, Singh et al. 2016). To classify the start and end point of the breeding season for each crane, we visually assessed the location of where the CPA was taken on the NSD plot and proceeded to trim the NSD plot using CPA until the graph resembled a horizontal plateau (Figure B.2.1). To be considered a breeding territory, the horizontal plateau had to occur for a minimum of three months within the period of March to October (Fronczak et al. 2017). If an individual did not have a defined plateau, we assigned them the mean arrival and departure dates calculated for all cranes with a definitive plateau for that respective breeding year.

Next, we considered whether an individual successfully bred using NSD plots to visualise movement exhibited throughout the breeding period and identify nesting periods (Figure B.2.*1*). Individuals were subsequently removed from our final analysis if they did not exhibit movement-specific behaviours associated with incubation. Because cranes are central place foragers, movement is spatially constrained by the frequency of return to a central location (Nilsson et al. 2020, Lalla et al. 2022). Throughout the breeding season, the central location often represents the return of a crane to the nest site and can thus be indicative of breeding-specific behaviours such as incubation (Picardi et al. 2020). Therefore, within our generated NSD plots, we assumed an approximate 30-day linear plateau, where movement was limited to ±2.5km, represented the incubation period of cranes. The 30-day plateau also had to occur anytime before mid-June as juveniles fledge 7-weeks following the incubation period and cranes begin to migrate to their wintering grounds around mid-September (McLean et al. *in prep*; Gerber et al. 2020).

3.3.3.2 Spatial analysis

We delineated breeding ranges by fitting 95% minimum convex polygons (MCPs) around each individual (Signer et al. 2019). Within each MCP, availability was sampled by randomly generating 1:2 ratio of used to available points within each home range (Johnstone et al. 2023). Nesting and roost site fidelity displayed by cranes can potentially lead to oversampling of these sites. Therefore, we ran a cluster analysis, using the *GPSeqClus* package (Clapp et al. 2021), for all used points within each home range to account for potential non-independence between sampled relocation data collected throughout the incubation period or at roost sites (Martin et al. 2009). *GPSeqClus()* parameters were based on both GPS accuracy and the behavioural characteristics of incubating cranes. Specifically, we set the search radius of each cluster to 40 meters, as determined by the GPS accuracy of our transmitters and HDOP values (Askren et al., 2022). The minimum temporal threshold (window_days) was set at 28 days to reflect the minimum incubation period of cranes, which typically lasts 28-30 days (Walkinshaw 1973*a*, *b*). To determine the minimum number of cluster locations within each cluster, we multiplied the recording frequency of GPS-GSM transmitters (every 30 minutes) by the minimum amount of time cranes spend at nest sites (males are responsible for only 30% of total incubation duties (i.e., approximately 7.2 hours per day at a nest site) (Nesbitt 1988, Gerber et al. 2014)). This product was then multiplied by the number of window days (28 days), resulting in a minimum requirement of 403 cluster locations within each cluster. We then buffered all used and available points by 45m to capture both the location and surrounding landscape, determined based on the grain of our spatial layer. For clustered locations, we identified the centroid within each cluster and buffered each centroid by 45m. All home range delineations and cluster analyses were conducted in R (R Core Team 2023).

Our RSF models included a pre-defined set of covariates we expected to be important predictors of crane occurrence and habitat use (Table 3.1). We classified general land cover based off the Annual Crop Inventory 2020-2023 raster layer (ACI 2023). Because high degrees of spatial overlap existed between the urban covariate in our ACI dataset and roads layer, we clipped urban features to the nearest city boundary (Statistics Canada 2017) and removed any urban features located either outside the city boundary or overlapped with the roads layer within the city. Regenerating cutblocks and naturally disturbed areas (e.g., wildfires) can also be found distributed across the landscape and can impact breeding territory selection (Lee et al. *in prep*). Therefore, we included forest disturbance (i.e., logging, cutblocks, and wildfires) as an additional land cover covariate in our analysis. The forest disturbance raster layer was obtained from Canada Landsat Derived Forest Harvest Disturbance 1985-2020 (Hermosilla et al. 2016). We limited the disturbance period to 2015-2020 to account for tree growth and stand height that could potentially restrict breeding habitat use. We also built road networks by combining layers obtained from the Ontario Road Network: Road Net Element (OMNRF 2019), Ontario Ministry of Natural Resources and Forestry Road Segments (MNRF 2019), and Addresses Québec AQréseau+ (AQR 2023). Non-road features such as railways and virtual roads, as well as winter roads were removed from our road networks. All road layers were originally downloaded as vectors which we later converted into a raster.

All habitat maps were processed in ArcGIS and assessed at a 30m spatial scale (ArcGIS Pro Desktop V3.1.2; ESRI Inc. 2022). Our final layer consisted of a land cover layer (ACI 2023) overlayed with a forest disturbance layer (Hermosilla et al. 2016) and road network. To reduce the total amount of covariates in our final models, we grouped similar covariates together based on similar habitat characteristics (Table 3.1). We extracted covariates using the *terra* package (Hijmans 2023) in R (R Core Team 2023). Extracted covariates were summarised as proportional cover and standardised by subtracting the mean and dividing by the standard deviation.

3.3.3.3 Model development

We built mixed effects logistic regression-based resource selection functions (RSFs) to quantify habitat selection of cranes at the third order. Due to multicollinearity between several of our habitat covariates and model convergence issues, we developed univariate mixed-effects logistic regression models to evaluate habitat selection for each of our habitat covariate. We included individuals as a random intercept to account for the hierarchical nature of our data. All covariates were standardised by subtracting the mean and dividing by the standard deviation. RSF model outputs with a positive coefficient of selection estimate (β value) indicated a selection for the respective habitat while a negative β-value indicated avoidance. If the confidence interval overlapped with zero, we assumed that there was no selection or avoidance for the respective habitat type. All models with $p < 0.05$ indicated significant selection or avoidance for the habitat type.

3.4 Results

We deployed transmitters on 122 adult cranes between 2019-2022. Location data were gathered from March to October between 2020-2023. We removed location data from individuals that experienced transmitter failure or mortality throughout the breeding season (n=65), had approximately 20 days or more of missing location data (n=4), bred outside the spatial coverage of our landscape layers (n=7), and a male who was likely paired with one of our females. Non-breeding individuals were removed from the analysis by visually assessing the net-squared displacement of the individual and identifying whether the 30-d linear plateau was present in the plot (n=58; Figure B.2.1). We also filtered the dataset and removed additional breeding data from individuals who bred in multiple years (n=25 additional breeding territories), ensuring that our final dataset comprised only of breeding data from one breeding year for each crane.

After filtering our dataset, we had a total of 238,364 locations from 42 breeding cranes. Of the cranes included in our analysis, the mean (± SD) breeding territory arrival and departure date were April 16 ± 8.0d and August 22 ± 18.4d, respectively, calculated using changepoints in the net-squared displacement of each crane (Figure B.2.1). Breeding territories size varied greatly between individuals, with the mean breeding territory size being 8.20 ± 26.2 km^2 and a range of 0.2 to 143.8 km^2 (Figure 3.1).

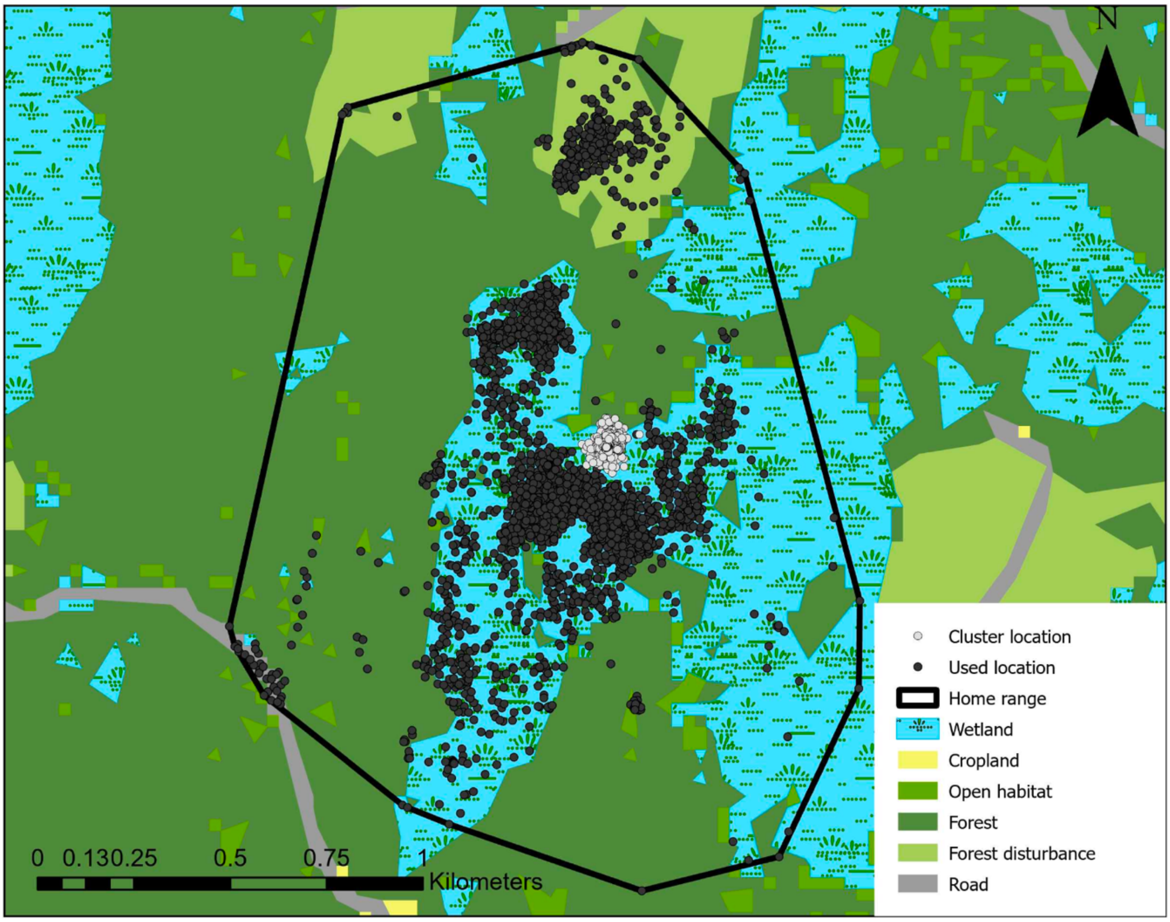

Figure 3.1 Example home range of a single crane throughout the 2023 breeding season in Ontario and Quebec, Canada. The black outline delineates the extent of the crane's home range. Points represent all used locations of the crane, while white points specifically indicate all locations found within an identified cluster which we classified as a nest site. Land cover and anthropogenic data were obtained from the Annual Crop Inventory Layer (ACI, 2023), CA Forest Harvest 1985-2020 (Hermosilla et al. 2016), Ontario Road Network: Road Net Element (OMNRF 2019), Ontario Ministry of Natural Resources and Forestry Road Segments (MNRF 2019), and Addresses Québec AQréseau+ (AQR 2023).

Based on the distribution of random points within each home range, the most dominant habitat types were forest (56.2%), open habitat (18.4 %), and wetland (11.9%), while cropland (3.2%), forest disturbance (3.0%), road (2.2%), urban (0.3%), and water (4.8%) were the least abundant (Figure 3.2). Our univariate GLMM models suggested that cranes strongly selected wetland, cropland, forest disturbance and water, weakly selected open habitat and roads, and avoided forest and urban habitats, relative to the proportion of habitat types available within each home range (Table 3.1 and Figure 3.3).

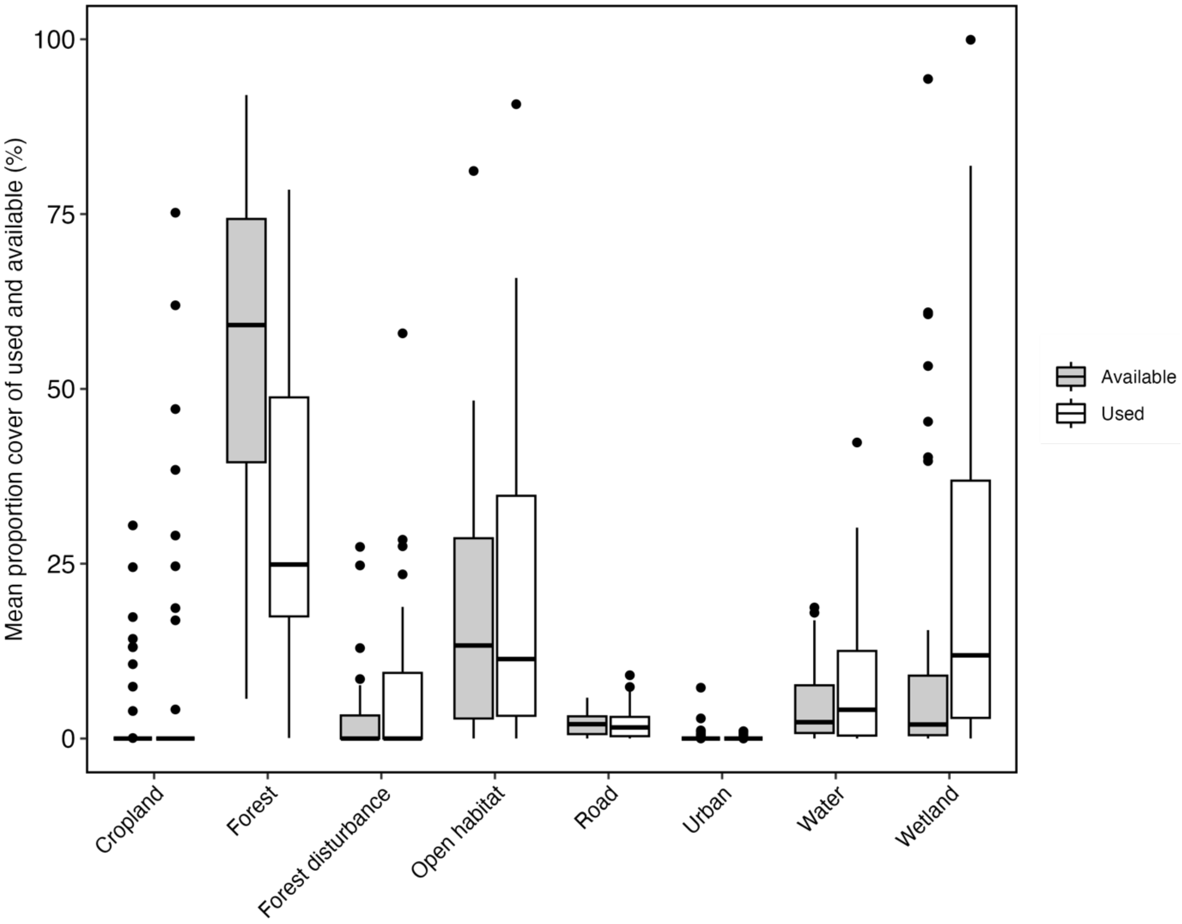

Figure 3.2. Proportion of habitat types between our used and available locations within the home ranges of cranes in Ontario and Quebec, Canada throughout the 2020-2023 breeding season.

Table 3.1 Land cover and anthropogenic covariates used to develop resource selection functions for cranes in Ontario and Quebec Canada, throughout the 2020-2023 breeding season. All covariates were summarised as proportional cover within each buffered point and analysed at a 30x30m spatial scale.

Covariate	Description	Unit	Reference
Land cover			
Forest	Conifer, broadleaf/deciduous, or mixedwood stands or treed areas.	%	ACI (2023)
Open habitat	Grassland, shrubland, or barren habitats.	%	ACI (2023)
Water	Bodies of water such as lakes, reservoirs, rivers, streams, and salt water.	%	ACI (2023)
Wetland	Areas where the water table remains near or above the soil surface. Includes semi-permanent or permanent wetland classes such as fens, bogs, swamps, sloughs, and marshes.	%	ACI (2023)
Anthropogenic			
Cropland	Areas used for the production of annual and perennial crops, perennial forage, and woody crops. Does not include naturally occurring grassland habitats.	%	ACI (2023)
Forest Disturbance	Areas recently impacted by wildfires or forest harvest.	%	Hermosilla et al. (2016)
Roads	Municipal roads, provincial highways, and resource and recreational roads.	%	MNRF (2019), OMNRF (2019), AQR (2023)
Urban	Built-up and developed areas.	%	ACI (2023)

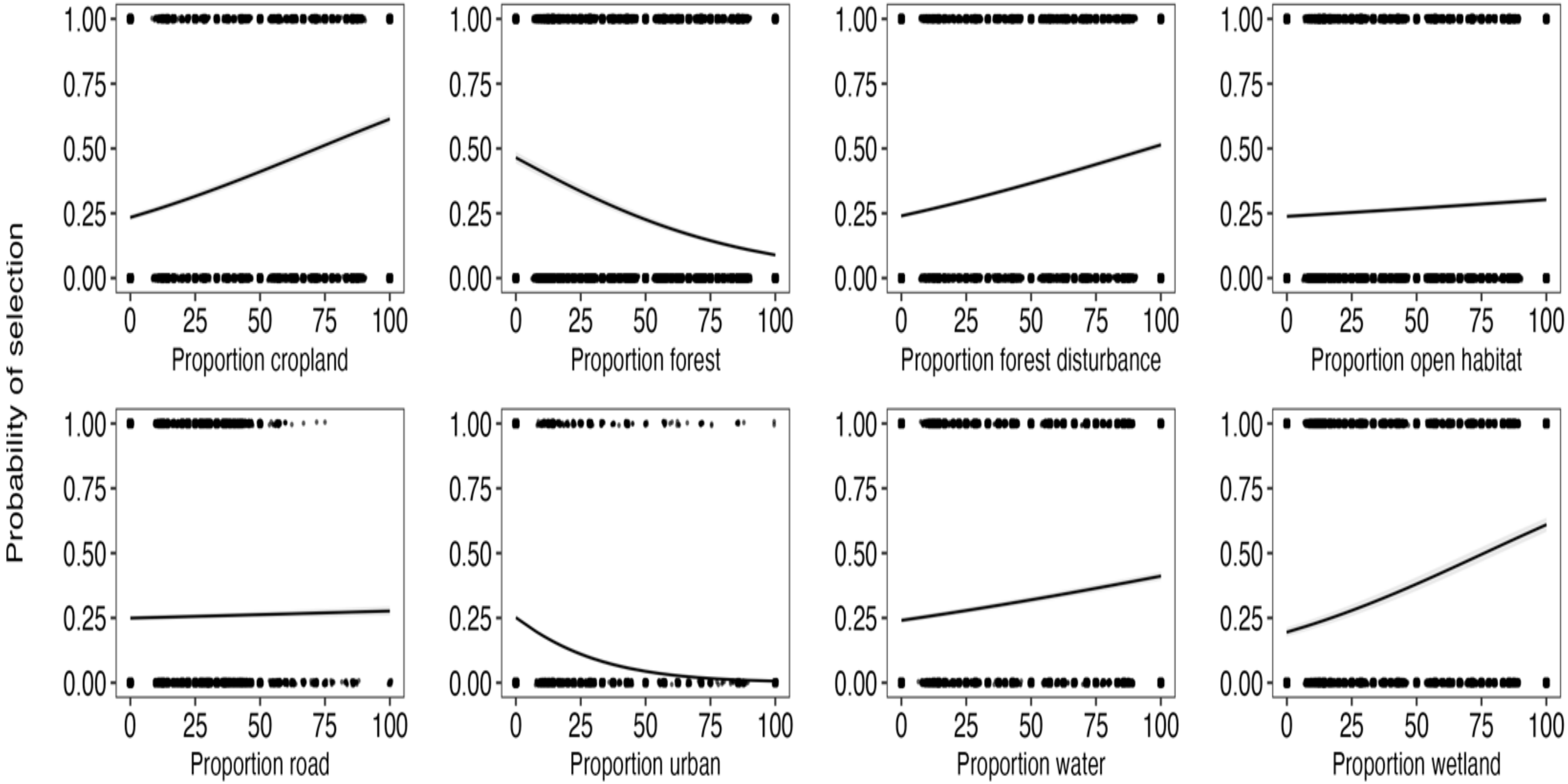

Figure 3.3. Predicted effects of land cover and anthropogenic covariates for breeding cranes in Ontario and Quebec, Canada between 2020-2023, with 85% confidence intervals. Units for all covariates are in proportions. Distribution of used and available points are represented by the points at the top and bottom of the graphs, respectively. Note that due to the scale of the graphs, confidence intervals may be difficult to see.

3.5 Discussion

As cranes continue to expand their breeding range into the Canada's eastern boreal forest, it becomes increasingly urgent to identify habitat characteristics at multiple scales that are important for breeding cranes to inform effective land management strategies. We used high-resolution satellite telemetry data to developed resource selection functions and quantify impacts of land cover and land use on third order selection (Johnson 1980) of breeding cranes in Canada's eastern boreal forest. Our research demonstrates the importance of wetlands for breeding cranes in this region and provides important insights into how cranes respond forestry practices and disturbance events, specifically logging and wildfires, in the boreal forest. We found that current levels of anthropogenic disturbance did not negatively affect habitat selection of breeding cranes in the boreal forest which is consistent with the small number of studies that previously investigated impacts of industrial development and forestry practices in other waterbird species within the boreal (Lemelin et al. 2007, Dyson et al. 2022, Johnstone et al. 2023).

Wetlands and open areas have previously been documented as important breeding habitat for cranes as these areas provide unobstructed views of the surrounding environment and freedom of movement across the landscape (Lovvorn and Kirkpatrick 1981, Baker et al. 1995, Su 2003, Lemelin et al. 2007). Wetlands are essential for breeding cranes and provide foraging, nesting, and brood-rearing habitat throughout the breeding season (Baker et al. 1995, McWethy and Austin 2009, Miller and Barzen 2016, Kruse et al. 2017, Casabona I Amat et al. 2022). Open habitats may have similar characteristics to wetland habitat where these habitats are inundated by spring snowmelt and run-off, creating seasonal wetlands (Kurkowski et al. 2023) available for cranes as they arrive on breeding grounds. In our study, cranes demonstrated stronger selection for water and wetland habitats, and weaker selection for open habitats within the home range. Stronger selection for wetlands and water highlights their significance even when open habitat is also available for use.

Variation in habitat use between wetlands, water, and open habitat may result from differences in microhabitat characteristics between habitats, as well as the seasonal duration during which open habitat resembles “wetland habitat” throughout the breeding season. Emergent vegetation around wetland and shore banks provides protective cover and visual concealment from predators, foraging resources for both the parents and offspring, and material to build nests (Drewien and Bizeau 1974, Urbanek and Bookhout 1992, Littlefield 1995, Donnelly et al. 2024). Wetlands also offer a greater diversity of potential prey items, particularly high protein animal prey which are important for cranes during egg production, nesting, and throughout the chick-rearing period (Nowald et al. 2018). Open habitat areas may lack additional components that wetlands provide such as vegetative structure and diversity of forage materials, resulting in decreased selection for open habitat. Cranes may also use wetland and open habitat differently throughout the breeding period, due to inter-annual variation in hydrological events that control the formation, duration, and persistence of seasonal wetlands. For example, seasonal droughts during late summer may limit the suitability of open habitat as viable wetland habitat (Donnelly et al. 2021, 2024, Bunting et al. 2022), resulting in decreased selection for open habitat towards the latter end of the breeding season. Permanent wetlands persist throughout the breeding season, likely leading to more consistent use of wetland habitat by cranes.

The "wetland" category in our spatial data represented an aggregation of multiple wetland habitat types including bog, fen, marsh, swamp, and open water. However, these wetland types can vary substantially in their hydrological and vegetation characteristics (Ducks Unlimited Canada 2011) and can have differential influence on breeding and nest site selection in cranes and other breeding waterbirds (Bennett 1992*b*, Dyson et al. 2022, Johnstone et al. 2023). While we observed selection for our aggregated wetland spatial data, classification of selection for different wetland types was limited based on the data available. Further refinement of spatial layers classifying different wetland types would result in concomitant refinement of our understanding of habitat selection within the breeding home range of cranes. Because seasonal wetlands also vary in availability year-round, the inclusion of time-varying covariates could also increase the accuracy and precision of habitat selection models.

We observed selection for forest disturbance areas and avoidance of intact forests within the home range. Avoidance of forest was consistent with previous research (Baker et al. 1995, Su 2003, Miller and Barzen 2016, Kruse et al. 2017) and may be due to increased predation risk and visual obstruction associated with forested habitats, as well as lack of forage (Urbanek and Bookhout 1992). Limited research exists regarding the impacts of forestry practices and industrial development on breeding cranes and other waterbird species within the boreal forest. Lemelin et al. (2007) found that cutblocks were positively associated ground nesting waterbirds such as Canada Geese (*Branta canadensis*) and American Green-winged Teals (*Anas crecca carolinensis*), while Johnstone et al. (2023) found that breeding Mallards (*Anas platyrhynchos*) avoided forest harvest areas. Other studies involving boreal breeding ducks have observed selection for industrial features such as borrow pits and well pads, with Dyson et al. (2022) and Johnstone et al. (2023) suggesting these areas mimic natural wetlands and provide important microhabitat characteristics that support breeding waterbirds. Similar to the habitat characteristics of borrow pits and well pads, we believe recently disturbed habitat in our study area resembled seasonal wetlands, resulting in cranes selecting for forest disturbance. Rapid succession of grassland plant communities and shrub species occurs following forest disturbance events such as forest harvesting or wildfires, (MacDonald et al. 2004, Ram et al. 2020), creating early successional communities that closely resemble open habitat. Snow melt throughout the spring can result in the creation of wetland features located in forest disturbance areas (MacDonald et al. 2004, Ram et al. 2020, Kellett et al. 2023) that could support breeding cranes. Disturbance events can also affect soil composition and thus may provide additional foraging opportunities for breeding cranes (Forsman et al. 2010, Austin 2018). It is important to note that forestry practices and industrial development often differ in the degree in disturbance and may have different relative effects on breeding habitat selection. Forestry practices typically involve single disturbance events where stands are cut and left to regenerate. Industrial development and associated infrastructure, such as borrow pits, well pads, compressor stations, and pipelines, often have higher degrees of human disturbance, as these sites require continual maintenance, monitoring, and traffic until the resource is depleted or no longer economically viable.

While we observed selection for recently disturbed areas, further research is required to understand how forest disturbance events affects breeding success and wetland use in cranes. Forest edges and cutblock areas can be positively associated with mammalian predators (Forman and Alexander 1998, Brodeur et al. 2008), which may act as ecological traps for cranes that breed in recently disturbed areas through increased predation risk. Modifications or changes caused by disturbance events can also impact riparian properties and water flow to other areas (Dubé et al. 1995, Smith et al. 2003), which may impact wetland use by cranes (Holopainen et al. 2015). Cranes are vulnerable to changes in water levels (Nesbitt 1988, Ivey and Dugger 2008) with lower water level increasing mammalian predator access (Sargeant and Arnold 1984, Austin et al. 2007), while high water levels may lead to flooded nest sites (Markham 1982, Bennett 1992*b*, Dwyer and Tanner 1992)

We observed strong selection for cropland, avoidance of urban areas, and weaker selection of roads within the home range. Cropland is an important foraging resource for cranes throughout the breeding season (Miller and Barzen 2016), with cranes often maximising time and energy foraging in agricultural fields for nutrient and energy-rich food (Downs and Horner 2008, Anteau et al. 2011, Nilsson et al. 2020, Hemminger et al. 2022). Strong inter-individual variation existed in cropland use in our study. This may be due to limited availability of cropland habitat across the boreal forest. The geology and relatively poor soil conditions of the Boreal Shield Ecozone are not suitable for agricultural development (Thiffault 2019), which limits the availability of cropland habitat relative to other habitats located within the region. Unsurprisingly, breeding cranes avoided urban areas as these areas do not support breeding habitat for cranes and high noise and human disturbance can negatively impact breeding success through nest abandonment and predation (Dwyer and Tanner 1992, Pearse et al. 2017). We also observed weaker selection for roads. It is difficult to discern effect of roads on breeding habitat selection given the very low road density in the region generally and within breeding home ranges, specifically. Previous studies have reported mixed results on selection of roads in cranes. Norling et al. (1992) observed avoidance for gravel and paved roads, while private roads did not affect selection choices. Pearse et al. (2017) documented avoidance of roads. While not measured directly during the breeding season, during the capture period when we deployed transmitters to cranes, we observed cranes using private or recreational roads when foraging around cropland (K. J. Lee, University of Waterloo, personal observation). Similar to the concerns mentioned above regarding the categorical resolution in wetlands, spatial data that accurately identifies different road classes may lead to finer resolution understanding of the influence of roads. We could not measure breeding success directly, but it is important to consider the potential impacts of roads on this life history parameter. Roads can act as travel corridors for mammalian predators (Frey and Conover 2006, Degregorio et al. 2014, Peterson et al. 2022) which may facilitate easier access into breeding habitat. Roads can also reduce habitat quality through noise production and visual disturbance (Forman and Alexander 1998). Dwyer and

Tanner (1992) also suggested that nesting around highways may cause adjacent nest sites to flood more rapidly.

The use of high-resolution satellite telemetry data provides unique opportunities to investigate patterns of habitat selection in remote areas of the boreal region and allows for a species-driven approach to quantifying patterns of breeding habitat selection. As demand for natural resources is expected to increase, forestry practices are likely to have greater impacts on the composition of habitats within boreal forest (Girona et al. 2023). Therefore, it is important to understand how anthropogenic disturbances impact habitat selection of breeding cranes. Although we report limited effects of anthropogenic disturbance on habitat selection patterns of breeding cranes, further research is required to investigate the underlying effects of disturbance events on nest site selection and breeding success in cranes. Given high breeding site fidelity and the potential impacts of forest disturbance events on wetlands, we recommend further research to investigate how anthropogenic disturbance impacts wetland use in the future. Wetlands continue to be an important predictor of breeding habitat use in cranes and further refinement of wetland layers is necessary (e.g., Ducks Unlimited Canada's Enhanced Wetland Classification raster layer; Ducks Unlimited Canada 2011) to elucidate effects of wetland type on breeding habitat selection of cranes.

Chapter 4: Conclusions

The boreal forest contains over 85% of Canada's wetlands and is a central breeding ground for many waterbird species (Holopainen et al. 2015), including cranes (Casabona I Amat et al. 2022). Breeding habitat is an important component of the crane's annual cycle, with the quality and availability of breeding habitats strongly influencing reproduction, survival, and overall population viability (Johnson 2007). Anthropogenic disturbance is a major threat to the boreal forest ecosystem (Venier et al. 2014) and can alter important ecosystem services including carbon storage, community composition, and wildlife habitats (Wilson et al. 2020, Boulanger and Pascual Puigdevall 2021). Impacts of disturbance events (e.g., forest harvest, logging, and wildfires) on breeding cranes remains largely unknown, necessitating further research to understand its effects on breeding habitat use. As cranes continue to expand their range and recolonize historical breeding areas in this region (Amundson and Johnson 2011, Fronczak et al. 2017, Casabona I Amat et al. 2022), it is important to understand ecological drivers of breeding habitat selection. These findings can be used to develop site-specific and range-wide management efforts that support the long-term viability of crane populations that breed in the boreal forest.

We examined second and third order habitat selection of breeding cranes in the boreal. Findings from our study revealed breeding habitat selection of cranes to be scale dependent and that model results varied across scales. At second order, our top model revealed selection for breeding territories containing greater proportions of cropland, forest disturbance, and wetland habitat. Competitive models also indicated selection for breeding territories with greater proportions of urban and roads and avoidance of areas containing greater proportions of forest, open habitat, and water. At third order, we observed strong selection for cropland, forest disturbance, water, and wetland, weaker selection for open habitat and roads, and avoidance of forest and urban areas. Differences in selection choices between second and third order suggests that habitat selection of breeding cranes is hierarchical in nature and that findings at broader ecological scales do not necessarily reflect the selection and activity patterns of cranes at finer scales. This can have important implications when findings are used to guide land management decisions that address conservation at either the population or individual level (Meyer and Thuiller 2006). For example, if land managers were presented with results from second order selection for management of habitat patches within the home range, they may mistakenly prioritise the protection of urban environments over water and open habitat. However, by examining patterns of habitat selection between scales, land managers are able to understand the relative importance of these land cover variables to cranes when establishing territories across the landscape compared to resource use within the home range. By carefully evaluating habitat selection at various scales, managers can ensure that management strategies effectively align with the specific habitat requirements of breeding cranes and prevent issues that may arise from a single-scale focus. Ultimately, this study illustrates the importance for future research to adopt multi-scale approaches in habitat selection analyses. Such strategies are essential to develop effective management plans that address both the broad landscape level requirements of crane populations at the second order as well as the specific habitat requirements of breeding individuals at the local (i.e., home range or third order) level.

We identified important land cover and land use features used by cranes throughout the breeding season and quantified patterns of habitat selection at the second and third order in the boreal forest. Overall, our results suggest that anthropogenic disturbance did not negatively affect breeding habitat selection of cranes and that wetland continues to be an important predictor of breeding habitat use. Findings from our study suggest that the boreal forest contains an abundance of habitat available to support cranes throughout the breeding season, such that current levels of anthropogenic disturbance in the boreal forest have minimal effects on territory establishment or habitat selection. However, as anthropogenic disturbance continues to expand in the boreal, results may differ with subsequent forest harvest and forestry management practices, requiring further research to explore the cumulative impacts of anthropogenic disturbance on breeding cranes over the long term. Long-term forestry practices may lead to changes in water dynamics (Shah et al. 2022) and wetland function (Richardson 1994, Shepard 1994, Wei et al. 2022) over time. Wetland use of waterbird species is closely linked to water availability and hydrolytic cycles that drive wetland function (Donnelly et al. 2022). Changes in wetland function, such as alterations in food source availability, predator access, and protective cover, may impact the overall habitat quality and availability of wetlands as viable breeding grounds for nesting cranes (Markham 1982, Sargeant and Arnold 1984, Austin et al. 2000, 2007, Brodeur et al. 2008, Dyson et al. 2022). Limited research exists regarding the relationship between wetland-forest disturbance events and crane habitat use. Therefore, we recommend further research that investigates whether the cumulative impacts of future forestry practices (e.g., cutblocks, logging, and forest harvest) will limit the availability of wetland as viable breeding habitat and if forest disturbance areas will replace wetlands as primary breeding habitats for cranes in the boreal forest.

While we observed selection for forest disturbance areas at second and third order, caution is warranted when applying these findings to land management practices. Selection for forest disturbance may be attributed to spring snowmelt flooding these areas, forming seasonally flooded habitats reminiscent of wetlands (Kurkowski et al. 2023) that appear to be suitable for breeding cranes. However, previous research in other waterbird species observed avoidance for these areas (Johnstone et al. 2023). Forest disturbance areas are associated with increased predator activity (Dyson et al. 2020) and nest predation risk (Pierre et al. 2001), and may potentially act as ecological traps (Hale and Swearer 2016) for breeding cranes. As a result, cranes that nest in forest disturbance areas may experience lower reproductive success compared to cranes that nest in wetlands. Therefore, we highly recommend further research that examines the reproductive success of cranes that nest in forest disturbance areas. This will provide a more comprehensive overview of the suitability of forest disturbance areas as viable breeding habitat for cranes in the boreal forest.

Overall, results from this thesis highlight the importance of conducting habitat selection studies across multiple scales to capture the complexity in which cranes respond to a broad range of land cover and land use classes. Findings at broad ecological scales can be applied to regional and provincial wildlife management and incorporated into land-use planning and reserve design that benefit cranes at the population level. Finer-scale selection results provide important insight for local habitat management that focus on the specific habitat requirements of individual cranes. Integration of breeding habitat selection results from other crane populations would be useful to provide a more comprehensive understanding of how cranes respond to land cover and land use classes. Not only will this approach extend the applicability of our findings to other boreal breeding populations (e.g., Mid-continental Population Krapu et al. 2011), but it can also be applied to other populations that breed outside the region (e.g., other Eastern Population and Mid-continental Population cranes; Krapu et al. 2011, Fronczak et al. 2017). Ultimately, this empirical approach can be applied to a variety of species across diverse landscapes to assess how ecological processes differentiate across spatial scales and can therefore contribute to improving the reliability of habitat selection analyses and support of large-scale conservation on a global scale.

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Appendix

6.1 Appendix A: Chapter 2

Table A.2.1. Home range size of breeding sandhill cranes within the boreal forest of Ontario and Quebec, Canada for each breeding season, determined using 95% minimum convex polygons. Date of arrival and date of departure represent the day an individual arrived and left the breeding territory. Duration represents the total number of days an individual spent on the breeding territory. Total locations denote the total amount of recorded location data from when an individual arrived and departed from their respective breeding territory, following the resampling of location data to 30-minute intervals.

Crane ID	Breeding year	Home range area (km2)	Date of arrival	Date of departure	Duration (days)	Total locations
AB044	2020	69.5	02/05/2020	30/08/2020	120	5599
	2021	8.7	20/04/2021	23/08/2021	125	5826
	2022	4.8	01/05/2022	14/09/2022	136	6313
	2023	1.7	27/04/2023	26/08/2023	121	5586
AB343	2020	4.0	01/05/2020	25/08/2020	116	5379
	2021	4.6	14/04/2021	30/08/2021	138	6403
	2022	7.8	22/04/2022	01/09/2022	132	6089
	2023	3.5	24/04/2023	14/09/2023	143	6646
AB350	2020	2.8	01/05/2020	25/08/2020	116	5395
	2021	1.2	19/04/2021	05/08/2021	108	5033
AB414	2020	10.7	29/04/2020	08/09/2020	132	5962
	2021	2.3	23/04/2021	26/08/2021	125	5708
	2022	19.4	29/04/2022	31/08/2022	124	5594
AB713	2021	45.1	24/04/2021	28/07/2021	95	3539
	2022	32.1	02/05/2022	08/09/2022	129	5788
	2023	11.2	27/04/2023	25/08/2023	120	5145
AB796	2020	7.5	28/04/2020	26/08/2020	120	5556
	2021	2.9	19/04/2021	01/08/2021	104	4830
	2022	7.3	25/04/2022	12/09/2022	140	6312
	2023	3.4	26/04/2023	06/09/2023	133	6156
AL165	2022	1.4	20/04/2022	20/09/2022	153	7157

AM484	2022	5.5	29/04/2022	04/09/2022	128	5659
	2023	4.5	24/04/2023	26/08/2023	124	5627
AU516	2022	5.2	13/04/2022	13/09/2022	153	7054
	2023	1.4	14/04/2023	26/08/2023	134	6211
AU870	2022	4.6	16/04/2022	16/09/2022	153	7144
AZ177	2022	8.2	24/04/2022	27/09/2022	156	7105
AZ231	2022	6.0	12/04/2022	26/08/2022	136	6275
AZ418	2021	5.5	13/04/2021	27/08/2021	136	6275
	2022	3.8	22/04/2022	06/08/2022	106	4868
AZ765	2022	5.1	20/04/2022	25/07/2022	96	4306
	2023	4.8	22/04/2023	22/08/2023	122	5082
CO761	2023	8.6	15/04/2023	30/08/2023	137	6566
MN112	2022	0.8	11/04/2022	01/09/2022	143	6314
MN605	2022	8.4	29/03/2022	19/08/2022	143	6635
	2023	0.5	06/04/2023	17/08/2023	133	6070
MN678	2022	0.2	11/04/2022	01/08/2022	112	5230
	2023	0.2	02/04/2023	15/08/2023	135	6290
MN753	2022	2.0	03/04/2022	21/08/2022	140	6481
	2023	0.4	10/04/2023	12/08/2023	124	5794
MN823	2022	1.5	08/04/2022	04/08/2022	118	5359
	2023	0.3	06/04/2023	02/08/2023	118	5509
MN837	2021	81.1	29/03/2021	27/09/2021	182	8309
	2022	13.0	07/04/2022	31/08/2022	146	6508
	2023	22.8	28/03/2023	23/08/2023	148	6693
MS234	2021	22.5	09/04/2021	11/08/2021	124	5764
MS242	2022	13.1	07/04/2022	01/08/2022	116	5350
	2023	4.9	25/04/2023	25/07/2023	91	3919
MS259	2021	1.5	03/04/2021	24/08/2021	143	6621
MS937	2022	89.3	22/04/2022	31/08/2022	131	6026
NL157	2023	2.6	07/05/2023	26/08/2023	111	5159
NL231	2020	12.0	04/05/2020	27/08/2020	115	5157
	2021	48.0	17/04/2021	25/08/2021	130	5883
	2022	11.2	22/04/2022	02/09/2022	133	5951

NL259	2021	143.8	19/04/2021	19/08/2021	122	5549
NL679	2020	8.0	28/04/2020	10/09/2020	135	5951
	2021	6.4	18/04/2021	14/08/2021	118	4985
	2022	9.0	22/04/2022	02/09/2022	133	5552
	2023	4.7	23/04/2023	05/09/2023	135	6051
NL762	2020	12.2	01/05/2020	30/08/2020	121	4892
	2021	30.6	09/04/2021	25/08/2021	138	4726
NL802	2020	17.6	28/04/2020	06/09/2020	131	6058
	2021	18.6	23/04/2021	25/08/2021	124	5728
	2022	20.1	30/04/2022	03/09/2022	126	5841
NL844	2020	11.1	16/04/2020	03/09/2020	140	6222
	2021	4.6	12/04/2021	28/08/2021	138	5782
	2022	19.9	20/04/2022	05/09/2022	138	6003
	2023	26.0	15/04/2023	27/08/2023	134	6067
NL850	2023	15.0	09/04/2023	21/08/2023	134	6084
NL868	2020	12.0	28/04/2020	06/09/2020	131	5910
	2021	28.3	19/04/2021	26/08/2021	129	5355
	2022	11.6	30/04/2022	12/09/2022	135	6001
NL937	2023	10.4	20/04/2023	11/09/2023	144	6587
SM001	2021	3.9	27/04/2021	01/08/2021	96	4300
SM225	2021	17.5	13/04/2021	29/07/2021	107	4391
SM655	2021	2.4	23/04/2021	26/08/2021	125	5497
	2022	4.2	28/04/2022	07/08/2022	101	4599
SM711	2021	25.8	13/04/2021	22/08/2021	131	5822
SM806	2021	8.2	14/04/2021	19/08/2021	127	5921
SM932	2022	5.0	17/04/2022	11/09/2022	147	4759
	2023	3.1	15/04/2023	05/09/2023	143	6845
SM934	2022	30.6	21/04/2022	31/08/2022	132	6270
SM936	2022	62.4	18/04/2022	12/09/2022	147	5139
SM938	2022	7.0	25/04/2022	06/08/2022	103	3335
TI758	2023	5.7	14/04/2023	19/08/2023	127	6068
TI762	2023	9.0	12/04/2023	10/08/2023	120	5760
TI763	2023	3.9	28/04/2023	29/08/2023	123	5903

TI770	2023	14.2	20/04/2023	30/08/2023	132	6292
VA916	2022	3.9	13/04/2022	16/09/2022	156	7279
	2023	2.9	23/04/2023	09/09/2023	139	6481

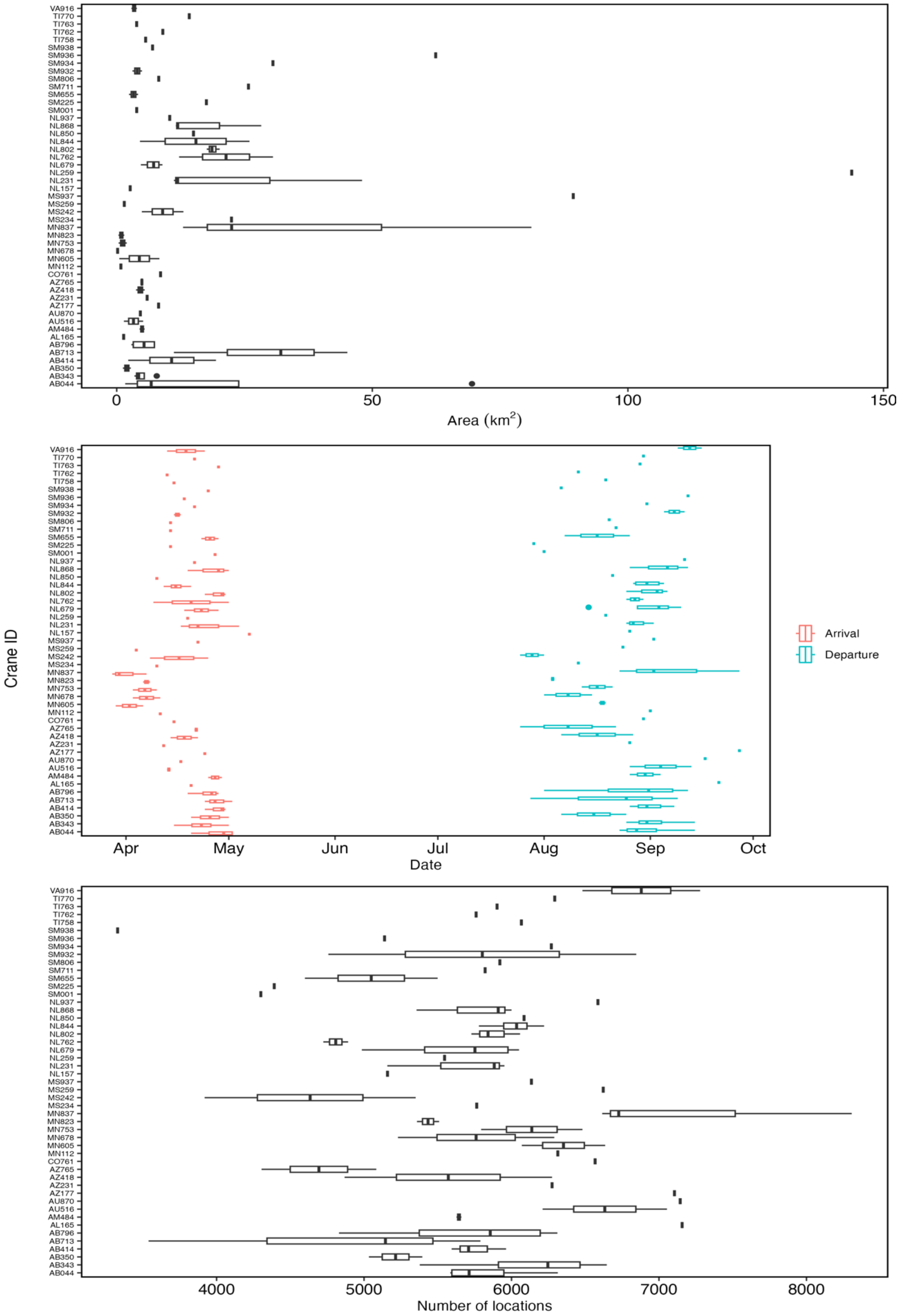

Figure A.2.1. Distribution of home ranges size, arrival and departure dates, and total number of locations taken throughout the 2020-2023 breeding season for each sandhill crane that bred within the boreal forest of Ontario and Quebec, Canada.

Table A.2.2. Distance between breeding territories for sandhill cranes with multiple recorded breeding territories within the boreal forest of Ontario and Quebec, Canada. Distance was calculated by fitting a 100% MCP around all recorded breeding territories and determining the centroid, which represented the average centre of all breeding territories combined. Additional centroids were then placed within each recorded breeding territory before computing the distance from each breeding territory's centroid to the centroid of the overall MCP. Mean distance indicates the average distance between breeding territories across all recorded breeding years. Year and Distance denote the distance from the respective year's breeding territory centroid to the distance of the overall MCP's centroid.

Crane ID	Number of breeding territories	Mean distance (km ± sd)	Year	Distance (km)
AB044	4	1.7 ± 1.0	2020	0.3
			2021	2.2
			2022	2.0
			2023	2.3
AB343	4	0.3 ± 0.2	2020	0.3
			2021	0.2
			2022	0.0
			2023	0.5
AB350	2	0.1 ± 0.1	2020	0.0
			2021	0.2
AB414	3	0.5 ± 0.4	2020	0.7
			2021	0.6
			2022	0.0
AB713	3	1.4 ± 0.8	2021	0.5
			2022	1.7
			2023	1.9
AB796	4	0.2 ± 0.1	2020	0.2
			2021	0.2
			2022	0.3
			2023	0.3
AM484	2	0.1 ± 0.1	2022	0.1
			2023	0.2
AU516	2	0.2 ± 0.3	2022	0.0

			2023	0.5
AZ418	2	0.2 ± 0.2	2021	0.1
			2022	0.4
AZ765	2	0.04 ± 0.0	2022	0.1
			2023	0.1
MN605	2	0.02 ± 0.0	2022	0.0
			2023	0.0
MN678	2	0.02 ± 0.0	2022	0.0
			2023	0.0
MN753	2	0.05 ± 0.1	2022	0.0
			2023	0.1
MN823	2	0.08 ± 0.1	2022	0.0
			2023	0.2
MN837	3	1.4 ± 1.1	2021	0.1
			2022	2.1
			2023	2.0
MS242	2	0.6 ± 0.7	2022	0.1
			2023	1.1
NL231	3	4.6 ± 2.4	2020	2.7
			2021	3.7
			2022	7.2
NL679	4	0.3 ± 0.2	2020	0.5
			2021	0.4
			2022	0.2
			2023	0.1
NL762	2	0.5 ± 0.6	2020	0.9
			2021	0.1
NL802	3	0.2 ± 0.1	2020	0.3
			2021	0.2
			2022	0.1
NL844	4	0.8 ± 0.6	2020	1.3
			2021	1.4
			2022	0.2

			2023	0.5
NL868	3	0.8 ± 0.6	2020	1.2
			2021	0.2
			2022	1.0
SM655	2	0.11 ± 0.2	2021	0.3
			2022	0.0
SM932	2	0.3 ± 0.2	2022	0.2
			2023	0.5
VA916	2	3.7 ± 5.2	2022	7.4
			2023	0.0

6.2 Appendix B: Chapter 3

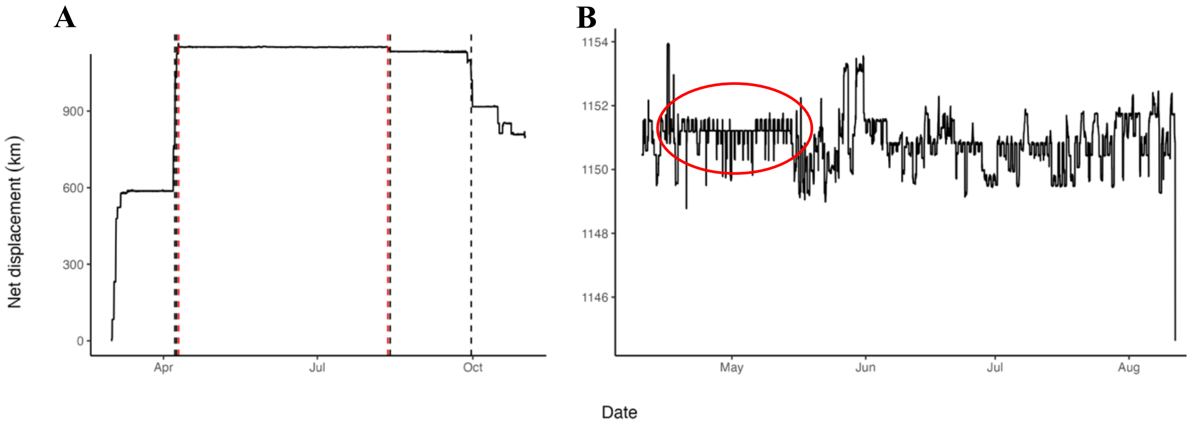

Figure B.2.1 Example net displacement and changepoint analysis of a single crane used to identify the timing of breeding territory arrival and departure dates and classify breeding individuals during the 2020-2023 breeding periods in Ontario and Quebec, Canada. Panel A represents the net displacement of a crane from March to October and identified changepoints (dotted lines) taken throughout the same period. The changepoints denoted in red represent the breeding territory arrival and departure dates. All location data outside of the arrival and departure timeframe were removed from our analysis. Location data between the changepoints represented the net displacement and total time the crane spent on their breeding grounds. Panel B shows the clipped net displacement segment and time spent on breeding grounds, based on the identified changepoints. The 30-day linear plateau, located between mid-April and mid-May (circled in red), indicates the individual crane successfully bred. We assumed the 30-day linear plateau represented the incubation period of a successfully breeding crane.