

Landscape Effects on Breeding Habitat Selection and Incubation Behaviour in Boreal Nesting Ducks

by

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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.

I understand that my thesis may be made electronically available to the public.

Statement of Contributions

The manuscripts presented in this thesis are the work of Ryan Johnstone, in collaboration with his co-authors and advisor. The co-authors include Dr. Brad Fedy, Dr. Matthew Dyson, and Dr. Stuart Slattery. Ryan Johnstone is first author on both of the manuscripts and responsible for the data collection on the home range manuscript. Dr. Matt Dyson is responsible for the data collection on the incubation dataset used in the manuscript. Ryan Johnstone was responsible for the data wrangling, analysis, writing, and preparation of all the following manuscripts, including figures and tables. The contents of the manuscripts were edited by co-authors.

The incubation manuscript is being prepared for submission to IBIS and meets their formatting requirements. The home range manuscript does not have a publishing journal of interest at this time, and therefore meets the requirements of IBIS for consistency.

Disclaimer

The research presented in the chapters of this thesis are the product of collaborative efforts from the co-authors and myself. Therefore, for the remainder of this thesis I will refer to these collaborative efforts using the collective “we/our” in accreditation for all of those involved.

Abstract

Canada's western boreal forest is the second most important breeding area for North American duck populations. Over the last several decades, this region has experienced a considerable expansion of industrial development that has drastically altered the structure of the landscape. Duck populations in North America are a significant and sought-after game species and thus require effective conservation and management. There is relatively limited research regarding boreal duck ecology and the impacts of industrial development on ducks breeding in this region remain largely unexplored. We investigated the effects of land cover and land use on second and third order habitat selection in boreal breeding female Mallards (*Anas platyrhynchos*). In addition, we developed a new method to identify nest attendance patterns, and applied this method to quantify incubation behaviour (i.e., daily recess frequency, duration, and incubation constancy) in four species of ground nesting ducks across a gradient of land cover and land use types. We modelled the effects of land cover, land use, and weather on incubation behaviour at the micro (i.e., nest site) and macro (i.e., home range) scale. We found that breeding female Mallards established home ranges with greater proportions of marsh habitat, graminoid fens, and well pads. Within their home ranges, female Mallards selected shrub swamps, marsh, graminoid fens, well pads, and borrow pits. Female Mallards also selected habitats that were close to roads and pipelines. Additionally, land cover, land use, and weather influenced incubation behaviour, and our results suggested that boreal nesting ducks took more recesses per day in response to greater densities of secondary roads and proportions of marsh habitat surrounding the nest. Overall, our results suggested that breeding Mallards selected and avoided a combination of land cover and land use features when establishing home ranges and selecting habitats within the home range. In addition, the

relationships between incubation behaviour in upland nesting ducks and land cover, land use, and weather are equivocal, requiring further investigation. Our research addressed important questions concerning ducks' behavioural response to the natural features and industrial development during the breeding period. With the expected continuation of industrial development in the boreal forest, this information is vital. It will serve as a baseline for future habitat selection and incubation research in the region; and, assist managers when making predictions about waterfowl population trajectories in the boreal and other ecosystems experiencing similar habitat changes.

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Dedication

This thesis is dedicated to my best friend, brother, and forever wingman Thomas Hurley Brown. May you soar with the eagles and ride the cold November winds.

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We must first change our role as conqueror of the land to citizen of the land

- Aldo Leopold, 1948.

Chapter 1: Literature Review

1.1 Ecology

Modern ecology stemmed from an interest in answering simple questions regarding what animals were doing, the drivers of these behaviours, and the limiting factors acting on them (Elton 1927, Andrewartha 1970). The pursuit of, and the answers to these questions have provided ecologists and population managers with valuable insight regarding the extrinsic factors that influence individual behaviour (McLoughlin *et al.* 2010) and subsequent individual or population level fitness (Boyce & McDonald 1999, Hebblewhite & Merrill 2008). Understanding how individuals interact with their surroundings and the subsequent outcomes is required to better explore central problems influencing the abundance and distribution of animals and populations across habitats and spatial scales (Brown 1984, Jones 2011, Lele *et al.* 2013, Matthews & Whittaker 2015). Therefore, to refine our understandings of animal ecology, we must first determine how individuals (or populations) interact with their habitat, and how habitat influences their decisions and fitness throughout their annual cycle.

1.2 Habitat

Habitat is a unique suite of biotic and abiotic environmental factors that influences the individual's behaviour (Holopainen *et al.* 2015) and limits the abundance and distribution of a species (Boyce & McDonald 1999, Kaminski & Elmberg 2014, Boyce *et al.* 2016) by affecting survival (Fretwell & Lucas 1968) and reproduction (Block & Brennan 1993, Jones 2001). In ducks, changes in habitat structure and composition have been shown to influence varying stages of the annual cycle including migration and staging (Krementz *et al.* 2012, Bengtsson *et al.* 2014, Meattley *et al.* 2019) and nest site selection and brood rearing (Yerkes 2000, Ludlow

& Davis 2018, Kemink *et al.* 2019, Dyson 2020). In addition, evidence suggests that habitat characteristics influence nest success (Dyson 2020, Skaggs *et al.* 2020), and female (Gue *et al.* 2013) and offspring survival (Roy 2018). Since these vital life stages are influenced by habitat structure, it is important to understand how habitat alterations can affect decisions and subsequent landscape interactions of individuals and populations throughout their annual cycle.

Industrial development threatens habitat and ecosystem function (Fahrig 2003, Fahrig & Rytwinski 2009, Beatty *et al.* 2014a, Roy 2018) at both the regional and local scale (Drapeau *et al.* 2000, Faleiro *et al.* 2013, Beatty *et al.* 2014a, Holopainen *et al.* 2015) by altering the landscape and community structure (Wiegand *et al.* 2005, Copeland *et al.* 2011), posing a major threat to global biodiversity (Turner *et al.* 2008, Hanski 2011, Lambin & Meyfroidt 2011, Hebblewhite 2017). This process is an inherent function of society that is linked to economic, technologic, and societal growth (Houghton 1994, Allred *et al.* 2015). With global populations on the rise (Wagner *et al.* 2016), energy use is predicted to increase, and a majority of this demand is expected to be supplied by fossil fuels (Faleiro *et al.* 2013, Jones *et al.* 2015).

In North America, industrial development is a major threat to terrestrial ecosystems (Allred *et al.* 2015, Hebblewhite 2017), and the fossil fuel extraction (i.e., oil and gas) industry has claimed ~3 million ha of land for production purposes (Hebblewhite 2017). The forestry industry operates concomitantly and rivals the oil and gas sector as the leading cause of land use change (Timoney 2003). There is growing interest to shift from fossil fuel dependent energy towards more carbon neutral platforms (Jones *et al.* 2015), which would reduce overall carbon emissions (Pimentel *et al.* 2002, McDonald *et al.* 2009) and climate change concerns

(Jacobson 2009). However, this change does not alleviate the landscape impact on the terrestrial environments. The cumulative land use requirements (i.e., industrial footprints) are similar, if not greater for carbon neutral energy alternatives (e.g., solar farms; McDonald *et al.* 2009), increasing the concern for terrestrial biodiversity and ecosystem dynamics.

The impacts of industrial development on species ecology has been well studied across mammalian taxa (Green & Elmberg 2014, DeMars & Boutin 2017, Dickie *et al.* 2017, Hebblewhite 2017, Muhly *et al.* 2019). Evidence suggests that anthropogenic changes to landscape structure benefit predator communities by facilitating movement (DeMars & Boutin 2017, Finnegan *et al.* 2018) increasing their efficiency (Abrams & Ginzburg 2000, Muhly *et al.* 2019, Mumma *et al.* 2019) resulting in unsustainable mortality rates that negatively affect prey population-level fitness (McLoughlin *et al.* 2005, Hebblewhite 2017). Efforts to mitigate these impacts require an extensive understanding of both species ecology and behavioural response to anthropogenic landscape alterations (i.e., industrial development; McLoughlin *et al.*, 2010). Therefore, it is vital that we identify the factors influencing animal behaviours and investigate the effects of anthropogenic change on ecosystem structure and function, which will assist in determining the cause of species decline.

Habitat selection (Johnson 1980) is a central component of animal ecology that has been investigated for many years (Kendeigh 1945, Fretwell & Lucas 1968, Cody 1981, Block & Brennan 1993). The hierarchically sequential process has received considerable recognition throughout the ecological literature (Wiens 1973, Jones 2001, Meyer & Thuiller 2006). The four orders of selection (Figure 1.1) define the seasonal range of a species or population within their geographic range (first order) that determines the seasonal home range (second order;

Johnson 1980). Selection then becomes demonstrative of resource use, and represents habitat patch (e.g., marsh) selection within the home range (third order); followed by the precise procurement of resources (e.g., nest sites) within those patches (fourth order; Johnson 1980, Meyer & Thuiller 2006). Though we must distinguish between habitat selection and use (Jones 2001). Habitat use represent the patterns and behaviours exhibited by an individual or species when using habitats; whereas, habitat selection is a process that results in the disproportionate use of habitats with the goal of increasing fitness and survival (Block & Brennan 1993, Boyce & McDonald 1999, Jones 2001, Lele *et al.* 2013). Ultimately, habitat selection occurs coarsely at the regional or population level and results in the precise selection of habitat components (i.e., habitat use) at the local or individual level (Johnson 1980, Jones 2001).

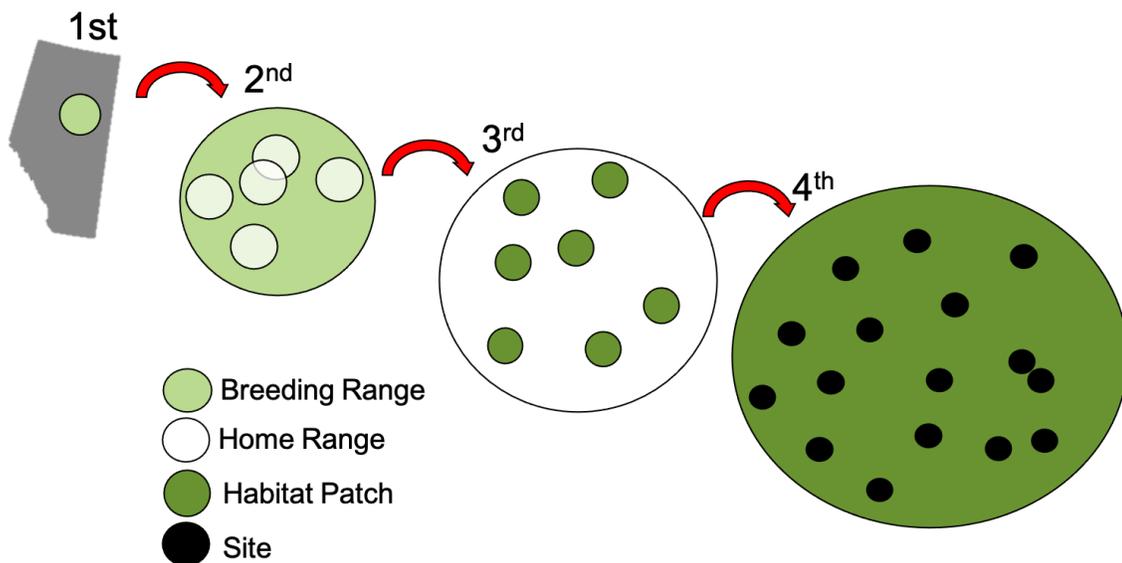


Figure 1.1 – Hierarchical orders of habitat selection based on Johnson’s (1980) natural orders of selection.

The motives to select a particular habitat may be disparate to the underlying reasons for their persistence within those habitats. For example, the fourth order settling patterns of

breeding ducks can be flexible (Johnson & Grier 1988) and influenced by philopatric behaviours (Rohwer & Anderson 1988, Gauthier 1990, Evrard 1999) or landscape characteristics (Singer *et al.* 2020). While post-breeding habitat selection at the third order can be influenced by nest success and habitat characteristics (Yerkes 2000, Roy 2018) or congregations of conspecifics (Block & Brennan 1993, Elmberg *et al.* 1997, Thomson *et al.* 2003, Kaminski & Elmberg 2014). Therefore quantifying habitat selection at relevant hierarchical levels (Johnson 1980, Meyer & Thuiller 2006) is essential for elucidating the underlying factors that influence decisions.

Habitat selection is a scale-dependent process (Mayor *et al.* 2009) that occurs at different spatial and temporal scales within the hierarchical levels (McGarigal *et al.* 2016). Therefore, we must consider and distinguish between scales when exploring habitat selection because scale-specific factors that limit overall fitness may influence the individual or population differently (Orians & Wittenberber 1991). For example, habitat selection during the breeding period is temporally distinct and unrepresentative of habitat selection during the non-breeding period. Additionally, breeding habitat selection is often different between sexes and species due to intra- and interspecific requirements (Afton & Paulus 1992, Jönsson 1997, Lamb *et al.* 2020), though it can be similar during the non-breeding period (Bengtsson *et al.* 2014, Lamb *et al.* 2020). Furthermore, breeding and non-breeding period objectives of opposite sexes can be influenced by landscape variables at different spatial scales (Hostetler 2001, Bloom *et al.* 2013, Beatty *et al.* 2014b, Dyson 2020). Thus, it is important that we explore habitat selection across all relevant hierarchal levels (Boyce 2006, DeCesare *et al.* 2012, Beatty *et al.* 2014b,

Kaminski & Elmberg 2014); and, at applicable spatial and temporal scales (Orians & Wittenberber 1991, Mayor *et al.* 2009, McGarigal *et al.* 2016).

1.2.1 Modelling Habitat Selection

Over the last decade, our ability to investigate and understand animal habitat selection has drastically improved as tracking technologies have become more advanced (Lele *et al.* 2013, Thurfjell *et al.* 2014, Signer *et al.* 2019) and statistical analyses have evolved, aiding our ability to process and interpret mass amounts of location data (Prokopenko *et al.* 2017, Signer *et al.* 2019, Joo *et al.* 2020). Of the various modelling approaches, resource selection functions (RSFs) offer a robust framework for quantifying and describing animal habitat selection (Fieberg *et al.* 2020). RSFs compare environmental covariates at used locations to those at randomly distributed available locations within an estimated availability range (Boyce *et al.* 2002, Signer *et al.* 2019) using logistic regression analysis to produce proportional probabilities of used versus available habitat (Boyce *et al.* 2016, Avgar *et al.* 2017, Fieberg *et al.* 2020). These models can then be extended further and used to predict the likelihood of selection (Boyce *et al.* 2016, Muff *et al.* 2019) and create habitat suitability maps (Johnson *et al.* 2004, DeCesare *et al.* 2012, Morris *et al.* 2016, Holbrook *et al.* 2017). Thus, RSFs are valuable tools for describing, visualizing, and predicting important habitat for focal species, but also predicting the likelihood of selection (Avgar *et al.* 2017, Muff *et al.* 2019) at the population or individual level (Forester *et al.* 2009, Thurfjell *et al.* 2014).

As with other habitat modelling approaches, RSFs are subject to limitations. When RSFs focus on populations, models provide insight into suitable habitat at the regional level; whereas, analyses that focus on the individual can detect variation in habitat selection at a finer

scale (i.e., within a home range) and highlight important habitats used by individuals (Forester *et al.* 2009). Either approach, however, results in spatially limited models that describe habitat selection within a defined availability domain (Johnson 1980, Boyce 2006, Muff *et al.* 2019), which limits the interpretation of the results (Johnson *et al.* 2004, DeCesare & Pletscher 2006, DeCesare *et al.* 2012). Unfortunately, there is a lack of consensus regarding the delineation of the availability domain (Avgar *et al.* 2016, Signer *et al.* 2019). Generally, an availability domain should be limited to the area that contains the daily activities of the individual or population across the focal season (e.g., population or individual breeding season home range; Meyer & Thuiller 2006) and can be defined using a high number of infrequent fixes over a long duration (Mitchell *et al.* 2019). This approach is widely applied, though its acceptance is questionable (Northrup *et al.* 2013) as defining availability in this way can also introduce more concerns as RSFs assume observations are independent (Hooten *et al.* 2016), which can be problematic when using high resolution location data (Forester *et al.* 2009).

RSFs allow researchers to investigate complex hypotheses surrounding both habitat selection and use, while predicting ecological patterns of selection across the landscape. Furthermore, RSFs provide insight into the effects of habitat change (e.g., industrial development) on individual and population behaviours, providing the necessary information to effectively target management objectives (Holbrook *et al.* 2017). However, RSFs require careful considerations of the spatial scale when used to inform species and habitat management (Holbrook *et al.* 2017) as the definition of availability can result in the misinterpretation or misapplication of predictions across spatial extents (Johnson *et al.* 2004, DeCesare & Pletscher 2006, DeCesare *et al.* 2012). Ultimately, RSFs are a descriptive tool for generating reasonable

hypotheses regarding potential habitat selection behaviours (Lele *et al.* 2013); and if they are applied and interpreted correctly, they serve as a valuable tool for predicting animal landscape relationships and highlighting important animal habitats.

1.3 Avian Ecology

1.3.1 Avian Habitat Selection

Avian taxa are highly volant and experience the landscape from a different perspective than terrestrial vertebrates; thus, the patterns and processes of avian habitat selection have long been an interest to ecologists (Kendeigh 1945, Hildén 1965, Block & Brennan 1993, Jones 2001). Early research explored community selection and species assemblages (Kendeigh 1945), describing the correlations observed between individuals and the characteristics of their immediate habitat (Hildén 1965, Cody 1981, Ricklefs 2000, Jones 2001). Conflicting explanations of species distribution among these habitats arose, attributing the patterns to competition, though habitat composition quickly became an important explanatory factor (Lack 1933, 1966) regarding distributions and habitat selection. The competing arguments and notions animal distribution were further clarified with the advanced theoretical modelling approaches (Fretwell & Lucas 1968) that ultimately guided habitat selection analyses (Nocera & Bett 2010). Concomitantly, the theoretical natural orders of selection (Johnson 1980) were proposed, and advancements in technology and modelling approaches set the foundation for which avian habitat selection research could progress and begin to investigate more detailed questions (Johnson & Grier 1988).

Researchers have commonly investigated avian habitat selection at fixed orders (Jones 2001, Beatty *et al.* 2014b) such as coarse order settling patterns (Johnson & Grier 1988,

Broughton *et al.* 2020, Singer *et al.* 2020), and finer habitat selection (Murkin *et al.* 1997, Clark & Shutler 1999, Lemelin *et al.* 2010, Dyson *et al.* 2019). This has generated a considerable understanding of how natural (Cody 1981, McCollin 1998, Broughton *et al.* 2020) and industrial (Hostetler 2001, Loss 2016, Injaian *et al.* 2018, Adams *et al.* 2019) landscape features influence avian habitat selection.

The hierarchical levels of selection (Johnson 1980, Meyer & Thuiller 2006) can be further decomposed into seasonal, or temporal scales (e.g., breeding, non-breeding) to further refine our understanding of the landscape factors that influence habitat selection in avian species across the annual cycle. Seasonal habitat selection represents the relationship between the individual and the surrounding habitat (Holbrook *et al.* 2017) at a given spatiotemporal scale, and provides insight into the landscape related factors that govern decisions (Prokopenko *et al.* 2017) and limit abundance and distribution. Ultimately, these findings elucidate the factors influencing individual and population level fitness (Block & Brennan 1993, Jones 2001, Kaminski & Elmberg 2014, Boyce *et al.* 2016). However, to fully comprehend the relationship between avian species and their habitat, and highlight the variables potentially influencing population dynamics, habitat selection must be considered across the hierarchical levels, relevant scales, and various qualities of habitat (Boyce 2006, DeCesare *et al.* 2012, Holopainen *et al.* 2015, Holbrook *et al.* 2017, 2019).

Migratory birds offer a unique opportunity to explore multi-level seasonal habitat selection (Kaminski & Elmberg 2014). In particular, ducks use various habitats throughout the annual cycle including stopover sites (Bengtsson *et al.* 2014, Beatty *et al.* 2017, O'Neal *et al.* 2018, Si *et al.* 2018), overwintering areas (Johnson *et al.* 1996, McDuie *et al.* 2019, Meattley *et al.*

2019, Palumbo *et al.* 2019) and breeding grounds (Yerkes 2000, Doherty *et al.* 2015, Kemink *et al.* 2020, Singer *et al.* 2020). Moreover, ducks are relatively abundant on the landscape, and indirectly provide a suite of ecosystem services for other niche-related taxa (Green & Elmberg 2014, Holopainen *et al.* 2015). Ducks may also be valuable indicators of ecosystem health and useful tools for measuring the effects of land use and climate change (Zhao *et al.* 2019).

We have a considerable understanding of habitat selection in ducks during the non-breeding season (Beatty *et al.* 2014b, Bengtsson *et al.* 2014, McDuie *et al.* 2019, Meatley *et al.* 2019, Palumbo *et al.* 2019), and during certain aspects of the breeding season including settling, nesting, and brood rearing at fixed orders and fine spatial scales (Yerkes 2000, Ludlow & Davis 2018, Roy 2018, Dyson *et al.* 2019, Kemink *et al.* 2019, Singer *et al.* 2020). However, we have comparatively less knowledge about coarse order breeding habitat selection, and we know almost nothing regarding the relationship between industrial development and breeding habitat selection. Exploring this relationship in ducks will generate a broader understanding of how ducks interact with their habitats, and reveal important behavioural responses of individuals and populations to changes in ecosystem structure during their most crucial life stage. Furthermore, habitat selection analyses can highlight key areas used during the breeding period, and reveal the change in importance at different spatial scales allowing for more targeted management objectives.

1.3.2 Incubation and Nest Attendance

Incubation is one of the most important aspects in avian reproduction (White & Kinney 1974, Afton & Paulus 1992). The behaviours exhibited by the attending parent(s) maintain optimal temperatures for embryonic development (Prince *et al.* 1969, Romanoff & Romanoff

1972, Webb 1987, Manlove & Hepp 2000, Hepp *et al.* 2005, Hepp & Kennamer 2012) resulting in faster development rates and healthier, more viable offspring all while reducing the risk of nest depredation (Afton & Paulus 1992, Hepp *et al.* 2006, Durant *et al.* 2013, Carter *et al.* 2014, Croston *et al.* 2020). However, maintaining optimal incubation temperature can be energetically costly for the attending parent (White & Kinney 1974, Tinbergen & Williams 2002, DuRant *et al.* 2013, Ringelman & Stupaczuk 2013, Croston *et al.* 2020), and since depredation is the primary cause of nest failure (Ricklefs 1969, Martin 1995, DeGregorio *et al.* 2016) there is increased risk for hen survival.

To maintain optimal incubation environments, various incubation behaviours have been adopted across avian taxa, each of which are characterized by unique nest attendance patterns. White & Kinney (1974) describes three methods of incubation supported by elementary survey data collected by Van Tyne and Berger (1959): the primary form of incubation in birds is biparental, or mutualistic in which both the male and female partners share the duty of incubation (54%); the secondary form is uniparental, which is often female only (25%), though certain species also exhibit male only (6%). The final form of incubation is considered intermediate, in which neither male, female, nor both are entirely committed to incubating (Van Tyne & Berger 1959, White & Kinney 1974). As with all categorization attempts of animal behaviour, there are also exceptions to incubation behaviour such as the incubator birds (family: *megapodiidae*) who rely on non-metabolic heat sources for incubation (Harris *et al.* 2014). Other unique cases include the Emperor Penguin (*Aptenodytes forsteri*) which the male relies entirely on lipid stores to incubate the egg propped up on the top of his feet, allowing him to remain nomadic for survival (White & Kinney 1974, Ancel *et al.* 2009); or the Asian

hornbills (family: *Bucerotidae*) where the female locks herself away in a tree cavity for the duration of the incubation period, receiving food provisions from her mate (Santhoshkumar & Balasubramanian 2010, Chadre *et al.* 2011, Kozłowski *et al.* 2015).

Disregarding the unique incubation behaviours, one of the most demanding incubation behaviours that emphasizes the stark trade-off between nest attendance, self-maintenance, and survival is uniparental incubation (Johnson *et al.* 1999, Cockburn 2006). Though there are exceptions (e.g., *Branta canadensis* mate guarding during incubation), most often the incubating parent receives minimal or no assistance from the partner in the form of shared incubation duties, food provisioning (Kozłowski *et al.* 2015), or predator vigilance while foraging (Fedy & Martin 2009). Thus, the attending parent must decide between the competing requirements of incubation, self-maintenance, and survival.

To further conceptualize uniparental care, we can consider the patterns of attentiveness on a spectrum that represents resource allocation. The ends of the spectrum signify the polar extremes of capital and income breeding strategies (Jönsson 1997). Capital breeders rely solely on endogenous stores, whereas income breeders rely almost entirely on compensatory forage to supplement nutritional requirements during incubation (Jönsson 1997, Langin *et al.* 2006, Houston *et al.* 2007, Stephens *et al.* 2009). The gradient of capital and income breeding strategies exhibited in avian species, coupled with intermittent foraging behaviour, results in highly variable incubation patterns (Skutch 1957, 1962, Afton 1980, Manlove & Hepp 2000). Understanding these patterns (i.e., attentive/inattentive periods) can provide valuable insight (Baldwin & Kendeigh 1927, Skutch 1957, 1962) into the intrinsic and extrinsic factors that influence incubation behaviour.

Ducks serve as an interesting topic for incubation analyses because they exhibit various incubation behaviours (e.g., biparental, uniparental, and parasitism; Afton & Paulus 1992) and breeding strategies (e.g., capital and income; Jönsson 1997, Hepp *et al.* 2006, Bentzen *et al.* 2010). Most commonly, we observe uniparental (female only) income breeding strategies that are characteristically similar across species in that nesting hens have inattentive periods where they leave the nest to replenish endogenous stores (Croston *et al.*, 2020). The result is distinct variations in incubation rhythms (Afton & Paulus 1992, Hepp *et al.* 2006) that represent the incubation behaviour of nesting ducks (Skutch 1957, 1962, Manlove & Hepp 2000).

Incubation behaviour in ducks has received considerable attention over the years (Skutch 1957, White & Kinney 1974, Afton & Paulus 1992, Deeming 2002) and generated a thorough understanding of the physiological demands (Korschgen 1977, Tinbergen & Williams 2002, DuRant *et al.* 2013) associated with avian incubation and embryonic development (Batt & Cornwell 1972, Caldwell & Cornwell 1976, Ringelman *et al.* 1982, Mallory & Weatherhead 1993, Hepp *et al.* 2006, Hepp & Kennamer 2012, Durant *et al.* 2013). In addition, nest attendance patterns of various duck species have been described (Ringelman *et al.* 1982, Mallory & Weatherhead 1993, Manlove & Hepp 2000) and used to quantify the extrinsic effects of weather (Afton 1980, Croston *et al.* 2020, Setash *et al.* 2020), food availability (Maccluskie & Sedinger 1999, Bentzen *et al.* 2010), habitat (Zicus 1995), and depredation on incubation behaviour in ducks (Ringelman & Stupaczuk 2013, Croston *et al.* 2018a). Nest attendance is vital for survival, reproduction, and recruitment. Therefore, understanding the patterns and behaviour of incubating ducks in response to environmental and habitat related variables plays an important role when untangling the drivers of population dynamics.

Research regarding the effects of industrial development on breeding ducks is emerging (Ludlow & Davis 2018, Roy 2018, Kemink *et al.* 2019, Dyson 2020, Skaggs *et al.* 2020), yet the relationships between industrial development and incubation behaviour have yet to be explored. Industrial features such as roads have shown to positively influence nest and brood success (Roy 2018, Dyson 2020, Skaggs *et al.* 2020), but their influence on incubation behaviour is unknown. In addition, evidence suggests that duck predators (Dyson *et al.* 2020) are more likely to use (Dyson 2020) and benefit from (DeMars & Boutin 2017, Dickie *et al.* 2017, Finnegan *et al.* 2018, Muhly *et al.* 2019, Mumma *et al.* 2019) industrially disturbed areas. Nesting ducks often avoid predators and defend their nest by flushing from the nest (Forbes *et al.* 1994, Guinness *et al.* 2001, Dassow *et al.* 2012). Increased predatory activity may result in greater avoidance, prolonging the duration of incubation and increasing the overall susceptibility to predators. Thus, it is important to understand how industrial development might affect ducks during such a vital stage, as industrial development may indirectly impact individual fitness and population dynamics.

1.4 Study System

1.4.1 Canada's Western Boreal Forest

The western boreal forest is an iconic region that is characterized by a myriad of aquatic and terrestrial habitats (Environment Canada 2013, Prairie Habitat Joint Venture 2014). Large scale natural disturbance such as wildfires and insect outbreaks (Schmiegelow & Mönkkönen 2002, Carlson *et al.* 2015, Thom & Seidl 2016) have continuously altered the boreal region, generating a heterogenous landscape composed of various successional habitats. The habitats affected by these natural disturbances include expanses of mixed-wood, deciduous dominated

upland forests that consist of Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*Populus balsamifera*) and White Spruce (*Picea glauca*). Lowland habitats are characterized by conifer dominated forests, consisting primarily of Black Spruce (*Picea mariana*). Scattered amongst these terrestrial ecosystems are various aquatic communities including large lakes, peatlands (e.g., bog and fen), and mineral wetlands (e.g., marsh, swamp) that provide a suite of biotic services and influence forest structure (Foote & Krogman 2006).

The unique collection of terrestrial and aquatic ecosystems supports a diversity of wildlife. Migratory waterbirds, including ducks, breed and raise offspring throughout the spring and summer months in the abundant wetlands (Foote & Krogman 2006, Prairie Habitat Joint Venture 2014). While the many lakes serve as resting habitat during duck fall and spring migrations. The forests and early successional grasslands also provide migratory song birds with habitats of comparable purpose and equal importance during the breeding and non-breeding seasons (Environment Canada 2013). Additionally, certain areas of the boreal forest also supports wintering caribou (*Rangifer tarandus*) and a variety of threatened or endangered species including Whooping Cranes (*Grus americana*), Trumpeter Swans (*Olor buccinator*), and Wood Bison (*Bison bison var athabascae*; Foote & Krogman 2006).

In addition to wildlife, the western boreal forest also supports a diversity of natural resources including oil and gas, and forestry. In recent years, however, the demand for these plentiful natural resources has increased considerably. Within the last decade, timber harvest was expected to account for approximately 6 million hectares in the boreal regions; while oil and gas exploration and infrastructure had already comprised approximately 46 million hectares, and was expected to increase (Wells 2011). This has resulted in extensive development and

fragmentation of boreal habitats (Schmiegelow & Mönkkönen 2002, Fahrig 2003, Hebblewhite 2017, Fisher & Burton 2018), increasing the concern for wildlife populations (Wells 2011).

The associated pressures from active development and infrastructure on bordering habitats impedes ecosystem function (Fahrig 2003, Fahrig & Rytwinski 2009, Polfus *et al.* 2011, Roy 2018) and alters the dynamics (McLoughlin *et al.* 2005, DeMars & Boutin 2017, Hebblewhite 2017, Finnegan *et al.* 2018) at varying spatial scales (Drapeau *et al.* 2000, Faleiro *et al.* 2013, Beatty *et al.* 2014b, Holopainen *et al.* 2015). For example, linear features (e.g., roads, seismic lines, pipelines) are narrow cutlines that result in limited habitat loss, but create extensive edge habitats in forested landscapes (Rich *et al.* 1999, Degregorio *et al.* 2014, Mumma *et al.* 2019, Dickie *et al.* 2020) and account for a considerable amount of industrial development in the western boreal forest. These features occur at high densities on the landscape, and therefore have the potential to influence wildlife populations at both coarse and fine spatial scales. Whereas, block features (e.g., well pads, pump stations) are relatively less abundant on the landscape. At coarse spatial scales, block features are abundant and their cumulative industrial footprint is large; though, at fine spatial scales, they can be less abundant, given their size and distribution.

1.4.2 Western Boreal Forest Ducks

In addition to forestry and energy development, Canada's western boreal forest plays an integral role in migratory waterbird annual cycles (Environment Canada 2013, Prairie Habitat Joint Venture 2014, Pavón-Jordán *et al.* 2017). The heterogenous aquatic communities in the western boreal forest (Foote & Krogman 2006) are regarded as the second most important

breeding area for North American duck populations (Slattery *et al.* 2011), second only to the prairie pothole region, supporting 12-15 million breeding pairs annually (Slattery *et al.* 2011). Unfortunately, some of these species are showing signs of decline due to unknown mechanism (Ducks Unlimited Canada 2014, Singer *et al.* 2020). This is concerning because we have not yet isolated the cause(s) of decline; and the western boreal forest is expected to become increasingly important to breeding ducks as prairie breeding areas continue to dry up due to land conversion for agricultural purposes and changes in annual climate regimes (Johnson *et al.* 2010, Holopainen *et al.* 2015).

Industrial development is predicted to continue to increase (Loss 2016), and many studies have investigated wildlife-development interactions in the boreal (DeMars & Boutin 2017, Dickie *et al.* 2017, Hebblewhite 2017). However, we are only beginning to understand this relationship in boreal ducks (Dyson 2020) and we know very little about how they respond to industrial development (Slattery *et al.* 2011, Burton *et al.* 2014, Singer *et al.* 2020). The lack of knowledge regarding the relationship between industrial development ducks breeding in the boreal reveals a critical gap in the concepts of duck ecology. Furthermore, this presents a unique opportunity to make a substantial contribution to waterfowl ecology and our overall understandings of the function of boreal forest ecosystems.

1.5 Objectives

The overall objective of this thesis is to improve our understanding of boreal waterfowl ecology by quantifying the effects of land cover and land use on habitat selection and incubation behaviours of ducks breeding in the western boreal forest. The research presented in this thesis aims to answer the following questions:

- I. What habitats are breeding female Mallards using in the boreal forest during the breeding season?
- II. How do land cover and land use influence breeding season home range establishment in boreal breeding female Mallards?
- III. How do land cover and land use influence breeding season habitat selection in boreal breeding female Mallards?
- IV. How does boreal breeding female Mallard habitat selection change across the second and third orders of selection?
- V. What are the incubation behaviour (e.g., recess frequency, recess duration, incubation constancy) metrics of boreal nesting ducks?
- VI. Do land cover, land use, and weather effect incubation behaviour in boreal nesting ducks?

Chapter 1 introduced the theoretical underpinnings of avian habitat selection and incubation behaviour in a detailed review of the literature. Chapter 2 explores breeding season habitat selection of female Mallards breeding in the western boreal forest, and quantifies the effect of land cover and land use on second and third order habitat selection during the breeding period. Chapter 3 presents a new approach for identifying nest attendance patterns in ducks, then applies this method to describe incubation behaviours (i.e., recess frequency, duration, and incubation constancy) in four species of ground nesting boreal ducks; and quantify the effect of land cover, land use, and weather on incubation behaviour at the micro (i.e., nest site) and macro (i.e., home range) scale. Ultimately, this research addresses important questions in avian ecology concerning species responses to anthropogenic changes in ecosystem structure and

function using waterfowl as a model species. The data from this research can be used to make predictions about waterfowl population trajectories relative to landscape change, and to inform conservation policy. This research will also contribute new theoretical knowledge to boreal forest ecology and waterfowl ecology, while simultaneously assisting in the identification of the mechanisms driving demographic variation in the region.

Chapter 2: Multi-level Habitat Selection of Boreal Breeding Mallards

2.1 Overview

Canada's western boreal forest is vital breeding habitat for North American duck populations. Recently, this region has experienced considerable demand for its valuable natural resources (e.g., oil and gas, forestry) resulting in an increase in industrial development (e.g., infrastructure), which is predicted to continue. The potential impacts of industrial development on breeding ducks in the western boreal forest, however, remains largely unexplored. We used backpack harness GPS transmitters to document habitat selection in breeding female Mallards across a gradient of industrial development in the western boreal forest of Alberta, Canada. We modelled breeding home range (second order) selection and habitat selection within the home range (third order) using resource selection functions; and, spatially predicted our models across the landscape to highlight important breeding areas. Contrary to our predictions, breeding female Mallards did not avoid all industrial development at the second and third orders, and demonstrated selection for natural and industrial features during the breeding period. Females established home ranges with greater proportions of marsh, graminoid fen, and wells, and decreasing proportions of forest. Within their home range, females selected shrub swamps, graminoid fens, marsh, well pads, and borrow pits, and avoided open water, swamps, treed peatlands, forests, harvest areas, and industrials. Females also selected habitats close to pipelines and roads. We also observed an increased precision of our coefficient estimates from the second to third order, implying stronger selection behaviours at the third order. Overall, our habitat maps highlighted the importance of the western boreal forest for breeding ducks. Additionally, our results suggested that the magnitude and direction of

breeding season habitat selection in female Mallards varies depending on the scale and landscape features; but, current levels of industrial development within our study area still allowed for the establishment of breeding home ranges. Our research emphasized the importance of understanding habitat selection across all relevant scales and levels; and, contributes to the increasing body of work surrounding the boreal ecology by improving our understanding of ducks in Canada's western boreal forest.

2.2 Introduction

Habitat selection is a fundamental aspect of species ecology (Kendeigh 1945, Fretwell & Lucas 1968, Cody 1981, Block & Brennan 1993) that represents the connection between the individual and their surroundings (Holbrook *et al.* 2017) and influences individual fitness and population performance (Jones 2001, Kaminski & Elmberg 2014, Doherty *et al.* 2015, Matthiopoulos *et al.* 2015, Boyce *et al.* 2016). In animals, habitat selection is a hierarchal process whereby individuals coarsely select habitat within their geographic distribution (first order), then becoming increasingly more refined in subsequent home range selection within their distribution (second order), habitat patch selection within their home range (third order), and resource selection within those patches (fourth order; Johnson 1980). It is important to consider habitat selection across these hierarchies (Boyce 2006, DeCesare *et al.* 2012, McGarigal *et al.* 2016, Holbrook *et al.* 2017, 2019) to better understand species ecology and guide management efforts. Our ability to quantify this relationship with empirical data has drastically improved over the last decade. The concomitant advancements of tracking technologies (Kesler *et al.* 2014, Kirol *et al.* 2020) and modelling techniques allow researchers to collect, process, and fit models to mass amounts of location data (Lele *et al.* 2013, Signer *et*

al. 2019, Joo *et al.* 2020). Resource selection functions (RSFs) are a popular and robust method for investigating the relationships between individuals and their surroundings (Boyce *et al.* 2002, Avgar *et al.* 2017, Holbrook *et al.* 2017, Muff *et al.* 2019) that can provide insight into the effect of resources on species distribution at the individual and population level (Block & Brennan 1993, Jones 2001, Forester *et al.* 2009, Kaminski & Elmberg 2014, Boyce *et al.* 2016).

Migratory birds, such as ducks, are ideal for investigating multi-level habitat selection because of their temporally distinct habitat requirements that drive the hierarchical selection of habitats at the various stages of the annual cycle (Kaminski & Elmberg 2014). Habitat selection occurs annually during the non-breeding (Bengtsson *et al.* 2014, Beatty *et al.* 2017, Meattley *et al.* 2019, Palumbo *et al.* 2019), and breeding periods (Johnson & Grier 1988, Yerkes 2000, Doherty *et al.* 2015, Kemink *et al.* 2020, Singer *et al.* 2020). The breeding period represents a temporal scale and a critical stage in the annual cycle of ducks when habitat structure and composition can influence reproduction and survival of nests, broods, and adults (Simpson *et al.* 2007, Boyer *et al.* 2018, Roy 2018, Dyson 2020, Skaggs *et al.* 2020). A majority of the breeding habitat selection research is in prairie (Gloutney & Clark 1997, Murkin *et al.* 1997, Clark & Shutler 1999, Yerkes 2000, Ludlow & Davis 2018) and arctic regions (Robertson 1995, Pratte *et al.* 2016, Gerall 2019, Lamb *et al.* 2020) and focuses on third and fourth order selection at specific phases of the breeding period (e.g., nest and brood sites). Thus, we have a limited understanding of coarse order breeding habitat selection in ducks (Johnson & Grier 1988, Krapu *et al.* 1997), and we have considerably less knowledge regarding breeding habitat selection in boreal ducks (Holopainen *et al.* 2015, Dyson 2020, Singer *et al.* 2020).

The relationship between industrial development (e.g., oil and gas) and duck ecology is a nascent area of research. Energy demand and industrial development are expected to continue to increase (Jones *et al.* 2015, Loss 2016). In addition, ducks are of significant cultural and economic value (Green & Elmberg 2014), and therefore, a priority of conservation and international management strategies (Doherty *et al.* 2015, NAWMP 2018). Recent studies have investigated the effects of industrial development on nest site selection, survival, and brood abundance (Ludlow & Davis 2018, Roy 2018, Kemink *et al.* 2019, Dyson 2020, Skaggs *et al.* 2020). Collectively, current research suggests that nesting ducks of some species are resilient to industrial development. However, this is only a glimpse of the breeding period. Thus, we require a more holistic understanding of how industrial development affects breeding habitat selection across the stages of the breeding period. For example, if breeding female ducks avoid industrial development (e.g., pipelines) during settling or territory establishment (Singer *et al.* 2020), we might fail to detect these behaviours in fine scale habitat or nest site selection analyses. Therefore, investigating how ducks select breeding habitat across hierarchical levels in the boreal will fill an important knowledge gap, and identify vital breeding areas that guide management efforts.

The western boreal forest is the second most important breeding area for North American duck populations (Slattery *et al.* 2011, Singer *et al.* 2020), though our understanding of breeding habitat is limited, and breeding habitat selection in boreal breeding ducks remains largely unexplored. Additionally, the boreal has experienced considerable amounts of industrial development (Schmiegelow & Mönkkönen 2002, Fahrig 2003, Slattery *et al.* 2011, Fisher & Burton 2018) in recent years that has drastically altered landscape structure (Wells

2011) and ecosystem dynamics (McLoughlin *et al.* 2005, DeMars & Boutin 2017, Hebblewhite 2017, Finnegan *et al.* 2018, Muhly *et al.* 2019). Therefore, we quantified habitat selection of breeding female Mallards using GPS transmitters in the western boreal forest of Alberta, Canada. Our first objective was to describe the habitats used by boreal Mallards during the breeding season. Our next objective was to quantify habitat selection at the second and third orders selection (Johnson 1980) using RSFs, to investigate how land cover (i.e., natural habitat) and land use (i.e., industrial development) influenced breeding habitat selection female Mallards. Our final objective was to develop spatially predictive maps of habitat selection to aid in the spatial prioritization of breeding habitats for ducks in the western boreal forest.

2.3 Methods

2.3.1 Study Area

Our study was located within the western boreal forest region (Prairie Habitat Joint Venture 2014) of Alberta, Canada within ~ 100 km radius of Utikuma Lake (Figure 2.1). This landscape is a mosaic of terrestrial and aquatic habitats composed of upland mixed-wood deciduous forests consisting of Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*Populus balsamifera*) and Jack Pine (*Pinus banksiana*), with Black Spruce (*Picea mariana*) dominated lowland habitats. Scattered amongst the terrestrial ecosystems are various aquatic communities including peatlands (e.g., bog and fen) and mineral wetlands (e.g., open water, marsh, swamp). Both terrestrial and aquatic communities have been regularly influenced by large scale natural disturbance such as wildfire and insect outbreaks (Schmiegelow & Mönkkönen 2002, Carlson *et al.* 2015, Thom & Seidl 2016). Within the last three decades, the western boreal has also experienced increased amounts of industrial development as a result of the demand for natural

resources including oil and gas, and forestry (Schmiegelow & Mönkkönen 2002, Foote & Krogman 2006, Slattery *et al.* 2011, Wells 2011, Pasher *et al.* 2013). Therefore, we categorized our landscape based on cumulative land use intensity (e.g., high, medium, low) and disturbance types (e.g., developed, harvested, burned), generating nine landscape strata, which we used to guide the distribution of our trapping efforts across our study area in an effort to mark birds across the range of landscape categories.

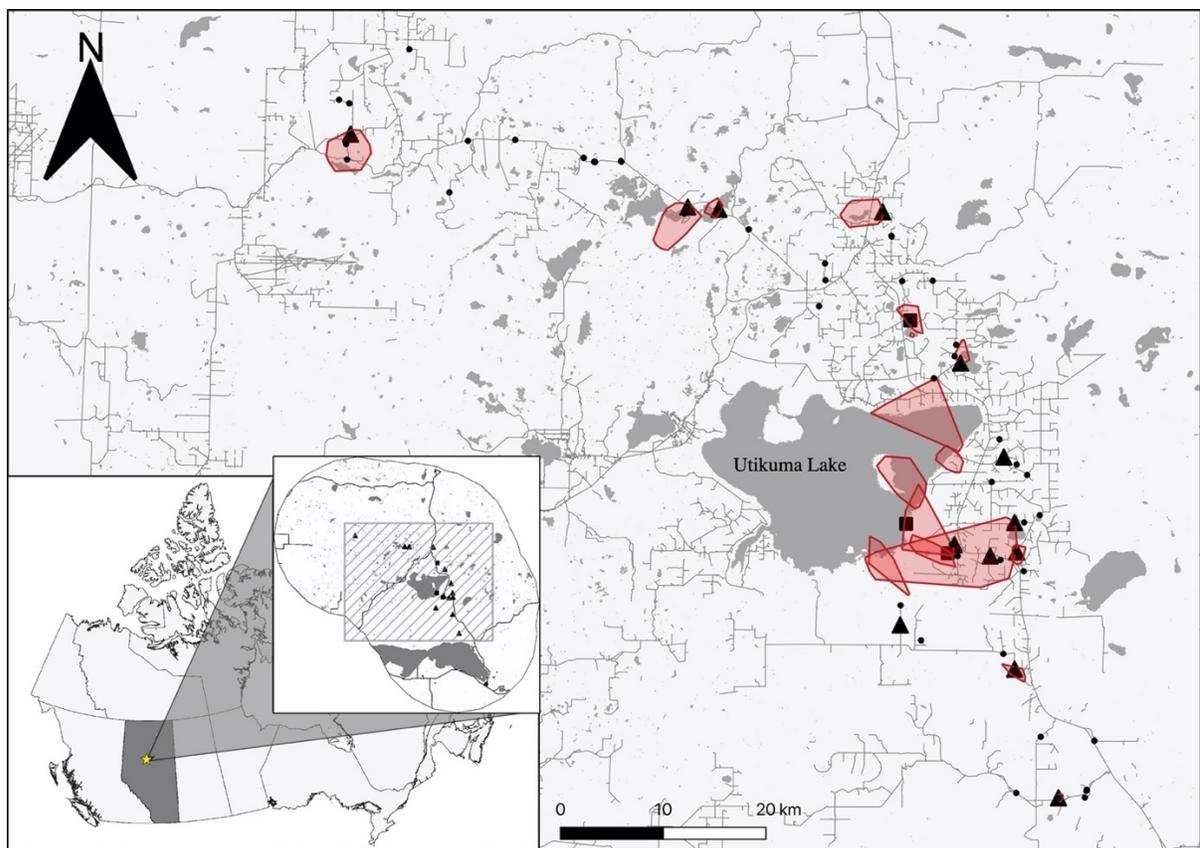


Figure 2.1 – General map of study area in the Slave Lake region of Alberta, Canada. Points represent all trap locations in 2019 (●), including capture sites of transmitter marked females using decoy traps (▲) and the airboat (■). The red outlined shaded areas represent individual home range boundaries for marked ducks used in the habitat selection analysis. The inlay indicates the location of the study area (hashed box) relative to the study extent within the province of Alberta and Canada.

2.3.2 Field Methods

2.3.2.1 Capture

We employed a combination of active and passive techniques to capture ducks in the spring (12 April – 26 May 2019) including decoy traps (Sharp & Lokemoen 1987, Kaminski *et al.* 2013, Brasher *et al.* 2014) and spotlighting from an airboat prior to nest initiation (Cummings & Hewitt 1964, Drewien *et al.* 1967, Buchanan *et al.* 2015). Our decoy ducks were ‘wild strain’ female Mallards (approximately 3-4 generations removed; Juniata River Game Farm, Lewistown, PA, USA) and a domestic hybrid (Rouen x Call; Tanjo Farms, Millbank, ON, Canada). We operated up to 10 traps per night. Decoy ducks were in traps for at least 24h and no more than 72h, at which point we replaced individuals with a rested female. We also captured females during two nights of airboat banding at two locations within the study area. We focused our airboat capture efforts on Mallard hens accompanied by drakes and only tagged hens that were captured with a drake. The presumed pairs were released together after processing.

2.3.2.2 Transmitter Attachment

When we captured females that weighed >1000 g, we banded them using a standard USGS aluminum leg band. We attached solar powered GPS-GSM-UHF (CREX, Ecotone, Poland) transmitters ($n = 20$) with an additional side mounted VHF transmitter (ATS, Asanti, MN, USA), using a modified backpack harness (Dwyer 1972, Krementz *et al.* 2012, Palumbo *et al.* 2019) made of Teflon ribbon (4.76 mm; Bally Ribbon Mills, Bally, Pennsylvania, USA), and secured the units with copper crimps (ID 4mm, OD 5mm copper tubing). Our harnesses also included round elastic band inserts across the horizontal straps allowing the cross straps to

extend by approximately 2.54 cm to accommodate for post-breeding/pre-migration mass gain of the individual. Complete transmitters (including the Teflon harness, neoprene pad, elastic band, copper crimps, GPS unit, and VHF unit) weighed ~30 g (< 3% female ducks body weight). Transmitters were acquired through Vertebrate Systems, LLC, Missouri, USA. We took careful consideration when making the harnesses to reduce the influence on the hen, and followed similar procedures to recently published literature (Krementz *et al.* 2012, Beatty *et al.* 2014b, Kesler *et al.* 2014, Palumbo *et al.* 2019, Kirol *et al.* 2020). In addition, when we discovered female mortalities ($n = 2$) or harness failures ($n = 1$), we confirmed the units were in operating order, attached a new harness, and redeployed the transmitters.

2.3.2.3 Tracking

Transmitters recorded female locations using GPS on two separate duty cycles and transferred the data using two separate communication systems. The first cycle recorded a single GPS location every 12 hours that was sent remotely through the GSM cellular (3G) network. The second duty cycle recorded a single GPS location every hour that was stored on the transmitter and could be actively downloaded via Ultra High Frequency (UHF) communication with a handheld download device (i.e., base station). In addition, data on the second duty cycle were received remotely via a File Transfer Protocol (FTP) at irregular intervals related to cellular connectivity (i.e., received over the GSM cellular network intermittently). This was particularly useful for cases where we could not retrieve data in the field using the base station (i.e., UHF).

We relocated individuals on a 3-5-day rotation using a combination of data sent via the GSM network and previously known locations. We visited the last known location and then

actively isolated the individual's current location using VHF. However, due to poor cellular coverage within our study area, the GSM system was not always a reliable source for identifying the last known location. Therefore, the VHF system played an important role in overcoming this issue by also allowing us to actively relocate females and get in range to download the most recent data using the UHF base station, monitor activity, and identify potential nesting activity and nest locations.

2.3.3 Analysis

2.3.3.1 Data Processing

We reduced our final location data set to only include locations during the breeding season following a multi-step process. Since majority of our trapping efforts targeted breeding pairs during the spring on small waterbodies, we assumed that females had already established a territory and breeding home range upon capture. Therefore, we included all location data from the date of capture for each individual in our initial dataset. We began by removing individuals from the data due to transmitter failure ($n = 1$), mortality ($n = 2$), emigration ($n = 1$), harness failure ($n = 1$), and insufficient data ($n = 1$). Next, we only included locations that fell within the western boreal forest (Prairie Habitat Joint Venture 2014). We then estimated a breeding period cut-off date (September 13) by determining the latest estimated nest initiation date (June 15) using boreal Mallard nesting data from 2016 – 2018 (Dyson 2020). Our estimated cut-off was consistent with Raquel et al. (2016), who suggested ~95% of prairie nesting Mallards have initiated their nest by June 17. We then added 90 days to account for laying (10 days), incubating (30 days), and pre-fledging (50 days; Southwick 1953) to define the end of the breeding season, and removed all locations from our data set that occurred outside of this time

frame. This produced location data for each individual from the date of capture to September 13 that fell within western boreal forest.

We also took into consideration molt-migration movements. Prior to molt, waterfowl sometimes leave their breeding grounds and congregate at molting areas (Salomonsen 1968, Jehl Jr. 1990, Yarris & McLandress 1994, Tonra & Reudink 2018). Therefore, we removed distinct movements that resembled molt-migrations and any location data thereafter. To do this, we used a heads-up changepoint analysis to identify changes in variance of the individuals' ordinal day net-displacement (Beatty *et al.* 2014b, Palumbo *et al.* 2019) using the pruned exact linear time (PELT) algorithm (Killick *et al.* 2012) with a manual penalty of $2 \cdot \log(\text{number of locations})$ in the *changepoint* package (Killick & Eckley 2014) for R (R Core Team 2019). We visually inspected each plot (Figure 2.2A) to confirm changepoint assignment (Figure 2.2B) and removed subsequent location data following movements that were greater than 50 km (Figure 2.2C). Finally, remoteness of our study location occasionally resulted in poor communication with cellular networks, causing variability in data resolution across individuals. As a final step, to remove any duplicate locations recorded by duty cycle overlap at the 12-hour mark, we standardized sampling rates across individuals at one-hour intervals consistent with the median sampling rate between consecutive locations using the *amt* (Signer *et al.* 2019) package in R (R Core Team 2019).

We then quantified land cover and land use covariates (Table 2.1) within our study extent using QGIS (QGIS version 3.14.0 - Pi; QGIS Development Team, 2020). To measure land cover, we used Ducks Unlimited Canada's Enhanced Wetland Classification raster layer (30 m resolution; Ducks Unlimited Canada 2011). We grouped similar land cover covariates based

on common characteristics to reduce the number of variables that we considered. For example, we combined all treed mineral wetland types as swamp (Table 2.1), but excluded shrub swamp in the grouping because we expected it to be an important land cover type for ducks.

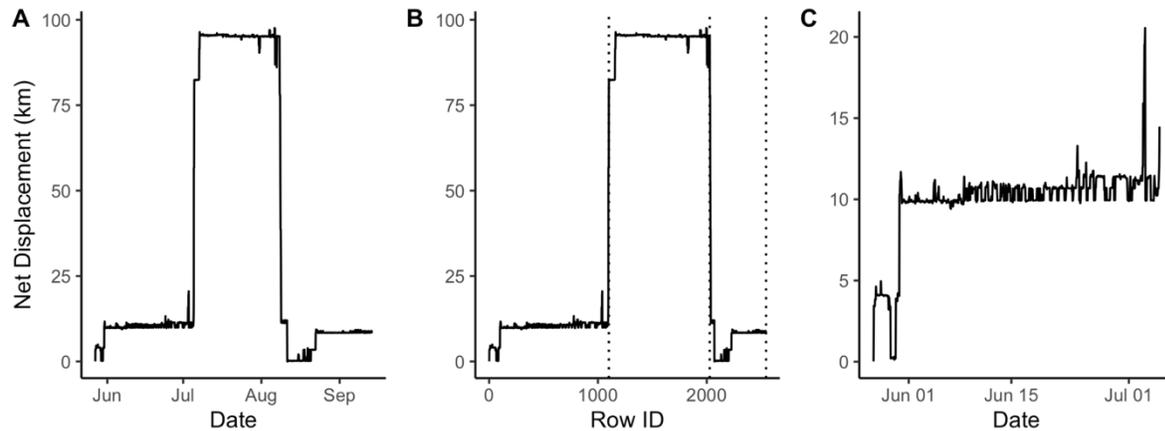


Figure 2.2 – Net displacement changepoint analysis for identifying and removing potential molt-migrations of female Mallards during the 2019 breeding season in the western boreal forest, Alberta, Canada. A) complete net displacement segment for a single female Mallard from date of transmitter deployment to September 13; B) complete net displacement segment for the same female Mallard with distinct changepoints (dotted line) identified. The first changepoint (~1000 Row ID) is characteristic of a presumed molt-migration movement and all data after this point are removed; C) clipped net displacement segment representing all locations prior to presumed molt-migration.

Table 2.1 –Descriptions and unstandardized range for grouped and individual fixed-effect predictors used in second and third order RSFs. Available values at the second and third order were summarized at the 1430 m and 45 m spatial scales, respectively. Second (2nd) order and third order (3rd) range represent the unstandardized range of land cover and land use covariates at their respective order. Predictors noted with (-) were not included in the model.

Covariate	Description	2 nd Order Range	3 rd Order Range
<i>*Land Cover</i>			
Marsh	Includes aquatic bed, mudflats, emergent, and meadow marsh. Transition zone between the open water and forests and/or graminoid fens. Saturated to permanently flooded hydrologic conditions, but often experiences periodic drawdowns and seasonal inundation. Measured as proportional area.	0 – 0.73	0 – 1
Swamp	Includes conifer swamp, tamarack swamp, mixedwood swamp, and hardwood swamp. Standing woody vegetation (> 10 m in height) with variable amounts of surface water. Transition between peatlands and forests. Measured as proportional area.	0 – 0.59	0 – 1
Shrub Swamp	Includes shrub swamp. >25% shrub coverage with large pools of water >2 m. Transition zone between marshes and forests. Measured as proportional area.	0 – 0.39	0 – 1
Open Water	Includes open water areas such as lakes, ponds, rivers, and other water bodies. Commonly associated with marsh, fen, and swamp. Measured as proportional area	0 – 1.0	0 – 1

Treed Peatland	Includes treed bog, shrubby bog, treed poor fen, treed rich fen, shrub poor fen, and shrub rich fen. All peatland types with trees >10m and shrubs, >20% <i>Sphagnum</i> spp cover, limited or no surficial hydrology, and varying nutrient availability. Measured as proportional area.	0 – 0.98	0 – 1
Graminoid Fen	Includes graminoid poor fen and graminoid rich fen. Shrubs < 2m in height and < 25% tree and shrub cover, > 20% <i>Sphagnum</i> spp cover, variable surface hydrology. Measured as proportional area.	0 – 0.41	0 – 1
Forests	Includes upland conifer, mixedwood, deciduous, and other forest/upland habitat types. Measured as proportional area	0 – 0.94	0 – 1
<i>Land Use</i>			
Distance to Roads	Average distance of individual location to roads (km)	-	0 – 5.21
Distance to Seismic Lines	Average distance of individual location to seismic lines (km)	-	0 – 5.28
Distance to Pipelines	Average distance of individual location to pipelines (km)	-	0 – 7.13
Roads	Maintained (e.g., paved and gravel roads) and unmaintained roads (e.g., winter roads and trails) measured as the average length (m) within a pixel, per home range.	0 – 3.94	-
Pipelines	Pipelines and transmission lines measured as the average length (m) within a pixel, per home range.	0 – 5.25	-

Seismic Lines	Seismic lines measured as the average length (m) within a pixel, per home range.	0 – 9.17	-
Industrials	Industrial block features (e.g., camps, facilities, oil and gas buildings, gas plants) measured as the average area (m ²) within a pixel, per home range.	0 – 115.94	0 – 900
Harvest Areas	Harvest areas measured as the average area (m ²) within a pixel, per home range.	0 – 680.51	0 – 900
Wells	Abandoned and active oil and gas well sites measured as the average area (m ²) within a pixel, per home range.	0 – 41.41	0 – 900
Borrow Pits	Borrow pits, sumps, dugouts, and lagoons measured as the average area (m ²) within a pixel, per home range.	0 – 51.67	0 – 900

*Descriptions derived from Smith *et al.* (2007)

We quantified land use layers using the Alberta Biodiversity Monitoring Institute's 2018 Human Features Inventory database vector layers (Alberta Biodiversity Monitoring Institute 2020) and also grouped similar land use covariates based on their characteristics (Table 2.1). For example, wells represent both active and inactive well sites, though we did not group them with other industrial features in order to isolate their potential effects on habitat selection. We summarized polygonal features to represent the area (m²) that is covered within a 30 m x 30 m pixel; and linear features to represent the sum of the length of each line feature within a pixel to be consistent with our land cover layers.

Linear features can influence multiple aspects of duck ecology during the breeding period (Roy 2018, Dyson 2020, Singer *et al.* 2020); thus, in addition to linear feature densities, we also generated distance raster layers to be consistent with our land cover layers (Table 2.1). Distance raster cells were assigned a value equal to the distance (km) from the edge of the cell to the nearest linear feature in question, and cells representing linear features were assigned a value of 0. We included distance rasters to account for the potential influence of linear features in the surrounding landscape at the finer spatial scale (third order), and capture the potential proximity related effects that may otherwise go undetected. Finally, we excluded land cover and land use features with minimal coverage across the study extent, and features that did not associate with any group criteria.

2.3.4 Habitat Selection

2.3.4.1 Second Order

At the second order, we constructed a habitat availability domain using all of the individuals in our sample (Meyer & Thuiller 2006) with the *amt* package in R (R Core Team 2019). We

fit a 100% minimum convex polygon (MCP) around all individual locations and buffered the MCP using a distance equal to the diameter of a circle equivalent in area to the maximum observed home range of a female Mallard from our sample (Holbrook *et al.* 2017). This buffered MCP contained every individuals' home range. Observed home ranges ($n = 17$) were our used locations. To sample potential available home ranges ($n = 1,700$), we randomly generated 1,700 (1:100, used to available; Northrup *et al.* 2013) points within the 100% MCP and buffered them by the diameter of a circle equivalent in area to the median (6.42 km²) Mallard home range from our sample (Holbrook *et al.* 2017). We used the median home range because our observed home range sizes were overdispersed. We determined whether home range size increased linearly with the location sample size (Powell 2000, Börger *et al.* 2006) by plotting the number of sampled locations against home range area and did not observe a significant correlation ($F_{1, 15} = 0.06$, $P = 0.80$, $r^2 = -0.06$). We extracted land cover covariates representing proportional estimates of land cover (0-1). To account for variation in home range size, we extracted individual areal land use features (e.g., well pads) as the average area (m²) of anthropogenic disturbance within a pixel, and linear land use features (e.g., pipelines) as the average length (km) of line feature within a pixel, and consider this an index of anthropogenic disturbance density.

Table 2.2 –Home range size and location data for female Mallard breeding in the western boreal forest of Alberta, Canada during the 2019 breeding season. Data are arranged by home range size in descending order. Total Locations indicates the number of locations following the standardization of sampling rates across individuals at one-hour intervals consistent with the median sampling rate between consecutive locations. Location days represents the number of days for which we have ≥ 1 location per individual. Duration is the time period between our first and last location for each individual female Mallard between April 13 and September 13, 2019.

Female ID	Home Range Area (km ²)	Home Range Weights	Total Locations	Location Days	Duration (Days)	Daily locations ($\bar{x} \pm SD$)
DEL_24	0.12	0.25	459	23	23	19.96 ± 5.27
DEL_19	0.32	0.5	2030	92	92	22.07 ± 3.44
DEL_15	1.71	0.75	232	16	72	14.50 ± 7.57
DEL_14	1.88	0.75	1601	137	137	11.69 ± 9.65
DEL_28	1.96	0.75	1204	53	53	22.72 ± 3.02
DEL_18	2.08	0.75	2363	114	114	20.73 ± 5.03
DEL_22	3.81	1	763	35	93	21.80 ± 4.93
DEL_11	4.35	1	2254	104	104	21.67 ± 3.73
DEL_25	6.43	1	2839	127	127	22.35 ± 2.77
DEL_16	8.56	1	451	24	24	18.79 ± 8.00
DEL_09	8.8	1	2673	128	128	20.88 ± 5.36
DEL_29	12.46	0.75	1709	76	76	22.49 ± 3.63
DEL_30	13.4	0.75	1256	65	65	19.32 ± 6.74
DEL_27	14.52	0.75	1233	56	56	22.02 ± 2.88
DEL_12	19.7	0.5	553	29	81	19.07 ± 7.99
DEL_23	29.36	0.25	862	40	40	21.55 ± 4.85
DEL_01	66.64	0.125	1517	70	70	21.67 ± 4.79

2.3.4.2 Third Order

We constructed individual home ranges for third order selection using 95% MCPs that represented the individuals' availability domain (Johnson 1980, Jones 2001). We investigated habitat selection at the third order using our individual home ranges where locations within the

home range (95% MCP) represented habitat use. Matching the available location sample size with the respective hierarchical level (e.g., third order selection) and scale of inference is important (Beyer *et al.* 2010, Northrup *et al.* 2013). Since the availability domain at the third order was more constrained than the second order, we generated randomly distributed available locations at a 1:2 used to available ratio within each individual home range. This allowed us to obtain an adequate sample of availability for each individual (Hebblewhite & Merrill 2008, Holbrook *et al.* 2017). We then buffered our used and available locations using a 45 m radial buffer to capture the location and the immediate surrounding landscape. We accounted for linear features using the distance rasters. We sampled habitat selection at used ($n = 23,999$) and available ($n = 47,998$) locations by extracting land cover and land use covariates representing proportional estimates of land cover (0-1), the average distance to linear features (m), and the average area for block features (m²). We extracted all land use and land cover covariates using the *raster* package (Hijmans *et al.* 2020) in R (R Core Team 2019).

2.3.5 Model Construction

We quantified the influence of land cover and land use covariates on second and third order habitat selection using fixed and mixed effects logistic regression based RSFs, respectively. We standardized covariates by subtracting the mean and dividing by the standard deviation, and did not allow highly correlated variables, Pearson's $r > |0.65|$, in the same model. Our global model included seven land cover and seven land use covariates (Table 2.1). At the second order, we used a weighted binomial logistic regression and weighted all home ranges to reduce the influence of observed home range sizes at the extreme ends of the distribution. We calculated the deviance from the median for every home range and assigned decreasing

weights to home ranges as they deviated from the median home range size which was used to estimate coverage in our available sites (Table 2.2). At the third order, we fit a mixed effects logistic regression with individual identification as a random intercept. We evaluated all potential model combinations of our global model using AICc, and removed nested subsets of the top model that contained uninformative parameters from our model sets, presenting all competing models within 1 Δ AICc at the second order, and 2 Δ AICc at the third order of the top model (Arnold 2010). We selected the top ranked model with the lowest Δ AICc for the generation of covariate effects plots (Burnham & Anderson 2004) and spatial predictions. We used the *lme4* (Bates *et al.* 2015) package in R (R Core Team 2019) to complete all modelling.

2.3.6 Habitat Mapping

We predicted our top ranked models across the landscape and generated maps that are reflective of the relative probability of selection of land cover and land use features at the second and third orders of selection (Johnson 1980, Meyer & Thuiller 2006). We produced equal-area quantile ranked selection probability maps at the second and third order. We standardized the landscapes using 1430 m radial moving window, consistent with the median home range size at the second order and a 45 m radial moving window at the third order. At the third order, we standardized the landscape using the sample mean and standard deviation from our third order sample data to align with our model. Furthermore, to avoid exceeding the limits of our predictive surface, we removed any landscape values that fell outside the range of our second and third order sample data and assigned NULL values to those pixels. We predicted the relative probability of selection across the second and third order landscapes

separately, and categorized selection probabilities using equal-area quantile ranking (Morris *et al.* 2016).

We used the model-predicted second and third order surfaces to generate two additional maps. We produced our scale-integrated map by multiplying our second and third order prediction probability surfaces together (DeCesare *et al.* 2012, Fedy *et al.* 2014, Holbrook *et al.* 2017), then categorized the integrated selection probability using equal-area quintile rankings (Morris *et al.* 2016). The scale-integrated maps are argued to be more representative of habitat selection than single-order maps characterize because they integrate selection probabilities from the second and third orders into a single map (DeCesare *et al.* 2012, Holbrook *et al.* 2017). Since there was not enough interpretable variation between equal-area quintile rankings 1, 2 and 3, we grouped quintiles into three bins (e.g., 1-3, 4, 5). We generated our change-in-rank map by subtracting the rank values from our third order equal-area quintile ranked map from the rank values of our second order equal-area quintile ranked map (Polfus *et al.* 2011). This map represents the importance of landscape relationships across hierarchical levels (i.e., second to third order habitat selection). All equal-area ranking and raster calculations were completed in ArcMap (Esri® ArcMap™ 10.7.1.11595, Redlands, CA, USA).

2.4 Results

We captured a total of 30 female Mallards between April 12 and May 26, 2019 using decoy traps ($n = 23$ hens) and an airboat ($n = 7$ hens). We outfitted 23 females with transmitters. We collected 52,568 GPS locations from 23 individuals during the breeding period (April 13 - September 13). Three of the 20 transmitters were redeployed including two from hens who

were depredated and one transmitter that was found in a small wetland, which we attributed to be a result of harness failure. We were unable to relocate one individual following release and attributed this loss to transmitter failure. Another female emigrated the study area shortly after capture, spending a portion of time in the prairies of southern Alberta, then travelling further south into Montana; and one individual had an insufficient number of locations ($n = 26$).

Following the removal of hens ($n = 6$) and data trimming, we had 23,999 GPS locations across 17 individuals (Table 2.2), with an average of $1,412 \pm 812$ observed locations per individual (range: 232 – 2,839 points). The median number of observed locations per day across individuals was 23 (IQR: 20 - 23) and the median home range size was 6.42 km^2 (IQR: $1.96 - 13.40 \text{ km}^2$).

2.4.1 Second Order Selection

Our top ranked model that best predicted second order selection included marsh, graminoid fen, forest, and wells (Figure 2.3). There were 3 competing models in our candidate set within 1 ΔAICc (Table 2.3). The remaining models were within 13 ΔAICc and included non-nested combinations of the top covariates. Our second order selection results produced considerable uncertainty in our estimates, but demonstrated that female Mallards established home ranges with greater proportions marsh ($\beta = 0.42$, 85% CI = 0.17 - 0.68), graminoid fen ($\beta = 0.22$, 85% CI = 0.02 – 0.39), and well pads ($\beta = 0.55$, 85% CI = 0.17 - 0.82), and avoided areas with greater proportions of forests ($\beta = -0.65$, 85% CI = -1.14 to -0.05; Figure 2.4).

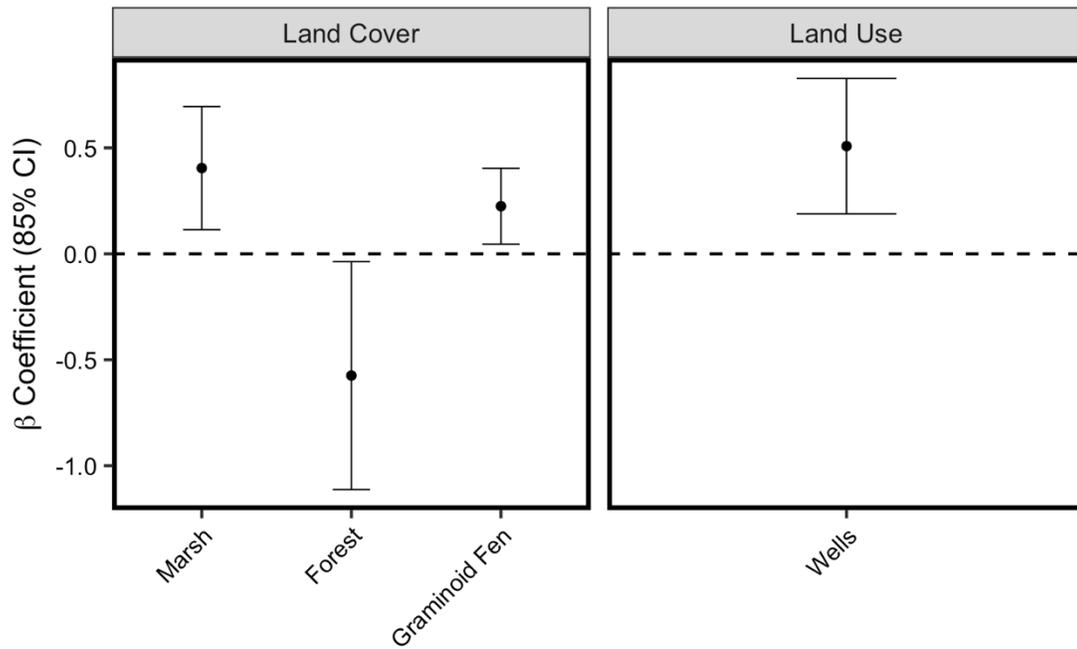


Figure 2.3 - Coefficient estimate plots for fixed effect covariates summarized at the 1430m spatial scale in the top ranked second order selection model for female Mallards breeding in the western boreal forest of Alberta, Canada during the 2019 breeding period. Error bars represent 85% confidence intervals.

Table 2.3 - Non-nested fixed and mixed effects resource selection functions, respectively, for second and third order for female Mallards breeding in the boreal forest of Alberta, Canada during the 2019 nesting season. Model sets represent non-nested competing models within 1 Δ AICc (second order) and 2 Δ AICc (third order) of the top ranked model.

Model	K	LL	Δ AICc ^a	w_i
<i>2nd Order</i>				
Graminoid Fen + Marsh + Forests + Wells	5	-61.22	0.00	0.18
Marsh + Forests + Pipelines	4	-62.28	0.11	0.17
Marsh + Forests + Wells	4	-62.47	0.50	0.14
Graminoid Fen + Marsh + Open Water + Treed Peatland + Wells	6	-60.70	0.96	0.11
<i>3rd Order</i>				
Swamp + Graminoid Fen + Marsh + Open Water + Shrub Swamp + Treed Peatland + Forests + Borrow Pits + Distance to Pipeline + Distance to Roads + Harvest Areas + Industrials + Wells	15	-37393.50	0.00	0.65
Swamp + Graminoid Fen + Marsh + Open Water + Shrub Swamp + Treed Peatland + Forests + Borrow Pits + Distance to Pipeline + Distance to Roads + Harvest Areas + Wells	14	-37395.14	1.28	0.35

^a Lowest AICc score for second = 133.57 and third = 74817.00 order resource selection functions

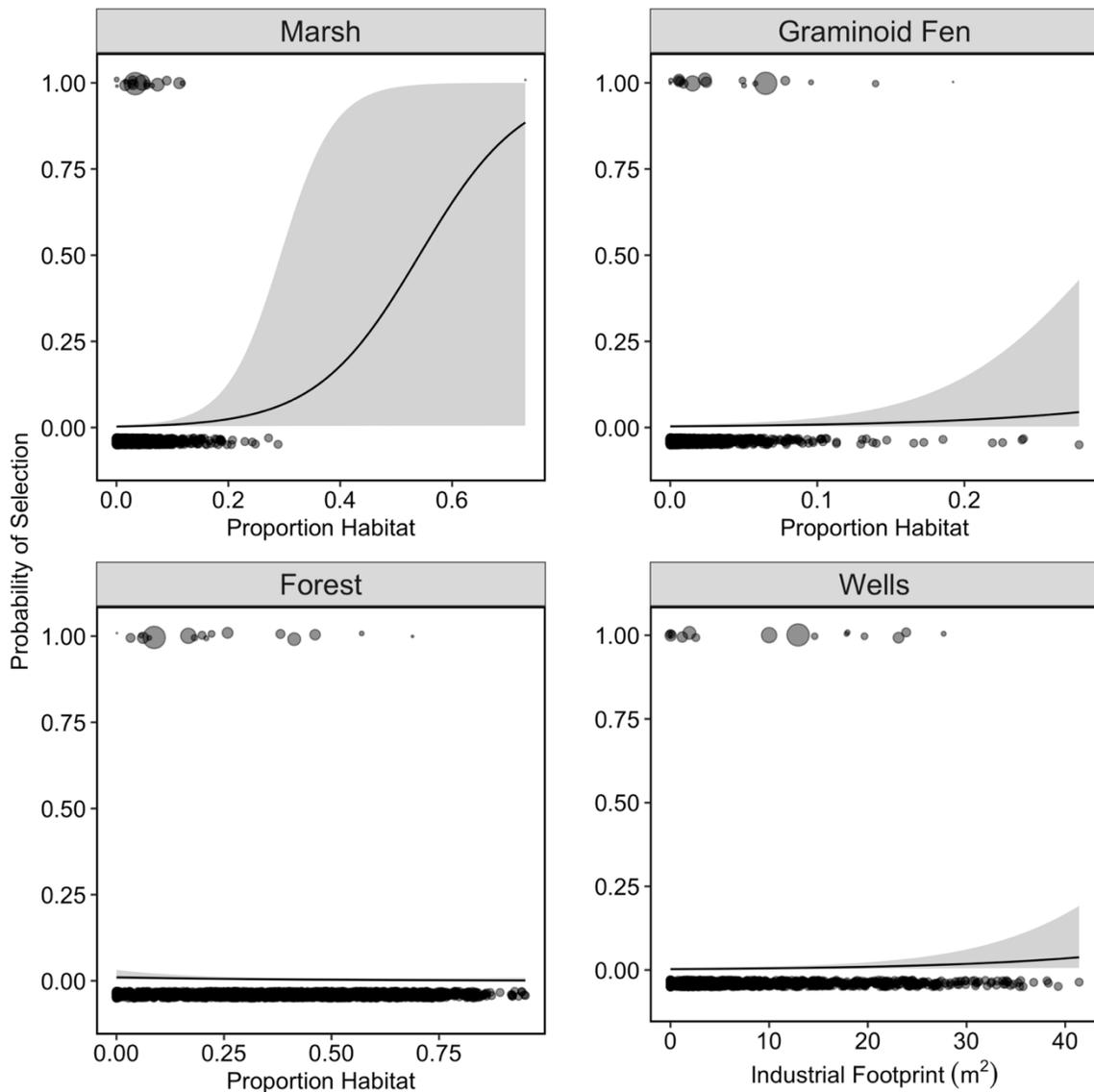


Figure 2.4 - Predicted effects of land use and land cover covariates on second order habitat selection for female Mallards breeding in the western boreal forest of Alberta, Canada during the 2019 nesting period. Plots represent the response from female Mallards to predictor variables. Shaded areas represent 85% confidence intervals. Circles across the top represent the distribution of used home ranges, and circles across the bottom represent the distribution of available home ranges. The size of each circle is representative of the relative home range size, and highlights the influence that home range size has on the predictor variables. Points have been jittered and made translucent for visualization purposes.

2.4.2 Third Order Selection

Our top ranked third order selection model included all land cover and land use covariates from our global model, except distance to seismic line (Figure 2.5). There was one competing model in our candidate set within 2 Δ AICc which excluded industrials and distance to seismic lines (-). The remaining models included non-nested combinations of the top covariates that were $> 14 \Delta$ AICc, and they were not considered. Breeding female Mallards selected habitats with greater proportions of shrub swamps ($\beta = 0.35$, 85% CI = 0.33 - 0.37), graminoid fens ($\beta = 0.30$, 85% CI = 0.28 - 0.315), and marshes ($\beta = 0.69$, 85% CI = 0.66 - 0.71); and avoided habitats with greater proportions of open water ($\beta = -0.49$, 85% CI = -0.52 to -0.46), swamp ($\beta = -0.20$, 85% CI = -0.22 to -0.18), treed peatland ($\beta = -0.31$, 85% CI = -0.34 to -0.28) and forest ($\beta = -0.13$, 85% CI = -0.16 to -0.10; Figure 2.6). Female Mallards also selected habitats with greater amounts of wells ($\beta = 0.16$, 85% CI = 0.15 - 0.17) and borrow pits ($\beta = 0.46$, 85% CI = 0.44 to 0.48), and avoided areas with greater amounts of harvest areas ($\beta = -0.10$, 85% CI = -0.11844760 - 0.083987587), industrials ($\beta = -0.018$, 85% CI = -0.034 to -0.0035), and increasing distance from roads ($\beta = -0.13$, 85% CI = -0.16 to -0.094) and pipelines ($\beta = -0.17$, 85% CI = -0.23 to -0.11; Figure 2.7).

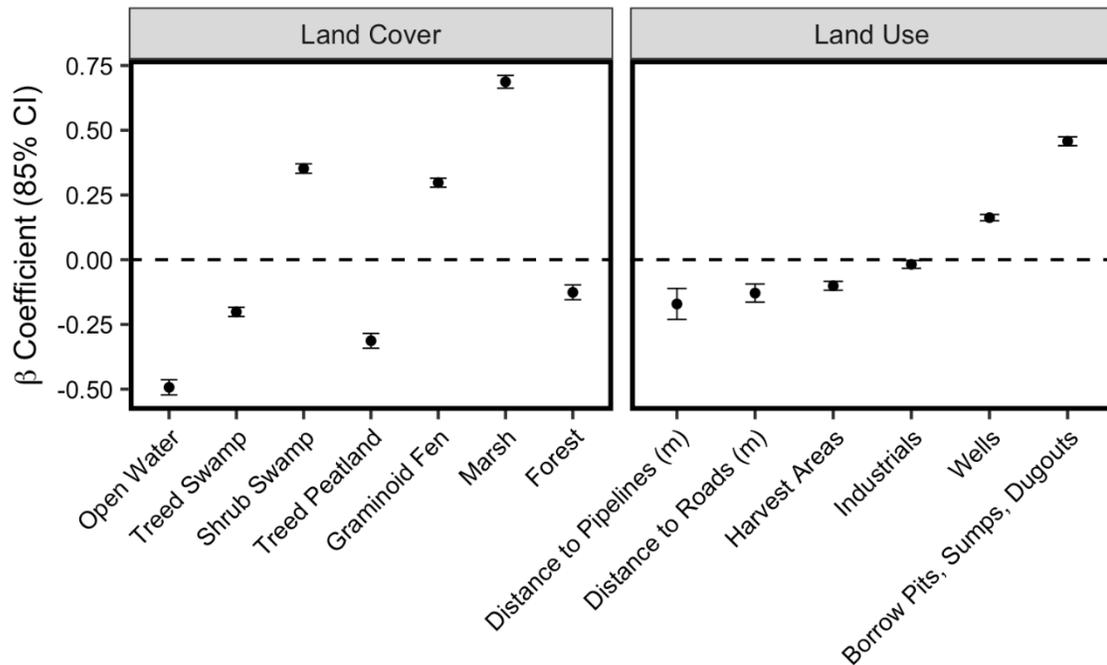


Figure 2.5 - Coefficient estimate plots for fixed effect covariates summarized at the 45m scale in the top ranked third order selection model for female Mallards breeding in the western boreal forest of Alberta, Canada during the 2019 nesting period. Error bars represent 85% confidence intervals. Variables were summarized using a 45 m buffer.

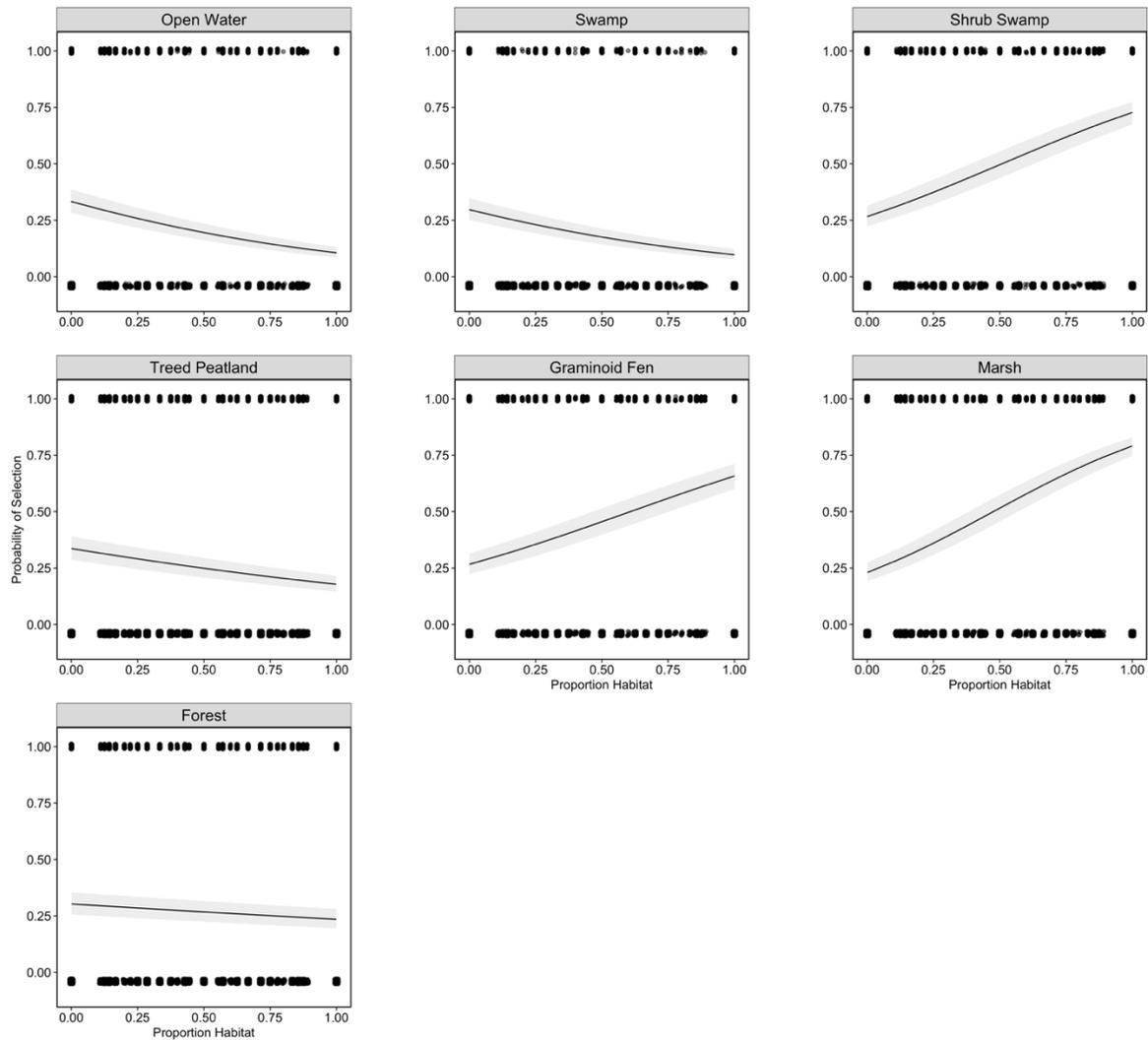


Figure 2.6 - Predicted effects of land cover covariates on third order habitat selection for female Mallards breeding in the western boreal forest of Alberta, Canada during the 2019 nesting period. Plots represent the response from female Mallards to land cover predictor variables. Shaded areas represent 85% confidence intervals. Circles across the top represent the distribution of used locations, and circles across the bottom represent the distribution of available locations. Points have been jittered for visualization

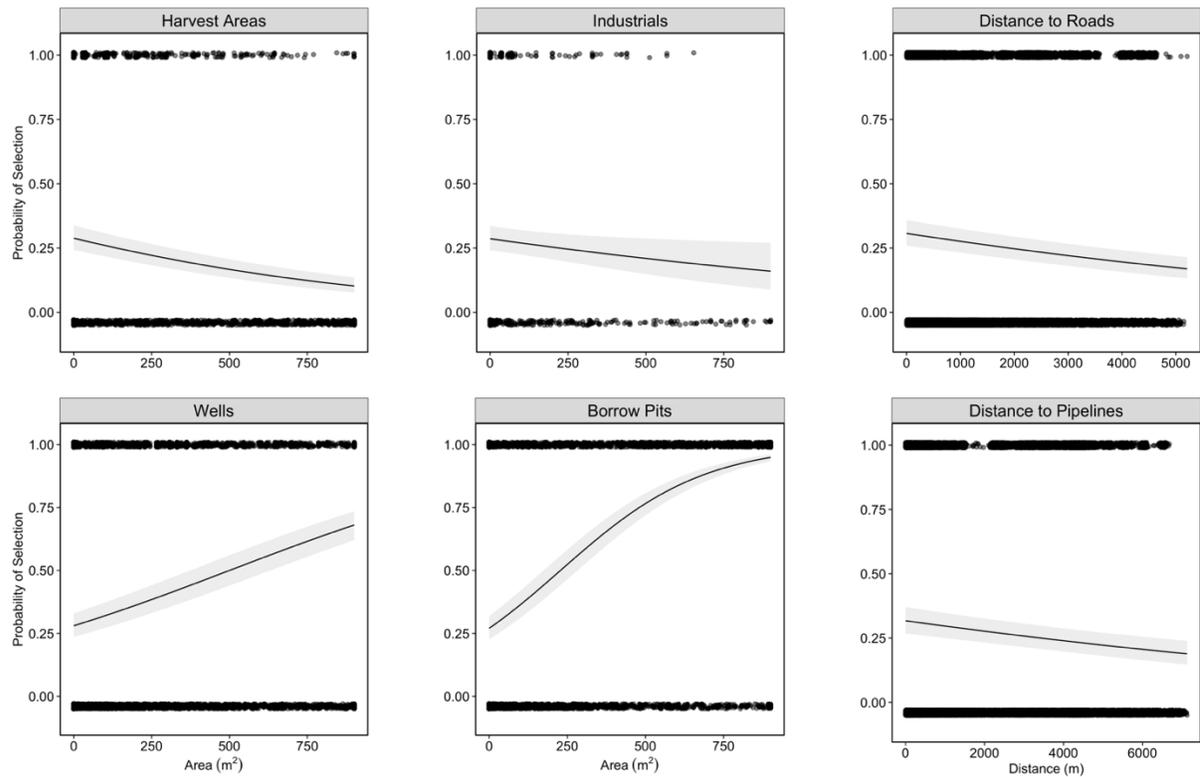


Figure 2.7 - Predicted effects of land use covariates on third order habitat selection for female Mallards breeding in the western boreal forest of Alberta, Canada during the 2019 nesting period. Plots represent the response from female Mallards to land use predictor variables. Shaded areas represent 85% confidence intervals. Circles across the top represent the distribution of used locations, and circles across the bottom represent the distribution of available locations. Points have been jittered for visualization purposes.

2.4.3 Habitat Mapping

Our fixed-level second (Figure 2.8A) and third order (Figure 2.8B) habitat maps displayed the spatially predicted relative probability of selection and avoidance at each individual hierarchical level. Our scale-integrated map (Figure 2.8C) represented the integrated relative probability of selection and avoidance. Finally, our change-in-rank map (Figure 2.8D) displayed the spatially predicted relative probability of selection and avoidance at the second, third, and both orders of selection.

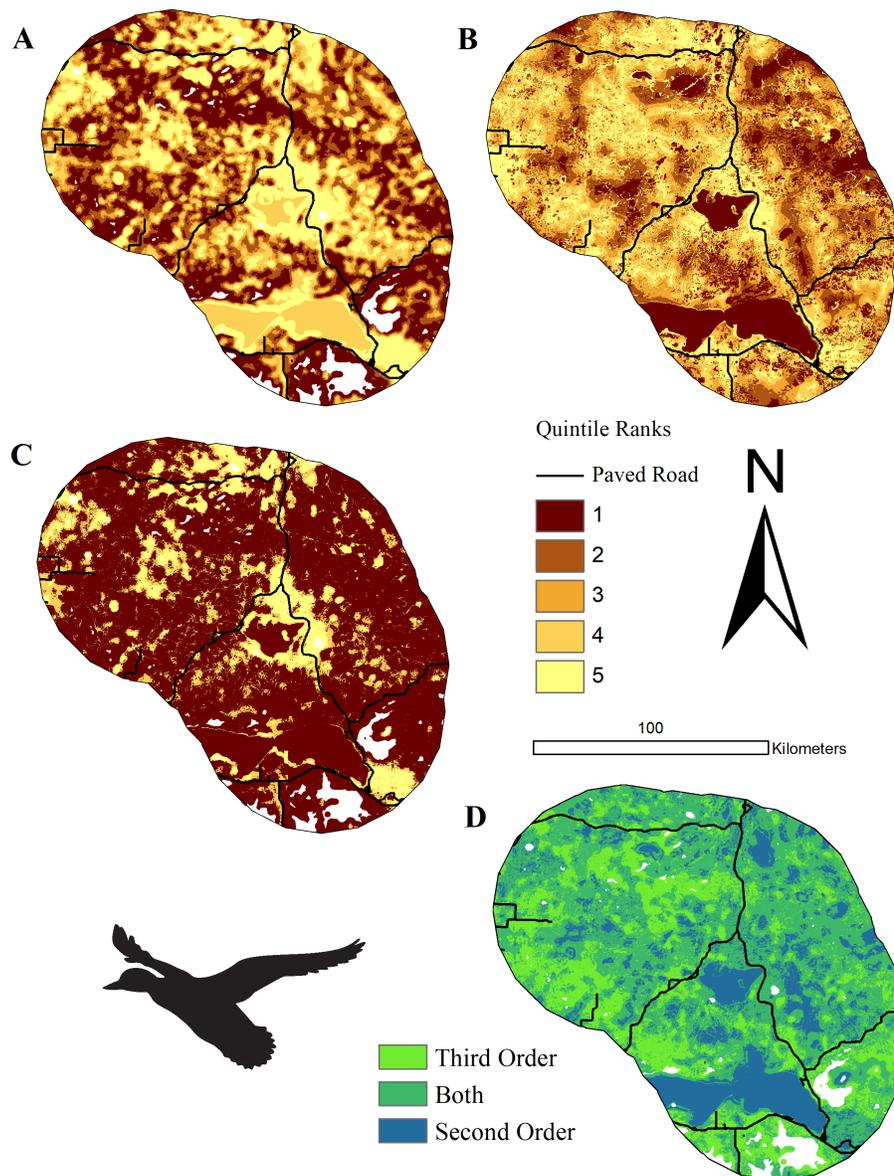


Figure 2.8 - Predicted probability of second (A) and third order (B) selection for female mallards during the breeding period in the western boreal forest of Alberta, Canada. These maps were generated using our top resource selection functions. We combined these maps to generate a scale-integrated prediction of habitat use by female Mallards (C) and a hierarchical ranked map of important habitats that are distinct or shared between second and third orders (D). For the quintile ranks, 1 indicates a low relative probability of selection and 5 indicates a high relative probability of selection.

2.5 Discussion

We quantified the effects of land cover and land use on the second and third orders of habitat selection (Johnson 1980, Meyer & Thuiller 2006) in boreal breeding female Mallards. In addition, we produced spatial predictions of important habitat for female Mallards during the breeding season at fixed spatial scales and across hierarchical levels. At the second order, breeding females demonstrated preference (Beyer *et al.* 2010) for marshes, graminoid fens, and well pads, and avoidance of forests. These covariates were included in our top model, though their effect was minimal given the uncertainty in coefficient estimates (Figure 2.3) and the large number of competing models within $2 \Delta AICc$. We observed the same effects of these variables and others at the third order. Breeding females selected shrub swamps, marsh, graminoid fens, wells, and borrow pits that were close to roads and pipelines; but avoided forests, treed peatlands, open water, swamps, harvest areas, and industrials (Figure 2.6, Figure 2.7). Contrary to our expectations, female Mallards did not avoid all industrial development when establishing home ranges or selecting habitat within their home range. Additionally, we revealed that land cover and land use influenced breeding female Mallard habitat selection across the hierarchical orders, such that fine-scale coefficient estimates at the third order were more precise than coarse-scale estimates at the second order. Most notably, the relationships highlighted the importance of investigating habitat selection across multiple hierarchical levels (Boyce 2006, DeCesare *et al.* 2012, Holbrook *et al.* 2017, Zeller *et al.* 2017) for volant species with highly variable annual cycles (Beatty *et al.* 2014b).

2.5.1 Habitat Selection

Breeding ducks arriving in Canada's western boreal forest encounter a myriad of lakes and wetland complexes that provide excellent breeding habitat (Foote & Krogman 2006, Slattery *et al.* 2011, Prairie Habitat Joint Venture 2014, Dyson 2020, Singer *et al.* 2020). Female Mallards responded to land cover and land use features when establishing a breeding home range at the second order (Figure 2.4), selecting marsh, graminoid fen, and borrow pits, while avoiding forest. At this level of selection, there were a large number of models within $\Delta 2$ AIC of the top model and the error associated with the covariate estimates approached zero. These patterns indicated that models at this order were not as discriminatory as those at the third order. Since the strength of habitat selection depends on the distribution of available sites, we suggest the most plausible explanation for the observed model uncertainty is that our study area provides abundant potential home range areas for breeding ducks (Prairie Habitat Joint Venture 2014), and we suspect that much of the habitat we considered 'available' would also provide adequate habitat for breeding female Mallards.

Wetlands are ideal habitat for breeding ducks (Kantrud & Stewart 1977, Cowardin & Golet 1995, Beatty *et al.* 2014a, Bartzen *et al.* 2017, Kemink *et al.* 2020). In our study, we considered five different wetland types including marsh, graminoid fens, shrub swamps, swamps, and treed peatlands (Table 2.1). Our third order results demonstrated variation in the strength and direction of selection coefficient estimates across these wetland types. Marsh was a grouped variable (Table 2.1), which characterized the transition zone between shrub swamp, graminoid fen, open water areas, and forests (Smith *et al.* 2007). Female Mallards selected marsh habitat across scales and these results were consistent with (Dyson 2020) who demonstrated boreal

ducks selected nest sites with greater marsh cover within 300 m of the nest. This is likely attributed to the foraging, resting, and nesting opportunities that marshes provide for ducks (Pearse *et al.* 2012, Beatty *et al.* 2014b, Stafford *et al.* 2016). Female Mallards also selected for graminoid fen land cover across levels. Since *graminoid* spp. (e.g., grasses, sedges, rushes) are considered important nesting vegetation for boreal ducks (Dyson *et al.* 2019), the habitat characteristics of graminoid fens (Smith *et al.* 2007) may provide females with ideal breeding habitat in our study region.

Within home ranges, we observed selection for shrub swamps and avoidance of swamps (Figure 2.6). Selection for shrub swamps is consistent with the limited available research; however, the avoidance of swamps was surprising given previous research that suggested ducks settling in the eastern boreal forest prefer wetlands with swamp peripheries (Lemelin *et al.* 2010). In terms of nest site selection in the region, nesting ducks exhibited a scale-dependent response and avoided swamps at coarse scales, but selected swamps at fine spatial scales (Dyson 2020). We suspect that shrub swamps provided forage opportunities (Straub *et al.* 2012) and dense vegetative cover for concealment. Avoidance of swamps was likely attributed to the standing woody vegetation (Smith *et al.* 2007) that may benefit predators, increasing the risk for breeding females (Simpson *et al.* 2007).

We observed avoidance of treed peatlands by breeding female Mallards (Figure 2.6). We suspect that avoidance is likely due to the lack of nesting habitat (Dyson *et al.* 2019, Dyson 2020). In addition, we documented avoidance of forest habitats at both the second and third order, which is consistent with previous research (Boyer *et al.* 2018, Dyson 2020). Dyson *et al.* (2020) identified important duck predators in the boreal, and given their species ecology,

we suspect that avoidance of forests and other treed habitats (e.g., treed peatlands, swamps; Dyson 2020) could be driven by greater predation pressure within these habitats.

Open water areas are important for breeding ducks (Yerkes 2000, Fast *et al.* 2004, Roy 2018), though evidence suggests that breeding Mallard pairs avoid using open water areas in lakes (total area > 8ha) and wetlands (< 25% standing vegetation) when settling in boreal regions (Lemelin *et al.* 2010). Similarly, breeding ducks also avoid nesting in areas with greater open water coverage (Dyson 2020). These findings are consistent with ours, such that we observed avoidance of open water within the breeding home range. During the breeding period, ducks are reliant on vegetation and protein sources (Fast *et al.* 2004, Straub *et al.* 2012, Stafford *et al.* 2016) and prefer sheltered waterbodies, but switch to open water areas during brood rearing (Yerkes 2000, Fast *et al.* 2004, Roy 2018). Avoidance of open water and selection of wetlands (e.g., marsh, shrub swamp, and graminoid fen) indicated that females selected small, productive waterbodies during the breeding season, which is consistent with other literature (Gilmer *et al.* 1975, Batt *et al.* 1992, Krapu *et al.* 1997, Dyson 2020).

There is limited support to suggest that ducks are negatively affected by industrial development during nesting and brood rearing (Ludlow & Davis 2018, Roy 2018, Kemink *et al.* 2019, Dyson 2020, Skaggs *et al.* 2020). However, it is likely that industrial development features vary in their influence. Borrow pits and well pads are abundant industrial features on the landscape in our study area. Ducks commonly use borrow pits (R Johnstone *pers. obs.*), and evidence suggests that nesting ducks select nest sites with greater proportions of borrow pits in close proximity (Dyson 2020). However, Skaggs *et al.* (2020) reported that prairie ducks may be avoiding nesting in habitats with high densities of wells, while Singer *et al.* (2020)

found no effect of wells on settling patterns in the boreal. We observed selection for borrow pits, which is unsurprising; though females also selected well pads. We believe borrow pit selection is associated with stable habitat conditions (e.g., vegetation, water levels) that mimic natural wetlands (Bendell-Young *et al.* 2000, Fast *et al.* 2004, Gurney *et al.* 2005, Kuczynski & Paszkowski 2010, 2012), while well pad selection may be associated with the early-successional vegetated peripheries that may provide nesting habitat for ducks (Emery *et al.* 2005, Ludlow & Davis 2018, Dyson *et al.* 2019). We could not separate active and inactive wells, thus selection for these categories is indiscernible. This warrants future research that explores how well pad activity (e.g., active vs inactive); and, well pad and borrow pit site characteristics (e.g., biotic communities, size, depth, forage) influence fine-scale breeding habitat selection.

In our study, females also avoided industrial block features (e.g., industrials, harvest areas) within their home range. Boreal ducks will avoid nesting in areas with greater proportions of industrial sites within 1000 m of a nest (Dyson 2020). This may be attributed to industrial noise and human activity at these features (Habib *et al.* 2007, Francis *et al.* 2009, 2011, Shonfield & Bayne 2017). Forestry is another major industry in the western boreal forest (Foote & Krogman 2006, Wells 2011, Prairie Habitat Joint Venture 2014), and contrary to previous research (Lemelin *et al.* 2007), females in our study avoided harvest areas within their home ranges. Mammalian boreal duck predators (Dyson *et al.* 2020) are positively associated with increasing industrial footprints (Dyson 2020), and forest edges promote predator activity (Pasitschniak-Arts *et al.* 1998, Flaspohler *et al.* 2001, Ball *et al.* 2008); therefore, ducks may be avoiding industrial sites and harvest areas due to increased predation risk.

Linear features (e.g., roads and pipelines) are narrow cutlines that result in limited habitat loss, but create extensive edge habitats in forested landscapes (Rich *et al.* 1999, Degregorio *et al.* 2014, Mumma *et al.* 2019, Dickie *et al.* 2020). Isolating the individual effects of linear feature can be difficult due spatial correlation, and their dissimilar biological functionality (e.g., travel corridors or travel obstructions; Degregorio *et al.* 2014, DeMars & Boutin 2017, Dickie *et al.* 2017, 2020, Mumma *et al.* 2019). Recent literature quantified the effects of roads and pipelines on ducks breeding in the western boreal and suggests they avoid settling and nesting in areas with greater densities of pipelines (Dyson 2020, Singer *et al.* 2020), but select nest sites with greater densities of roads (Dyson 2020). Consistent with current literature, females selected habitats in close proximity to roads (Figure 2.7). Many potential predators avoid paved roads (Pasitschniak-Arts *et al.* 1998, Tucker *et al.* 2018), consequently increasing the probability of duck nest and offspring survival (Roy 2018, Dyson 2020, Skaggs *et al.* 2020). Thus, paved roads may serve as a predator refugia for breeding ducks. Contrary to current boreal duck research, and inconsistent with our expectations, females also selected habitats close in proximity pipelines. Vegetation regrowth on pipelines is restricted, and they can act as travel corridors for predators (Slattery *et al.* 2011, Mckenzie *et al.* 2012, Degregorio *et al.* 2014, Dickie *et al.* 2017, 2020), potentially providing easier access to previously secluded breeding habitats; though, the attractive features of proximity habitats associated with pipelines is unknown. Thus, we are uncertain of an explanation regarding the nature of the relationship between ducks and pipelines. Future research should investigate additional characteristics of pipelines (e.g., vegetative communities, stage of regrowth) and their spatial association with

breeding habitats, which may help clarify the relationship with boreal breeding ducks at finer spatial scales.

2.5.2 Predictive Mapping

Habitats that support large numbers of waterfowl annually should be the focus of duck habitat conservation initiatives (Doherty *et al.* 2015, Janke *et al.* 2017, Kemink *et al.* 2020); therefore, the western boreal forest should be a priority for waterfowl managers. We generated four landscape-scale maps that represent spatial predictions of our top models to identify female Mallard breeding habitat in the western boreal forest (Figure 2.8). Our spatially predictive maps offer a suite of applications depending on the extent and resolution of management. Our second (Figure 2.8A) and third (Figure 2.8B) order maps are useful for identifying important habitats at coarse (1430m²) and fine (45m²) spatial scales, respectively. Our scale-integrated habitat map (Figure 2.8C) is useful for identifying the most important habitat (i.e., Ranks 4 and 5) across spatial scales. Similarly, our change-in-rank map (Figure 2.8D) can be used to identify the general importance of habitat at and across scales. Our maps are valuable management tools (DeCesare *et al.* 2012, Fedy *et al.* 2014, Morris *et al.* 2016, Holbrook *et al.* 2017) that provide reference for boreal breeding female Mallard habitat prioritization; however, their application beyond Mallards will require species-specific refinements given the generalist behaviour of Mallards (Sauter *et al.* 2012, Kleyheeg *et al.* 2017).

2.6 Summary

By assessing habitat selection across multiple hierarchical levels, we quantified the behavioural process of habitat selection (Johnson 1980, Boyce 2006, Meyer & Thuiller 2006) and produced spatial predictions of important habitat for female Mallards during the breeding period. Contrary to expectations, female Mallards do not avoid all industrial development. In addition, the increased precision of our coefficient estimates from the second to third order suggests stronger selection behaviour at the smaller spatial scale, and imply that current levels of industrial development still allow for the establishment of breeding home ranges in our region. We recommend that conservation initiatives focus on habitats with greater proportions of shrub swamp, marsh, and graminoid fens. Further focus should be placed on marsh habitat, as this is also an important variable in nest site selection (Dyson 2020). Indeed, there is also ample opportunity for additional research in this region. Based on our results, we suggest exploring the relationships between selection and fine-scale habitat characteristics of wetland communities (e.g., invertebrate and vegetation communities, vegetative community structure) and important industrial features (e.g., well pads and borrow pits) and linear features (e.g., roads and pipelines) across other species of breeding ducks. Overall, our research addressed important questions concerning behavioural responses of ducks to changes in habitat structure during the breeding season, and elucidated the effects of industrial development on habitat selection in boreal breeding female Mallards. Industrial development in Canada's western boreal forest is expected to continue, therefore our research may be a valuable tool for identifying and conserving vital breeding duck habitats, while also serving as an example for future breeding habitat selection studies in the boreal forest and other breeding regions.

Chapter 3: Multi-scale Landscape Effects on Incubation Behaviour in Boreal Nesting Ducks

3.1 Overview

Incubation plays a crucial role in embryonic development and influences nest and adult survival in birds. Among most North American duck species, only females incubate eggs and therefore face a tradeoff between self-maintenance and incubation. These patterns of attendance represent incubation behaviour and are influenced by various external factors that can affect the overall fitness of females and their offspring. However, we are lacking a thorough understanding of how habitat structure and composition affects incubation behaviour. We measured incubation recess frequency, duration, and incubation constancy in four ground-nesting duck species across a gradient of natural resource development in the western boreal forest of Alberta, Canada. We then examined the effects of land cover, land use (i.e., industrial development), and weather on the variation in incubation behaviour using generalized linear mixed-effect models. To quantify incubation patterns, we developed a behaviour identification method using a combination of observer-mediated changepoint analyses and generalized additive models. Average daily recess frequency for all species was 2.81 ± 0.251 ($\bar{x} \pm \text{SE}$) breaks per day with an average break duration of 3 hours (183.49 minutes \pm 29.52). Across species, individuals spent on average 67% (0.67 ± 0.038) of their day incubating. Daily recess frequency was positively correlated with secondary roads (e.g., winter roads, trails, unmaintained roads), overhead cover at the nest site, marsh habitat, and air temperature. Recess duration was positively correlated with average air temperature; and incubation constancy was negatively correlated with average air temperature and overhead cover. Our results suggested

that incubating females take more recesses per day in response to increased land cover, land use, and weather; and adjust the duration of recesses and incubation constancy in response to warmer weather. Our research yields baseline information regarding incubation behaviours of boreal ducks, and quantified the effects of habitat structure and composition on incubation behaviour in ground nesting ducks in the western boreal forest using a new quantitative approach.

3.2 Introduction

Nest attendance plays a crucial role in avian reproductive success (White & Kinney 1974, Afton & Paulus 1992) by maintaining temperatures within a narrow range promoting optimal embryonic development (Prince *et al.* 1969, Webb 1987, Manlove & Hepp 2000, Hepp *et al.* 2005, Hepp & Kennamer 2012). Prolonged period of active incubation also results in faster development rates and healthier, more viable offspring while reducing the risk of nest depredation (Afton & Paulus 1992, Hepp *et al.* 2006, Durant *et al.* 2013, Carter *et al.* 2014, Croston *et al.* 2020). However, maintaining incubation temperatures for embryonic development is energetically costly (White & Kinney 1974, Tinbergen & Williams 2002, Durant *et al.* 2013, Ringelman & Stupaczuk 2013, Croston *et al.* 2020), therefore, incubating individuals face a tradeoff between competing requirements of incubation and self-maintenance (Brown & Fredrickson 1987).

Incubation behaviour varies widely across duck species, linked to life history traits. Ducks exhibit various incubation strategies (Afton & Paulus 1992, Hepp *et al.*, 2006), including the energetically demanding uniparental or female-only incubation, which emphasizes the stark tradeoff between nest attendance and self-maintenance (Johnson *et al.* 1999, Cockburn 2006).

The incubating female receives no assistance from the male parent in the form of food provisioning or predator vigilance while foraging (Fedy & Martin 2009). Thus, the incubating female must meet her own metabolic needs through resource allocation strategies whereby the female passively relies on limited endogenous reserves, or intermittent foraging bouts for compensatory supplementation to meet the nutritional requirements of incubation (Ankney 1984, Jönsson 1997, Langin *et al.* 2006, Houston *et al.* 2007, Stephens *et al.* 2009). Compensatory foraging results in characteristically similar inattentive periods when females leave the nest to replenish energy reserves (Croston *et al.* 2020), producing a highly variable incubation pattern (Skutch 1957, 1962, Manlove & Hepp 2000). These behaviours are quantifiable and can provide valuable insight into extrinsic factors that influence incubation and reproductive success.

Given the importance of nest attendance for reproductive success, there is a long history of research investigating patterns of attendance (i.e., sessions and recesses; Baldwin & Kendeigh, 1927, Skutch 1962) and constancy of incubation (Skutch 1962). These patterns have been described in ducks (Skutch 1957, White & Kinney 1974, Afton & Paulus 1992, Deeming 2002) and highlight the significance of incubation temperature for embryonic development (Prince *et al.* 1969, Batt & Cornwell 1972, Webb 1987, Hepp & Kennamer 2012, Durant *et al.* 2013), and the physiological demands of incubation on the attending parent (Korschgen 1977, Tinbergen & Williams 2002, DuRant *et al.* 2013). The extrinsic effects of factors such as weather (Afton 1980, Croston *et al.* 2020, Setash *et al.* 2020), food availability (Maccluskie & Sedinger 1999, Bentzen *et al.* 2010), and depredation (Ringelman & Stupaczuk 2013, Croston *et al.* 2018a) on attendance patterns in ducks have also been well documented, and results vary.

Remarkably though, few studies have investigated the effects of habitat structure and composition on incubation, and no one has explored these effects at the macro (i.e., home range) and micro (i.e., nest site, home range) spatial scales. Furthermore, we do not know how industrial development might affect incubation patterns. Given that habitat characteristics influences duck nest site selection (Dyson *et al.* 2019, Dyson 2020) across multiple scales, and industrial development alters predator-prey dynamics (Abrams & Ginzburg 2000, Dickie *et al.* 2017, 2020, Muhly *et al.* 2019, Mumma *et al.* 2019), exploring the effects of habitat structure and composition may reveal the mechanisms that influence incubation behaviour in boreal ducks.

It is difficult to obtain accurate data on incubation patterns and nest attendance (Ringelman & Stupaczuk 2013) because it requires constant monitoring of the nesting individual (Croston *et al.* 2018b) which can be detrimental to both the incubating hen and nests (Korschgen & Dahlgren 1992, Esler & Grand 1993, Olson & Rohwer 1998, Bolduc & Guillemette 2003). Several solutions exist including the use of temperature sensors placed in the nest to infer the presence or absence of a hen (Afton 1980, Flint & Maccluskie 1995, Loos & Rohwer 2004, Bentzen *et al.* 2010, Croston *et al.* 2020), visual identification of the hen's attendance behaviour using cameras (Hoover *et al.* 2004, Croston *et al.* 2018b, a, Setash *et al.* 2020), or the use of radio telemetry (Ringelman *et al.* 1982). Each of these approaches and their variations, of course, come with concomitant tradeoffs. For example, false eggs with temperature probes accurately measure incubation temperatures experienced by eggs (Flint & Maccluskie 1995), but the addition of one egg can increase energetic demands for incubating females (Durant *et al.* 2013). The use of simple temperature sensors that do not involve the addition of a false egg

is less invasive and has been used to track nest attendance behaviour in various avian species (Cooper & Mills 2005, Schneider & McWilliams 2007, Fedy & Martin 2009, Dallmann *et al.* 2016). The use of cameras may act as a visual cue for potential nest predators and are often inefficient for documenting ground nesting species because nest activity can be challenging to document through dense ground vegetation (DeGregorio *et al.* 2016, Weston *et al.* 2017).

In addition to considering trade-offs in data collection, the high volume of data required to accurately identify incubation rhythms requires that researchers also consider trade-offs in terms of data processing. In both temperature sensor and camera approaches, nest attendance is regularly classified using manual identification of recesses through visual inspection of videos or photographs from cameras (Manlove & Hepp 2000, Hoover *et al.* 2004, Loos & Rohwer 2004, Dallmann *et al.* 2016, Setash *et al.* 2020), or visual inspection of variation in temperature data (Bentzen *et al.*, 2010; Hepp *et al.*, 2005). It can be difficult to accurately differentiate between incubation recesses using temperature data alone due to the high sensitivity of the sensors that can result in indistinct temperature fluctuations. Additionally, using only visual inspection can be time-consuming, especially with large datasets; and leads to concerns regarding objectivity, replicability, and internal validity if multiple researchers are involved (Hoover *et al.* 2004, Schneider & McWilliams 2007, Capilla-Lasheras 2018). Several temperature data processing approaches have been developed to help address some of these concerns; however, they can be cumbersome with large datasets (Capilla-Lasheras 2018); depend upon specialized software (Cooper & Mills 2005), or *a priori* knowledge of species incubation temperatures and behaviour to establish required temperature thresholds used for the identification of incubation recesses (Croston *et al.* 2018c). Therefore, an approach that is

capable of processing high volume temperature data in open access software, is replicable, applicable to novel species and environments, and identifies incubation recesses in highly variable temperature data would prove useful for quantifying incubation behaviour.

Our study was located in the western boreal forest of Canada. This area is an ideal landscape for exploring incubation behavior in ducks for several reasons. First, despite its importance to North American duck populations (Slattery *et al.* 2011), we know relatively little about the basic life history of ducks in the boreal region compared to ducks in prairie and arctic ecosystems. Additionally, the landscape has recently experienced considerable industrial development (Fahrig 2003, Slattery *et al.* 2011, Steffen *et al.* 2011, Wells 2011, Hebblewhite 2017, Fisher & Burton 2018) and resource exploration and infrastructure, such as road networks and extraction sites, that has resulted in extensive landscape alterations (Wells 2011, Hebblewhite 2017) and fragmented the boreal habitat (Schmiegelow & Mönkkönen 2002, Fahrig 2003, Fisher & Burton 2018). Finally, anthropogenic alterations to the landscape benefit predator communities (Degregorio *et al.* 2014) by facilitating movement (DeMars & Boutin 2017, Dickie *et al.* 2017, 2020, Finnegan *et al.* 2018) and increasing their efficiency in capturing prey (Abrams & Ginzburg 2000, Muhly *et al.* 2019, Mumma *et al.* 2019). Since nest survival is not negatively affected by industrial development in this region (Dyson 2020), investigating the multi-scale effects of habitat structure on incubation attendance may elucidate the adaptive behaviours adopted by nesting females in response to increased predator activity.

The goals of our research were to describe the patterns of incubation for multiple species of ground nesting ducks, and assess the effect of important macro and micro habitat characteristics that influence nest site selection (Dyson *et al.* 2019, Dyson 2020) on incubation

patterns. We developed an efficient and replicable approach for processing high volume temperature data obtained from common and affordable temperature sensors using standard analysis software (e.g., R) to identify incubation sessions and recesses and address the gaps in our notions of life history and ecological processes of incubation. We examined incubation attendance in four ground-nesting species of ducks across a gradient of industrial development in the western boreal forest of Alberta, Canada during the 2017 and 2018 breeding seasons. We hypothesized that land cover, land use, and weather would affect incubation attendance. More specifically, we predicted that nesting habitats with greater amounts of linear features (e.g., seismic lines, primary and secondary roads) and industrial block features (e.g., industrials, wells) would result in shorter and more frequent incubation breaks due to avoidance of increased predator and industrial activity. We also predicted that increased amounts of marsh habitat within proximity to the nest would result in shorter, more frequent incubation breaks due to increased accessibility of foraging habitat. Additionally, increased air temperatures and nest site concealment (i.e., lateral and overhead cover) would increase the number of breaks taken and prolong the time females spent off the nest due to reduced risk of embryonic shock and detection of the nest. Finally, we predicted no effect of land cover or land use variables on incubation constancy as hens would adjust frequency and duration behaviours to maintain nest microclimates, but warmer weather would decrease incubation constancy due to reduced need for nest microclimate regulation.

3.3 Methods

3.3.1 Study Area

Our study area was located within the western boreal forest of Alberta, Canada, north of Slave Lake and south of Red Earth Creek, within ~ 100km radius of Utikuma Lake (Figure 3.1). Upland habitats included mixed-wood, deciduous dominated forests that consist primarily of Trembling Aspen, Balsam Poplar, White Spruce, and Jack Pine. Lowland habitats were characterized by conifer dominated forests, consisting primarily of Black Spruce, and multiple wetland communities. In the boreal forest, terrestrial and aquatic communities are regularly influenced by large scale natural disturbance such as wildfire and insect outbreaks (Schmiegelow & Mönkkönen 2002, Carlson *et al.* 2015, Thom & Seidl 2016). The western boreal forest has also experienced an increased demand for natural resources (oil and gas, and forestry), which adds to the existing anthropogenic footprint (Schmiegelow & Mönkkönen 2002, Slattery *et al.* 2011, Wells 2011, Pasher *et al.* 2013). We selected study sites that represented the natural landscape and anthropogenic disturbance gradients by incorporating development intensities based on cumulative energy development and land cover characteristics. In addition, we considered regional duck density estimates (Ducks Unlimited Canada, 2014) and site accessibility. We did not consider any sites that experienced wildfire or logging activity within 20 years. More details on study site selection and description can be found in Dyson *et al.* (2019).

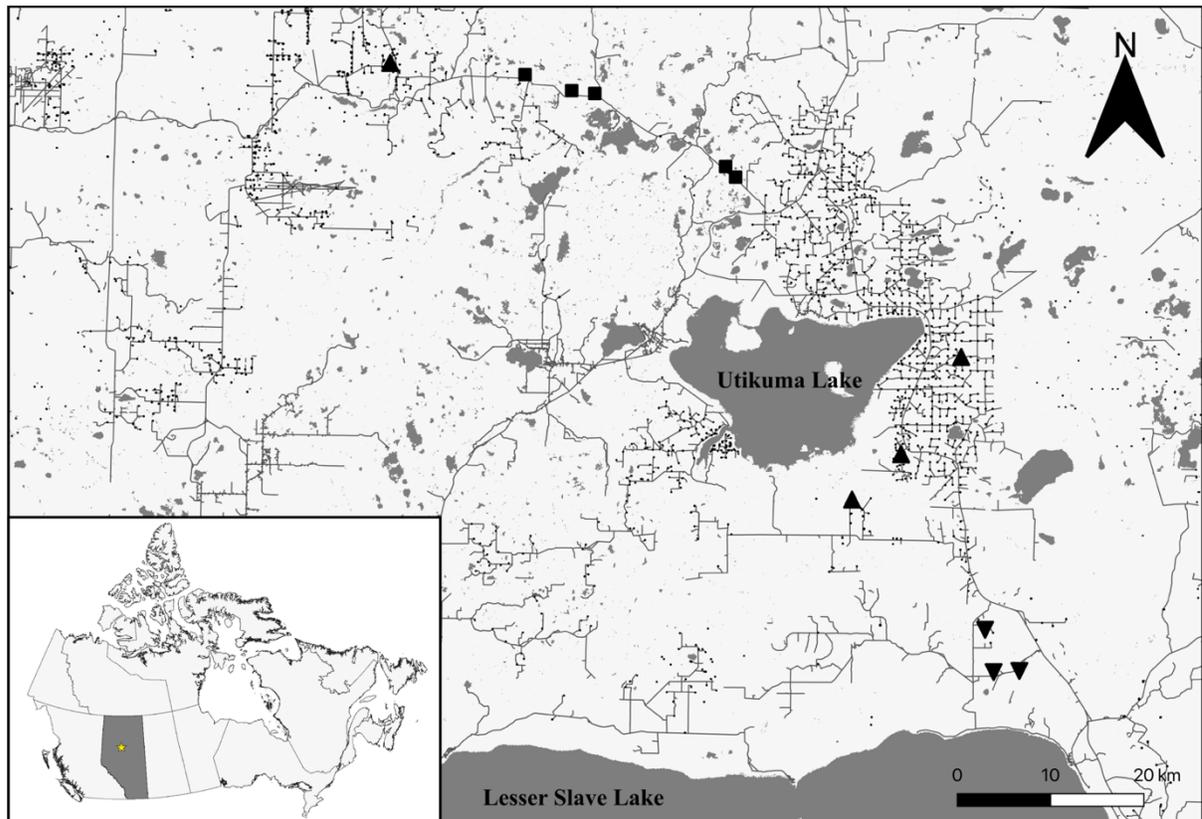


Figure 3.1- Map of study area in the Slave Lake Region of Alberta, Canada. Points indicate study site locations where nests were located and are categorized by the cumulative extent of industrial development (low: ▼, medium: ■, high: ▲). The inlay indicates the location of the study area relative to the province of Alberta and Canada.

3.3.2 Nest Searching

We searched for nests at 24 sites in 2017, and 25 sites in 2018 on a 3-week rotation (15–25 days) between 08:00 and 16:00. We conducted nest-searches on foot with a 'willow switch' (~1.2 m willow branch) to disturb vegetation and increase the probability of flushing an incubating female (Klett *et al.* 1986). The searching process involved 3–6 technicians walking in unison around wetlands ~5–20 m apart and parallel with the shore. In 2018, we piloted the use of transmitters in addition to nest searching and located three Mallard nests using radio telemetry. At each nest, we identified the species, recorded the number of eggs, and estimated

the incubation stage using a combination of egg candling and floating (Weller 1956). We recorded nest site variables including lateral and overhead cover, which were measured within 5 days of a nests predicted or actual hatch date (McConnell *et al.* 2017). We estimated overhead cover of nest bowl vegetation using a 12.5 x 12.5 cm grid with individual 2.5 x 2.5 cm squares from 120 cm above the nest bowl (Guyn & Clark 1997, Borgo & Conover 2016, Dyson *et al.* 2019); and lateral cover using a Robel pole (Robel *et al.* 1970, Nudds 1977, Dyson *et al.* 2019). For a complete description of nest searching and vegetation sampling methods, see (Dyson *et al.* 2019).

3.3.3 Nest Temperature Recording

We recorded nest bowl temperatures using Maxim Integrated iButton® temperature datalogger (Maxim Integrated Products Inc., San Jose, CA, USA; Model Number DS1921G-F5; hereafter iButton) from date of nest discovery until termination at 5-minute intervals. We sampled up to 30 nests of upland nesting ducks each year using iButtons. To optimize the spatial distribution of our nest bowl temperature samples, we opportunistically placed iButtons in a limited number of nests to avoid oversampling a site with iButtons. We attached iButtons to 5.8 cm roofing nails using silicone and pressed iButtons into the ground through the bottom of the nest bowl making sure the iButton was slightly protruding above the nest bottom and in contact with the eggs (Ringelman & Stupaczuk 2013). We replaced iButtons on a 7-10-day schedule during regular nest monitoring activities and chose the 5-min interval to ensure we did not exceed the internal storage capacity of the iButton between monitoring events. The location of the iButton meant that temperatures recorded were not indicative of true incubation temperatures experienced by eggs, but served as an accurate index of nest microclimate

(Fawcett *et al.* 2019) which we used to identify incubation sessions and recesses (Ringelman & Stupaczuk 2013).

3.3.4 Data Processing and Recess Detection

We uploaded temperature data from each iButton using Maxim's iButton Blue Dot™ receptor (Model DS1402D-DR8) and OneWireViewer software (Maxim Integrated Products Inc., San Jose, CA, USA). This produced files for each iButton which included a unique identifier, date, time, and temperature records for the predefined time intervals. We replaced iButtons during nest monitoring, therefore, most nests had data contributed from multiple iButtons. We referred to these unique iButton temperature time series within nests as "segments". As a precaution, we trimmed all temperature time series using deployment and removal dates to ensure temperatures recorded during transport were not included. We processed all temperature time series data using a four-step approach including: 1) trim the temperature time series data using a changepoint analyses to isolate the incubation period, 2) smooth incubation rhythms using generalized additive models to better represent the cyclic pattern of the data, 3) identify sessions and recesses using peak and trough identification and variation in temperature change to estimate the duration and patterns of incubation attendance, and 4) a final "heads-up" visual refinement of incubation rhythms to ensure accurate and precise quantification of incubation patterns. Our approaches to each step are outlined below.

We trimmed the raw temperature data to identify behavioral changes (e.g., laying, incubating, termination) in our temperature times series and restrict the data to the incubation periods. We identified changepoints based on the raw temperatures for each nest segment using the pruned exact linear time (PELT) algorithm (Killick *et al.* 2012) with a manual penalty of

$2 \cdot \log(\text{number of temperature records})$ in the *changepoint* package (Killick & Eckley, 2014) for R (R Core Team 2019). This approach allowed us to detect distinct changepoints in the nest attendance temperature time series (e.g., laying, incubating, termination). We visually inspected each identified changepoint (Figure 3.2A) and selected the changepoints that identified the initiation and termination of the incubation period (Figure 3.2B). This resulted in the removal of segments that did not represent incubation (i.e., laying, abandonment, or post-termination).

Step two involved smoothing our temperature time series data to better reveal the cyclic patterns of nest bowl temperatures during incubation. This approach reduced the noise and helped us efficiently and objectively identify sessions and recesses. We smoothed incubation rhythms by fitting a generalized additive model (GAM) with a gaussian distribution (Figure 3.2C). We calculated the degrees of freedom used for smoothing by multiplying the length of the time series for each segment by 0.25. This represented a good trade-off between retaining the detail in the raw data and identifying the major patterns in the data. All GAMs were fit using the *mgcv* (Wood 2011) package for R (R Core Team 2019). All subsequent steps were implemented on the model-predicted values.

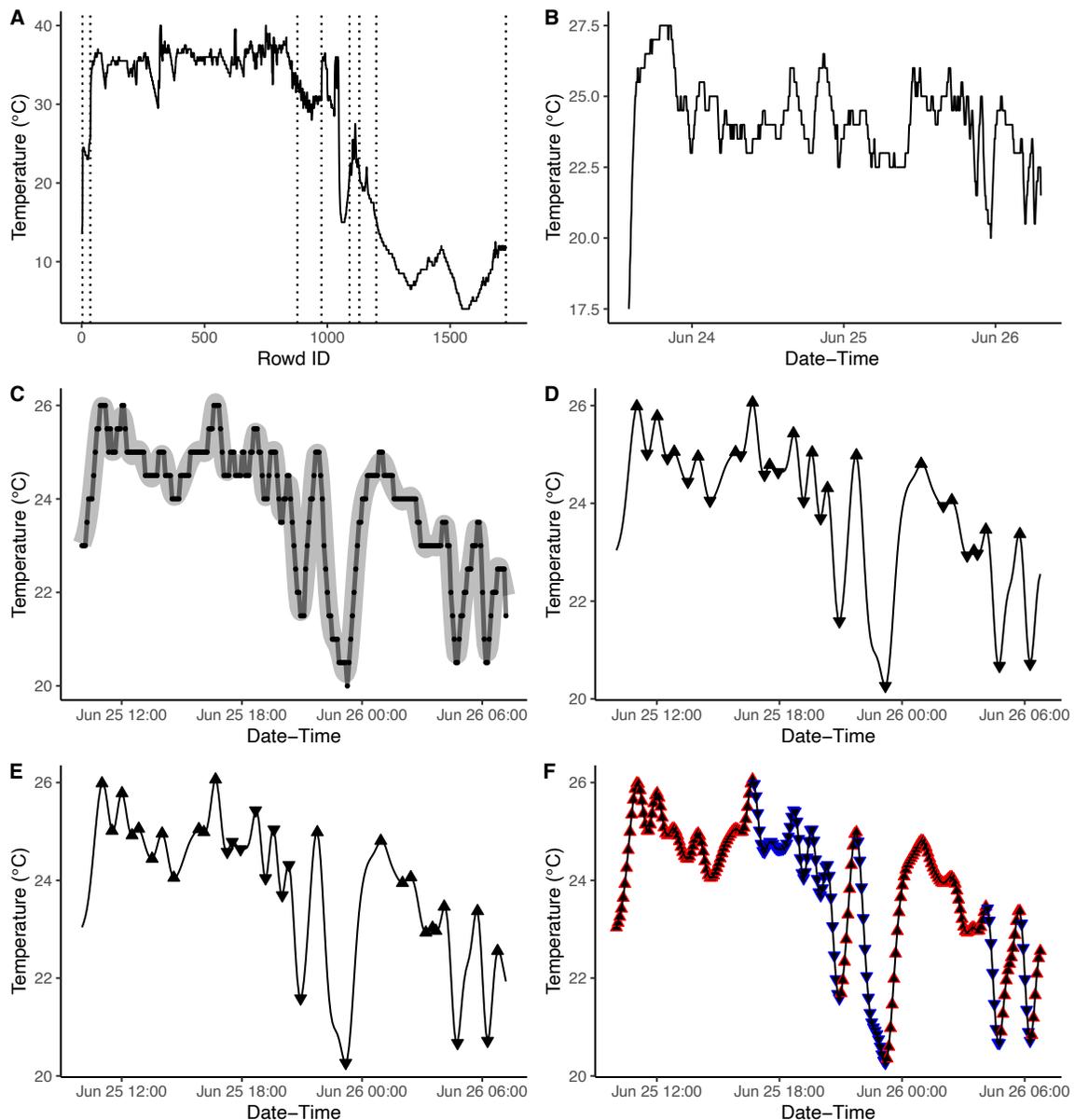


Figure 3.2 – Process plots highlighting key steps in the ‘heads-up’ analysis for temperature time series data from a single nest segment. A) Raw temperature data collected from iButton probes (solid black line) with changepoint locations (hashed line); B) Changepoint adjusted temperature time series representing the incubation rhythm in the segment; C) 48hr segment of the model predicted incubation rhythm (bolded gray buffer) with raw incubation rhythm overlay (dark gray line) and raw temperature records (black points) overlay; D) 48hr portion of the model predicted incubation rhythm (black line) with over-estimated peaks (\blacktriangle) and troughs (\blacktriangledown); E) 48hr portion of the model predicted incubation rhythm (black line) with threshold-adjusted peaks (\blacktriangle) and troughs (\blacktriangledown). F) 48hr portion of the model predicted incubation rhythm (black line) with colour coded sessions (\blacktriangle) and recesses (\blacktriangledown).

Step three required the identification of the start and end of incubation sessions and recesses. We achieved this goal through the identification of peaks and troughs (local minima and maxima) which indicated the start and end points of incubation sessions and recesses using model predicted temperature values and an inflection function. We used a conservative threshold in the inflection function for the identification of peaks and troughs, intentionally biasing our data towards Type I errors and identifying all peaks and troughs (Figure 3.2D). Incubation sessions were indicated by an increase in temperature and recesses were indicated by a decrease in temperature. A false positive in these types of data represents the identification of either the beginning or end of an incubation recess or session. Filtering false positives is commonly completed using a change in temperature (Δtemp) threshold where any temperature change that is $< x^{\circ}\text{C}$ is not considered a ‘true’ change in the incubation status.

Various thresholds have been reported for recess detection in waterfowl (Manlove & Hepp 2000, Hoover *et al.* 2004, Loos & Rohwer 2004, Bentzen *et al.* 2010, Croston *et al.* 2018b); however, variation among individuals and species means these thresholds are likely not appropriate for all temperature data (Loos 1999, Hoover *et al.* 2004). This is important because small variations in temperature (e.g., 1°C) can have dramatic effects on the estimation of the duration and frequency of incubation sessions and recesses. Rather than choosing an absolute change in temperature value for all nests and species, and since we are working with model predicted values, we used the distribution of the model predicted temperature data for each nest segment to inform the selection of an appropriate value. We calculated the change between sequential peaks and troughs and refer to these values as the *Trend Temperature* (TT). For example, the change in temperature between a peak and trough is assigned a recess *Trend*

Temperature (Recess_{TT}), and the change in temperature between that trough and the next sequential peak is assigned session *Trend Temperature* (Session_{TT}). We then used the distribution of each nest's specific *Trend Temperature* (i.e., Session_{TT} and Recess_{TT}) to set a nest independent change in temperature value. Our change in temperature value was determined for each individual nest segment using the standard deviation (SD) of *Trend Temperature* in each segment. If the *Trend Temperature* between adjacent peaks and troughs was greater than the *Trend Temperature* SD, we considered it a 'true' session or recess. Using the 'true' peaks and troughs (Figure 3.2E), we filled the gaps with our remaining model predicted values and assigned behaviour-specific identifiers (Figure 3.2D).

As the final (4th) step, we trimmed nest segments that started or finished with a recess to the first and last distinct session to remove any recesses caused by technician disturbance or termination (e.g., hatch, abandonment, depredation). In addition, we removed all nests with \leq 48 hours of data following session and recess identification.

3.3.5 Analysis

3.3.5.1 Variable Development

We used three daily metrics that describe incubation behavior. Recess frequency was a count of the incubation breaks (i.e., recesses) taken between 00:00 and 23:59. Recess duration was measured as the average amount of time a female spent in recess, between 00:00 and 23:59 each day. Incubation constancy was measured as the proportion of time a female spent incubating (i.e., in session) each day. We calculated daily constancy by dividing the total daily duration of sessions by the sum of the duration of all sessions and recess for a given day (Skutch 1962). We estimated sunrise/sunset time (05:30–21:30) across the study period and considered

a recess to have occurred during the day if it took place between 05:30 and 21:30, and at night if it occurred outside of those hours. We did not always have nest temperature records for an entire 24-hour period (e.g., date of discovery, memory shortage) but felt it was unnecessary to remove incomplete days (<24 hours) that were part of complete segments. Therefore, we included all temperature records for incomplete days during the incubation period and accounted for varying period lengths statistically. We report means and standard errors for each metric unless otherwise noted ($\bar{x} \pm SE$).

To measure effects of habitat on incubation behaviour, we evaluated important nest site characteristics (e.g., lateral and overhead cover) that influence nest site selection at fine spatial scales (Dyson *et al.* 2019). In addition, we developed landscape covariates using spatial layers that represented land cover (i.e. habitat) and land use (i.e. industrial development) features known to influence nest site selection at broader spatial scales in the region (Dyson 2020). Land cover variables were developed from Ducks Unlimited Canada's Enhanced Wetland Classification layer (Ducks Unlimited Canada 2011), and include nest site variables. Land use layers were developed from the Alberta Biodiversity Monitoring Institutes (ABMI) Human Features Inventory database (ABMI 2017). Polygonal features, such as well pads and pump stations, represented the percent area within a 30m x 30m pixel; and line features, such as pipelines and roads, were represented as the sum of the length of each line feature (km) in a 30m x 30m pixel. All land use and land cover covariates were then summarized based on a 1000 m radial buffer with the nest location as the centroid (Table 3.1).

To assess the influence of weather, we paired each nest with local climate data from the nearest active weather station. We obtained average daily temperature (°C) from the Alberta

Agriculture and Forestry meteorological station in Marten Hills (-114.5600, 55.5300) accessed through Alberta Climate Information Service (ACIS) systems.

3.3.5.2 Model development

We modeled the influence of all covariates on each of our three response variables representing incubation patterns (i.e., frequency, duration, and constancy) using generalized linear mixed effects models (lme4 package, Bates *et al.* 2015) in R (R Core Team 2019). We included important land cover and land use variables identified by the top micro and macro nest site selection models proposed by (Dyson 2020). Variables were not included in the same model if Pearson's $r > |0.65|$. When we identified highly correlated variables, we selected individual variables that were the most relevant for exploring our questions and underlying hypotheses. For example, roads and pipelines in the western boreal are often constructed in unison and sometimes share the cleared corridors through the dense forest landscape. However, evidence suggests roads (i.e., primary and secondary) play an important role in boreal duck nest site selection (Dyson 2020), and primary road (i.e., paved, gravel) densities are positively correlated with nest survival (Roy 2018, Dyson 2020), thus, we selected roads as a practical predictor variable. Prior to analysis, we standardized all predictor variables and visually inspected the species-specific distribution of our response variables using box and whisker plots to confirm overlap among species and justify the pooling of all species in our data.

Our global model for each of the three response variables incorporated three land cover, four land use, and one weather covariate as fixed effects (Table 3.1) and a unique nest identifier as a random effect. Recess frequency data are discrete counts and were fit using a Poisson distribution with a log link (Zurr *et al.* 2009). Prior to analysis, we log-transformed recess

duration to meet the requirements of homoscedasticity (Zurr *et al.* 2009) and fit models to these data using a Gamma distribution with an inverse link function (Hardin & Hilbe 2007). The incubation constancy data were proportional and therefore we fit linear mixed effects models to these data using a weighted binomial distribution with a logit-link function (Bolker *et al.* 2009, Zurr *et al.* 2009, Bates *et al.* 2015). We weighted observations using the combined daily duration of sessions and recesses (i.e., daily total) to account for days with < 24 hours of data. For each response variable, we ranked models using Akaike's Information Criterion corrected for small sample size (AICc) and removed nested subsets of the top model that contained uninformative parameters and present all competing models within 2 Δ AICc scores of the top model (Arnold 2010). We selected the top ranked model with the lowest Δ AICc score for interpretation (Burnham & Anderson 2004).

Table 3.1 – Descriptions and unstandardized ranges for fixed-effect land cover and land use predictors used in our frequency, duration, and incubation constancy models for four species of upland nesting ducks in Alberta’s western boreal forest.

Covariate	Scale	Description	Range
<i>Land cover</i>			
Marsh	Landscape	Land cover - Aquatic Bed, Mudflats, Emergent, and Meadow Marsh measured as proportional area (%)	0 – 10
Lateral Cover	Nest site	Land cover -Nest site measurement of percent lateral cover from all cardinal directions represented as average proportion for all directions (%)	9.08 – 83.96
Overhead Cover	Nest site	Land cover -Nest site measurement of percent overhead cover from 1m above the nest presented as average proportion (%)	7.6 – 100
<i>Land Use</i>			
Primary Roads	Landscape	Land Use - Maintained roads (i.e., paved and gravel roads) measured as total length (km)	0 – 13.69
Secondary Roads	Landscape	Land Use - Unmaintained roads (i.e., winter roads and trails) measured as total length (km)	0 – 3.89
Seismic Lines	Landscape	Land Use - All seismic lines measured as total length (km)	5.81 – 35.07
Industrials	Landscape	Land Use - Industrial block features (i.e., camps, facilities, oil and gas buildings, gas plants etc.) measured as proportional area (%)	0 – 2
<i>Weather</i>			
Air temperature	Landscape	Average air temperature for a 24-hour period (°C)	5.09 – 20.50

3.4 Results

We were able to use iButton data from 29 nests (25% iButton failure rate) including 5 Mallards, 12 Blue-winged Teal (*Spatula discors*), 5 Green-winged Teal (*Aanas crecca*), and 7 American wigeon (*Mareca americana*). Our use of the inflection function to detect peaks and troughs resulted in a total of 823 recesses across all species and nests. We documented 163 incubation recesses for Mallards and 73% occurred during the day (05:30-21:30). For Blue-winged Teal, we identified 249 recesses, of which 81% were during the day. Data availability for American Wigeon and Green-winged Teal were similar with 208 and 203 recesses, of which 67% and 72% were taken during the day, respectively. Approximately 35% of recesses were detected at night (213 at night and 610 during daylight) across all species (Figure 3.3).

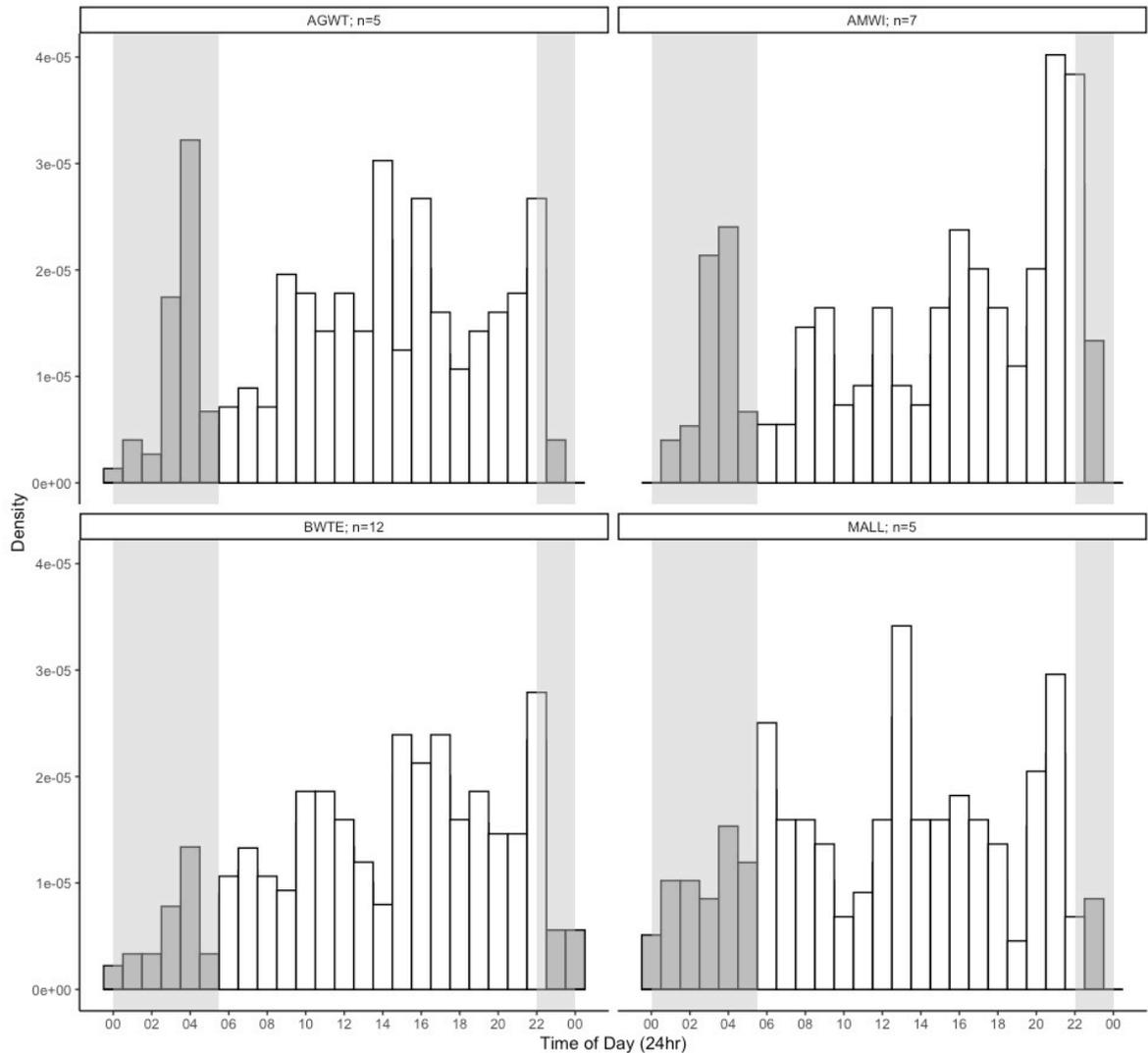


Figure 3.3 – Density distributions of recess start times during the 24-hour day for four species of upland nesting ducks in Alberta’s western boreal forest. Shaded areas with dark bars represent estimated night (21:30-05:30). Individual plot sub-titles indicate species four letter USGS codes, and n represents the number of nests. Species codes: AGWT = Green-winged Teal, AMWI = American Wigeon, BWTE = Blue-winged Teal, MALL = Mallard.

Summary statistics for measures of incubation behaviour varied across species (Table 3.2). Mean daily recess frequency was the greatest numerically for Green-winged Teal and the lowest for American Wigeon. The max number of recesses recorded in a single day was 7 in

Mallards, and 6 in all other species. Mean recess duration was greatest numerically in American Wigeon. The minimum recess duration we detected was in Blue-winged Teal and the longest was in American Wigeon. Mean incubation constancy was greatest numerically in Mallards, and the maximum and minimum incubation constancy we observed within a complete 24-hour time period was in American Wigeon.

Table 3.2 – Summary of recess frequency, duration, and incubation constancy in four species of ground nesting duck species in the boreal forest, Alberta, Canada during the 2017-2018 nesting period. Mean values represent $\bar{x} \pm SE$.

	All species	Green-winged Teal (n=5)	American Wigeon (n=7)	Blue-winged Teal (n=12)	Mallard (n=5)
Frequency					
Mean	2.81 ± 0.25	3.45 ± 0.29	2.54 ± 0.21	2.62 ± 0.22	2.85 ± 0.27
Max	-	6	6	6	7
Min	-	1	1	1	1
Duration					
Mean	183.50 ± 29.52	163.52 ± 26.16	208.53 ± 42.78	177.29 ± 19.90	178.23 ± 21.47
Max (hrs)	-	25.75	32	15.8	22.5
Min (min)	-	20	25	25	25
Constancy					
Mean	0.67 ± 0.038	0.65 ± 0.036	0.66 ± 0.041	0.67 ± 0.037	0.69 ± 0.036
Max	-	0.871	0.925	0.891	0.883
Min	-	0.035	0.010	0.069	0.066

Our top ranked recess frequency model included land cover, land use, and weather covariates (Table 3.3). There were four competing models in our candidate set within 2 Δ AICc scores. The remaining models were within ~ 6 Δ AICc scores and included non-nested combinations of the top covariates. We observed a response by nesting females to secondary roads (e.g., winter roads, trails, unmaintained roads; Figure 3.5) such that an increase in road density (i.e., total length) surrounding nests was correlated with an increased number of recesses taken daily (Figure 3.5). We observed a positive response to overhead cover at the nest site, suggesting increased overhead cover increased the number of recesses. We also detected an effect of marsh habitat on daily recess frequency, such that increased marsh habitat within 1 km of the nest resulted in increased daily recess frequency.

Table 3.3 – Non-nested generalized linear mixed model set for incubation recess frequency, duration, and constancy in four species of ground nesting duck species in the boreal forest, Alberta, Canada during the 2017-2018 nesting periods. Model sets represent non-nested competing models within 2 AICc scores of the top ranked model.

Model	K	LL	Δ AICc ^a	w_i
Recess Frequency				
Avg. Air Temperature + Marsh + Secondary Roads + Avg. Overhead Cover	4	-505.4	0	0.26
Marsh + Secondary Roads + Avg. Overhead Cover	3	-506.62	0.35	0.21
Avg. Air Temperature + Secondary Roads + Avg. Overhead Cover	3	-506.93	0.98	0.16
Marsh + Secondary Roads	2	-508	1.06	0.15
Secondary Roads + Avg. Overhead Cover	2	-509.26	1.57	0.12
Recess Duration				
Avg. Air Temperature	1	-253.23	0	0.82
Incubation Constancy				
Avg. Air Temperature + Avg. Overhead Cover	2	-950.85	0	0.58
Avg. Air Temperature	1	-952.19	0.62	0.42

^a Lowest AICc score for Recess Frequency = 1023.09, Recess Duration = 514.60, and Incubation Constancy = 1909.82.

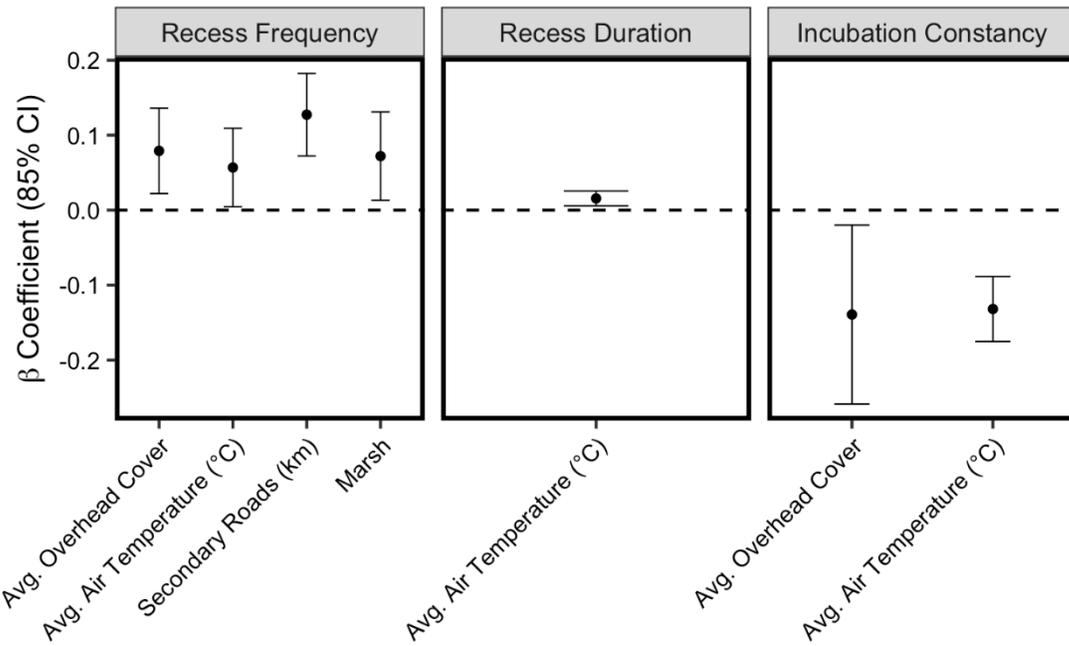


Figure 3.4 – Coefficient estimate plots for fixed effects in the top ranked recess frequency, duration, and incubation constancy models for upland nesting ducks in the boreal forest, Alberta, Canada, from 2017-2018. Error bars represent 85% confidence intervals.

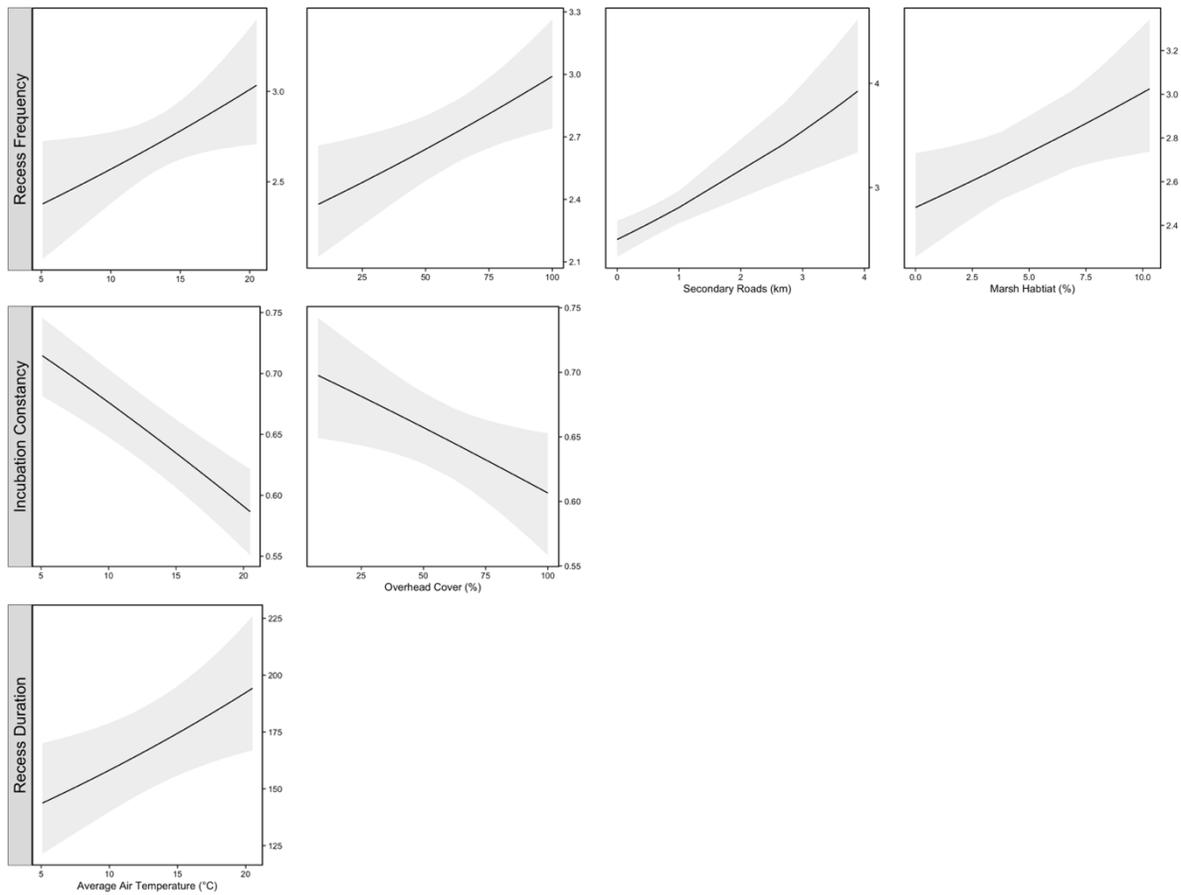


Figure 3.5 – Predicted effects plots for incubation recess frequency, duration, and constancy in ground nesting ducks in the boreal forest, Alberta, Canada from 2017-2018 nesting periods. Plots represent the response from ground nesting ducks to predictor variables. Shaded areas represent 85% confidence intervals.

For recess duration, our best model included only average air temperature and no land cover or land use covariates (Table 3.3). The next competing model, excluding all nested combinations, was $> 3 \Delta AICc$ scores and was the null model. We observed a positive effect of average air temperature on recess duration suggesting warmer temperatures resulted in longer incubation recesses (Figure 3.5).

Our top ranked model in our model set for incubation constancy included average air temperature and overhead cover, and did not include land use covariates (Table 3.3). Excluding

all nested combinations, the next competing model was $< 1 \Delta\text{AICc}$ score and did not include overhead cover. The remaining model was $> 17 \Delta\text{AICc}$ scores and was the null model. We detected a negative effect of average air temperature on incubation constancy (Figure 3.5) such that females spent a greater proportion of time off the nest during warmer weather (Figure 3.5). We observed a weak, negative response to overhead cover at the nest site (Figure 3.5), indicating that increased overhead cover reduced daily incubation constancy (Figure 3.5). Although, visual inspection of the residuals suggested a weak model fit at the upper and lower extremes of our model. In addition, we did not observe any differences across species for any of our three models.

3.5 Discussion

We described incubation patterns and presented quantified measures of incubation attendance for ducks nesting in the western boreal forest. Our design and implementation of the heads-up changepoint analysis and use of GAMs provides an effective, efficient and reproducible approach to quantifying incubation behaviour from temperature probe data. Our results provide a valuable baseline for incubation studies in the boreal forest and contribute new information on boreal waterfowl life histories and ecology. Overall, our findings were generally consistent with our predictions such that increased amounts of marsh habitat and greater densities of secondary roads (e.g., winter roads, trails, unmaintained roads) within proximity to the nest led to increased recess frequencies but did not affect recess duration or incubation constancy. Inverse to our predictions, recess frequency was positively correlated with warmer weather (i.e., air temperature); though we did observe a prolongment of recess durations and reduced incubation constancy, consistent with our predictions. Interestingly, and

also inverse to our predictions, overhead cover at the nest site and incubation constancy were negatively correlated. We did not detect an effect of industrial block features on any of our three incubation behaviour measures.

Previous approaches to quantifying incubation behaviour in ducks often use time-consuming and costly methods (Hoover *et al.* 2004, Schneider & McWilliams 2007, Capilla-Lasheras 2018) that require constant observer mediation (Cooper & Mills, 2005) or a prior understanding of the study species (Croston *et al.* 2018b). Our heads-up approach provides a fast, effective, and reproducible method for defining the incubation period and identifying sessions and recesses using standard statistical software across species. The use of iButtons offered a cost-effective alternative for accurately recording nest bowl microclimates (Fawcett *et al.* 2019) that reduced the amount of observer and equipment disturbance at the nest site compared to alternative approaches (i.e., false eggs; Durant *et al.* 2013, Erikstad & Tveraa 1995). A highlight of our approach involves using a flexible temperature threshold based on the distribution of model predicted nest bowl temperatures that accounted for the inter- and intraspecies variation, easing concerns regarding applications of thresholds across species (Loos 1999, Hoover *et al.* 2004). One limitation of our approach was iButton sensitivity and the efficiency, which may have hindered our ability to detect the onset of short recesses and sessions, primarily because ducks insulate their nest with a dense layer of down, potentially masking minor temperature fluctuations.

Comparison of incubation behaviors across species (i.e., Mallard vs Blue-winged Teal) is limited by the large variation in waterfowl nesting behaviors (e.g., cavity, upland, over water) and breeding strategies (i.e., capital and income). However, genetic evidence regarding species

relatedness (Wilson *et al.* 2012), breeding strategies and nesting behaviours (Connelly & Ball 1984) suggests that Blue-winged Teal and Cinnamon Teal (*A. cyanoptera*) do not cohere to interspecies variation, and therefore it is reasonable to compare measures of incubation across teal species. Setash *et al.* (2020) presented patterns for breeding Cinnamon Teal, reporting an average daily recess frequency of 2.02, with durations ranging from 0.1 – 1.5 hours (6.57 – 96.8 minutes) and an incubation constancy of 0.894. Blue-winged Teal in our study took comparatively more recesses per day (2.54) with longer recess durations (177 minutes), and lower incubation constancy (0.67). Within species, previous research on Mallards reported a daily recess frequency of 1.69 and recess duration of 1.75 – 2.5 hours (106.11 – 155.39 minutes; Croston *et al.* 2020). Similarly, Ringelman & Stupaczuk (2013) reported a combined daily recess frequency in Mallards and Gadwall of 1.7, with recess durations of ~3 hours (171 minutes). Our average daily recess frequency for Mallards was 40% higher (2.85); however, our recess duration in Mallards was similar to the two previous studies at ~3 hours (178.23). Overall, this suggests that Mallards and Blue-winged Teal nesting in the boreal consistently took more daily recesses, which were longer for Blue-winged Teal but similar in duration for Mallards when compared to previous research.

Within species variation in incubation patterns are influenced by several factors including habitat (Ringelman *et al.* 1982, Maccluskie & Sedinger 1999, Bentzen *et al.* 2010). Our results are consistent with patterns reported for other species in which populations further north tend to take more incubation breaks. For example, female Northern Shovelers (*Spatula clypeata*) took twice as many breaks and had lower constancy at a northern study site in Alaska compared to those nesting in the south in Manitoba, but recess duration was similar (Maccluskie &

Sedinger 1999). The measures of recess frequency, duration and incubation constancy that we report represent ducks in the western boreal forest and indicate that Mallards and teal take more breaks than their southern breeding conspecifics (Ringelman & Stupaczuk 2013, Croston *et al.* 2020, Setash *et al.* 2020). These differences may be further evidence of latitudinal variation in incubation patterns (Chalfoun & Martin 2007). If consistent, the differences may also represent behavioural adaptations required to meet the demands of incubation in more northerly climates such as increased foraging due to food limitations (Maccluskie & Sedinger 1999) and predator avoidance in response to elevated risk of female mortality (Martin 2002). However, the exact mechanisms driving this variation would require further examination.

The influence of local ambient temperature have been the focus of many studies because it influences incubation behavior, such that warmer ambient temperatures are generally associated with increased recess frequency, longer recess durations, and decreased incubation constancy within study sites (Afton 1980, Ringelman *et al.* 1982, Ringelman & Stupaczuk 2013, Croston *et al.* 2020). Our results were congruent with this previous research and all three of our top models indicated females took longer, more frequent breaks, and spent less time on their nest during warmer days. Incubation breaks in ducks often occur during the warmest part of the day (Brown & Fredrickson 1987) to assist in nest microclimate regulation. Microclimates can be different between nest sites (Gloutney & Clark 1997), therefore, to accurately model the effects of ambient temperature on incubation behaviour, future research may consider recording ambient temperature using additional iButtons outside of the nest bowl or installing weather stations to report a more localized ambient temperature pattern than we had available for this research.

The habitat a species occupies influences all aspects of the individual's behaviour and fitness (Block & Brennan 1993, Jones 2001, Kaminski & Elmberg 2014, Boyce *et al.* 2016). Incubation behaviour can impact both survival and reproduction, and has been studied for multiple duck species across North America (Afton 1980, Ringelman *et al.* 1982, Mallory & Weatherhead 1993, Maccluskie & Sedinger 1999, Hoover *et al.* 2004). However, few studies have quantified the effects of habitat structure on incubation behaviour. Previous research suggested that microscale (e.g., nest site) habitat characteristics such as overhead cover did not have an effect on incubation behaviour (Setash *et al.* 2020). However, we observed a positive response to overhead cover in our top recess frequency and incubation constancy models; likely because of the added benefits it provides during incubation (e.g., nest concealment and microclimate regulation; Fogarty *et al.* 2017, Gloutney & Clark 1997). Our recess frequency results are consistent with Zicus (1995), such that females took more recesses when functional foraging habitat (i.e., marsh) was in close proximity to the nest, presumably to forage (Afton 1979, 1980); however, we did not observe any effect of marsh habitat on recess duration nor incubation constancy. This may indicate a trade-off between self-maintenance and incubation attendance such that hens are reducing the duration of their breaks to maintain overall constancy and optimize microclimate for embryonic development. Remarkably, our findings serve as the first quantified evidence regarding the multi-scale effects of nest site and surrounding habitat characteristics on incubation behaviour in ducks.

The influence of industrial development on nest success in ducks has received attention in prairie (Ludlow & Davis 2018, Skaggs *et al.* 2020) and hemi-boreal (Roy, 2018) regions, and we are only beginning to understand the relationship between industrial development and

ducks in the western boreal forest (Slattery *et al.* 2011, Dyson 2020). Additionally, previous studies have yet to explore the relationship between industrial development on incubation behaviour. Our inclusion of road categories was illuminative as primary road (i.e., paved, gravel) densities and nest survival are positively correlated (Dyson 2020, Roy 2018) likely because many mammalian predators avoid roads (Tucker *et al.* 2018). However, our results indicated that nest sites surrounded with high densities of secondary roads (e.g., winter roads, decommissioned vegetated roads, trails) had a higher recess frequency which can negatively influence survival and embryonic development.

Predator avoidance and increased foraging behaviours are two potential hypotheses that explain the correlations with secondary roads. Linear features (e.g., secondary roads) have shown to facilitate predator movement (DeMars & Boutin 2017, Finnegan *et al.* 2018), and the characteristics of secondary roads make them ideal travel corridors (Trombulak & Frissell 2000, Randa & Yunger 2006, Fahrig & Rytwinski 2009, Roy 2018) that could increase foraging success rates (Abrams & Ginzburg, 2000; Muhly *et al.*, 2019; Mumma *et al.*, 2019). Depredation is the primary limiting factor of nest success in ducks (Martin 1995, Clark & Shutler 1999, Simpson *et al.* 2005, Pieron & Rohwer 2010, Howerter *et al.* 2014) and flushing off the nest is a defense tactic used by attending females (Forbes *et al.* 1994, Gunness *et al.* 2001, Dassow *et al.* 2012), thus increased recess frequency may be indicative of females flushing to avoid depredation. For example, if greater secondary roads densities increases nest depredation risk (i.e., elevated predator activity), then females should devote less energy to their nest due to reduced likelihood of survival (Ringelman & Stupaczuk 2013) and are more likely to flush from the nest in response to predator induced disturbance (Dassow *et al.* 2012).

Inversely, nesting habitats with higher densities of secondary roads may have fewer predators and provide females with increased foraging opportunities because of decreased predator pressure. If recesses were taken at appropriate times (i.e., during the warmer periods of the day; Brown & Fredrickson 1987), nest microclimates could be maintained for embryonic development (Webb 1987) with limited concern for nest concealment (Kreisinger & Albrecht 2008). Depending on forage availability, this behaviour could also be more energetically costly (Caldwell & Cornwell 1976) and extend the incubation period, increasing the potential for abandonment (Korschgen & Dahlgren 1992, Esler & Grand 1993) and depredation (Afton & Paulus 1992, Bolduc & Guillemette 2003). Although secondary roads did not influence incubation constancy nor recess duration, suggesting that while hens took more breaks, they did not spend more time off the nest, alluding to predator-induced recesses or increased foraging recesses. A companion study investigating the occupancy of boreal duck predators (Dyson *et al.* 2020) found increasing probability of site occupancy for bear, wolves, and coyotes with increasing human footprint, but was unable to differentiate impacts between primary and secondary roads (Dyson 2020). Thus, future research may consider investigating the exact mechanisms driving increased recess frequency.

Ducks nest at low densities in the boreal forest, making it difficult to locate nests. Previous research adapted for the prairie regions suggested that the optimal time to search for duck nests was between 08:00 and 14:00 (Gloutney *et al.* 1993). We detected incubation recesses at every hour during the entire 24-hour day (Figure 3.3). Given that the observers are dependent on flushing the hen to locate the nest, traditional upland nest searching methods (Klett *et al.* 1986) and time-frames may not be a feasible option. Though we cannot recommend an optimal time

to search for nests, the implementation of alternative nest searching approaches such as drones (Bushaw *et al.* 2020) may allow researchers to cover larger areas in shorter amount of time, increasing the success rate of finding nests.

3.6 Summary

We developed a new method to objectively and efficiently quantify incubation behaviour in ground nesting ducks using cost-effective temperature loggers. We then used that approach to produce baseline life history information regarding the recess frequency, duration, and incubation constancy in four species of boreal ground nesting ducks. This also allowed us to further investigate the multi-scale relationships between land cover, land use, weather and incubation behaviour. Our findings support our hypotheses that land cover, land use and weather affect incubation behaviour and are generally consistent with our predictions. Females took frequent, short recesses when ambient temperatures were high, resulting in reduced incubation constancy. Females also took more recesses when nests were surrounded with greater densities of linear features (i.e., secondary roads) and foraging habitat (i.e., marsh), and when nests were better concealed with dense overhead cover, reducing incubation constancy. The increased measures of recess frequency that we report are the first quantified effects of land use characteristics on incubation behaviour in ducks and represent the potential impacts of continued industrial development on boreal nesting ducks. Ultimately, our research addresses important questions concerning the behavioural response of ducks to changes in ecosystem structure and function during their most crucial life stage. Therefore, these data and our findings may prove useful for making predictions about waterfowl population trajectories relative to landscape change in the future.

Chapter 4: Conclusions

Industrial development is a major threat to terrestrial ecosystems (Allred *et al.* 2015, Hebblewhite 2017) as infrastructure removes and fragments habitat for many wildlife species (Ryall & Fahrig 2006). Industrial development in the boreal forest is expected to continue, and the impacts on boreal breeding ducks remains largely unknown. When focus is placed on the perceived drivers of change and coupled with rigorous conservation research, the results hold the potential to elucidate the unknowns (Pavón-Jordán *et al.* 2017). Therefore, disentangling the relationships between industrial development and breeding ducks will help identify the potential mechanisms of decline and provide the knowledge required to better manage boreal duck populations.

We identified important habitats used by female Mallards during the breeding season and quantified the influence of industrial development on second and third order habitat selection. Overall, our results suggest that the western boreal forest presents ducks with ample habitat that can provide support throughout the breeding period, and that current levels of industrial development do not negatively affect home range establishment or habitat selection of breeding female Mallards. However, with the continued expansion of industrial development across the western boreal region, it is important that we continue to explore the relationship between breeding ducks and industrial development. Brood survival is a major factor that contributes to population dynamics (Raven *et al.* 2007), yet we know nothing about brood survival in the western boreal forest, and there is limited research regarding the effects of industrial development on this important life stage (Roy 2018). Therefore, future research may consider exploring various aspects of the brood rearing period including survival and habitat

selection (Raven *et al.* 2007), taking into consideration the important breeding habitats highlighted by our research.

Given the importance of the western boreal forest to North American duck populations, this region should be a priority for waterfowl management objectives. Studies in the prairie regions have highlighted the importance of small, secluded wetland habitats during various aspects of the breeding period (Gloutney & Clark 1997, Clark & Shutler 1999, Yerkes 2000, Kemink *et al.* 2019). Based on our results, we suggest that habitat management projects in areas with varying industrial development intensities should prioritize habitats with greater proportions of shrub swamp, marsh, and graminoid fens. Wetland habitats provide attractive forage opportunities and vegetation communities (Bendell-Young *et al.* 2000, Gurney *et al.* 2005, Straub *et al.* 2012, Stafford *et al.* 2016) associated with these features have the potential to provide ducks with stable, valuable habitat throughout the breeding period (Emery *et al.* 2005, Kuczynski & Paszkowski 2012, Dyson 2020).

Though we observed selection for well pads, borrow pits, roads, and pipelines, we caution reclamation of these features. Selection for these industrial features may, in fact, be due to their attractiveness over other natural features in the boreal forest (Bendell-Young *et al.* 2000, Gurney *et al.* 2005). However, they may also represent adaptive behaviours such that competition for top-notch natural habitats resulted in the selection of sub-optimal ones. Therefore, we suggest that managers allow borrow pits and well pads to experience natural succession, as this is a cost-effective alternative to active reclamation. We also suggest that future research investigates the fine scale habitat characteristics (e.g., benthic invertebrate communities, vegetative community structure) of important wetland communities (e.g., shrub

swamp, marsh, and graminoid fens) and industrial block (e.g., well pads, borrow pits) and linear features (e.g., roads and pipelines) that promotes habitat selection.

We developed a new method to identify nest attendance in ground nesting ducks using temperature loggers. We believe our heads-up changepoint analysis is a practical method that is of considerable value to the avian research community; and suggest that future research consider employing this method on other species of ducks with different breeding strategies (e.g., capital) and nesting behaviours (e.g., cavity and over water nesters). Though, we recognize that this approach requires refinements and proof of concept before it can be applicable across other avian taxa, such as songbirds. Ultimately, however, this method is an efficient and effective way to quantify incubation behaviour metrics which provide valuable life history knowledge, and may also be important predictors that can be incorporated into nest and brood survival models (Bloom *et al.* 2013).

We applied our novel approach to quantify incubation patterns and produced baseline life history information regarding the incubation behaviour of boreal nesting ducks; and insight into the multi-scale effects of land cover, land use, and weather on incubation behaviour. The influence of secondary road densities and marsh habitat on daily recess frequency was informative, and generated two potentially dissimilar hypotheses that require further investigation. In particular, the correlation with secondary roads may represent increased depredation avoidance tactics (i.e., flushing) due to increased predator activity, or increased foraging behaviour due to a lack of predators and increased foraging habitat. Future research may also consider incorporating a nest-site specific predator activity aspect (e.g., occupancy rates) in their incubation behaviour models, which may help clarify the exact mechanisms that

influence incubation behaviour in boreal ducks. Our results provide a valuable reference point for incubation studies in the boreal forest and contribute new information to the growing repository of research surrounding duck life histories.

In this thesis, we explored how industrial development influenced breeding habitat selection and incubation behaviours in boreal nesting ducks, while also considering natural land cover features. We highlighted key habitats used by breeding female Mallards and quantified the effects of industrial development on the habitat selection process across multiple hierarchical levels. Furthermore, we quantified the effects of industrial development on incubation behaviour in four ground nesting species of boreal breeding ducks, and developed a novel approach for exploring incubation behaviour in avian species. The findings from our research will help facilitate the efficient allocation of management efforts and conservation dollars to develop effective conservation policy and population management initiatives. Additionally, our findings will guide future research that explores the relationships between industrial development on breeding ducks in the region. Our research contributes to our unique understanding of the novel boreal ecosystem by providing new theoretical knowledge to boreal forest and waterfowl ecology, and valuable insight into landscape interactions, ultimately contributing to conserving North American duck populations.

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