

Detection probability of the Pileated Woodpecker (*Dryocopus pileatus*): Implications for developing habitat use models

by

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## **Abstract**

As old-growth forest ecosystems become increasingly scarce in North America, the need to accurately and efficiently survey, monitor, and model old-growth specialists and keystone species, such as the Pileated Woodpecker (*Dryocopus pileatus*), becomes increasingly important. Little is known about the behaviour and habitat associations of the Pileated Woodpecker at the northern edge of its range in Alberta, Canada. Attempts at modeling Pileated Woodpecker habitat use for this region by the Alberta Biodiversity Monitoring Institute (ABMI) have high uncertainty, particularly for vegetation types. One explanation is that the data used to build these habitat selection models comes from surveys done in June, which may not capture the peak of Pileated Woodpecker detectability and breeding behaviour. As a large-bodied bird with an expansive home range, it is unknown how or if occupancy (traditionally used as the response variable in many habitat models) can effectively represent Pileated Woodpecker habitat associations. To model Pileated Woodpecker habitat, I first determined periods of peak detectability and evaluated how different methods of measuring and estimating use influence habitat models.

I explored temporal variation in Pileated Woodpecker behaviour using passive acoustic monitoring methods. Peak detection periods for Pileated Woodpeckers were near sunrise in early April. Mean daily temperature and day length were the most influential environmental variables that affected the drumming of Pileated Woodpeckers. Based on these findings, I provide minimum recommendations for future survey efforts regarding the timing and number of surveys required to ensure accurate data collection for the Pileated Woodpecker in Alberta, Canada. These guidelines can be used for planning future surveys and methods to utilize existing non-optimized surveys to ensure the accuracy of Pileated Woodpecker site occupancy.

Using these guidelines, I optimized data collection and built regional habitat models for the boreal forest in Alberta, Canada. These models evaluated how different response metrics, land cover data sources, and scales affect Pileated Woodpecker habitat associations and the predictive accuracy of models. I compared two response metrics, occupancy and intensity of use, to determine Pileated Woodpecker habitat use. Biomass and canopy closure were important environmental variables for both response metrics. However, these models were not particularly predictive, possibly due to errors in land cover data, the nature of the acoustic sampling strategy, the species' biology, or a combination of these factors. Additionally, I determined that land cover data sources can greatly affect model predictive capacity and the number of reliable predictors identified. Furthermore, I determined that broad-scale land cover data, which may represent the environment at the landscape level, may be more predictive in determining Pileated Woodpecker habitat use than local definitions of land cover. From these results, I outlined considerations regarding sampling and modeling techniques for future Pileated Woodpecker studies and identified important habitat characteristics for the Pileated Woodpecker in Alberta, Canada.

## **Preface**

### **Author Contributions**

This thesis is an original work by Austin Zeller.

Chapter 2 of this thesis is an unpublished manuscript: A.C. Zeller, E.M. Bayne, and C.L. Mahon “Temporal variation in Pileated Woodpecker behaviour: ecological explanations and management implications.” I was responsible for concept formation, data analysis, and writing the manuscript. E.M. Bayne was responsible for providing data, concept formation, and writing the manuscript. C.L. Mahon provided feedback on concept formation and writing of the manuscript.

Chapter 3 of this thesis is an unpublished manuscript: A.C. Zeller, A. de Rosa, E.M. Bayne, and C.L. Mahon “Pileated Woodpecker habitat use in the boreal forest of Alberta: The relative importance of response variables, land cover, and scale”. I was responsible for concept formation, data analysis, and manuscript writing. A. de Rosa assisted in and provided feedback on data analysis. E.M. Bayne was responsible for providing data, concept formation, and writing the manuscript. C.L. Mahon provided feedback on concept formation and writing of the manuscript.

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I want to thank all Bayne Lab members and technicians who have helped collect data, commiserated model results, and listened to my “*jokes*”. I especially would like to thank Taylor Hart for putting up with my shenanigans; Isabelle Lebeuf-Taylor for nerd-ing out with me; Carrie Ann Adams for her honesty and thoughtfulness; Anna Jacobsen for putting the capital “A” in the A-team; Alberto de Rosa for being my Bayesian sensei; Lionel Leston for being so helpful and approachable; and Cami Hurtado for surviving the pandemic grad school experience with me. Additional thanks go out to Tharindu Krishin Kalukapuge, Sejer Meyhoff, Juan Andres Martinez Lanfranco, Alessandro Franceschini, Andrew Crosby, Brendan Casey and Sergio Poo Hernandez for making the lab space full of positive, inspiring and exciting energy. Thanks to Alex McPhail for his help with Wildtrax and data management questions. Thanks to Hedwig Lankau for ensuring field operations and ARU data organization were successful. Technicians Keeya Beausoleil, Kyle Field, and Michel Vorasane were particularly important to the implementation and success of this project. I am grateful for the opportunities to work with the Canadian Wildlife Service (Whitehorse Branch) during my degree. I especially want to thank Logan McLeod, Jean François Jetté, and Joachim Bertrands, who made the field seasons full of laughs, epic views, and gnarly hikes. I would also like to thank my supervisors, Dr. Erin Bayne and Dr. C. Lisa Mahon, for allowing me to explore, learn, and make mistakes over the years. Additional thanks go to Dr. Scott Nielsen and Dr. Kimberley Mathot for their feedback on this thesis.

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# Table of Contents

1.	Chapter 1. Introduction .....	1
2.	Chapter 2. Temporal variation in Pileated Woodpecker behaviour: ecological explanations and management implications.....	5
3.	Chapter 3. Pileated Woodpecker habitat use in the boreal forest of Alberta: The relative importance of response variables, land cover, and scale .....	29
4.	Chapter 4. Conclusions .....	62
5.	Bibliography .....	66
6.	Appendices.....	79

## List of Tables

Table 2.1 Predictor variables that describe the relationship between time and Pileated Woodpecker behaviour. ....	13
Table 2.2 The model set used to examine how Pileated Woodpecker (PIWO) drumming patterns change on a seasonal and daily scale. ....	15
Table 2.3 The model set used to examine what environmental factors drive Pileated Woodpecker (PIWO) drumming patterns to change over a seasonal scale. ....	17
Table 2.4 The model set of generalized linear models used to examine how daily variations in weather affect Pileated Woodpecker drumming patterns. ....	18
Table 2.5 Model results and Akaike information criterion (AIC) scores for models describing the relationship between Pileated Woodpecker drumming and seasonal predictor variables. ....	21
Table 2.6 Model results for multivariate GAMMs which include the most predictive static (Julian date and day length) and dynamic (mean temperature) interannual environmental variables. ....	23
Table 2.7 Table showing the results of the generalized mixed effects models describing the relationship between Pileated Woodpecker drumming behaviour and daily fluctuations in weather described by the model variable. ....	24
Table 3.1 Variables selected from the Beaudoin <i>et al.</i> (2017) dataset (250 meter resolution). Italicized variables are exclusive to this dataset. ....	40
Table 3.2 Variables selected from the NTEMS dataset (30 meter resolution) Italicized variables are exclusive to this dataset. ....	40
Table 3.3 Model Set 1 describes variables in the base occupancy models (binomial). ....	43
Table 3.4 Model Set 2 describes variables included in the base intensity of use models (Poisson). ....	44



Table 3.5 Model Set 3 describes variables scale and response metrics used in creating models exclusively in the Beaudoin <i>et al.</i> 2017 dataset.....	45
Table 3.6 Pearson’s correlation coefficients for variables extracted from the Beaudoin <i>et al.</i> (2017) and NTEMS datasets at 565 meters (used as a representative scale).....	50
Table 3.7 Occupancy model’s reliable variables with the calculated posterior distribution of beta values and model accuracy based on cross-validation results. ....	53
Table 3.8 Intensity of use model’s reliable variables with the calculated posterior distribution of beta values and model accuracy based on cross-validation results.....	54
Table 3.9 Table of habitat covariates that consistently influence Pileated Woodpecker occupancy.. ....	55
Table 3.10 Table of habitat covariates that consistently influence Pileated Woodpecker intensity of use. ....	56
Table 6.1 Ridge regression model results for the multivariate models containing interannual static and flexible terms.. ....	82
Table 6.2 Model results for multivariable models with/without interactions between variables explored in Chapter 2, objective 3. ....	82

## List of Figures

Figure 2.1 Map of Alberta, Canada, showing the sites where Pileated Woodpeckers were surveyed. ....	9
Figure 2.2 Example spectrograms of a Pileated Woodpecker drum (A) and call (B) in Alberta, Canada.....	11
Figure 2.3 The predicted probability of detecting a Pileated Woodpecker drum on a seasonal scale.....	20
Figure 2.4 The predicted probability of detecting a Pileated Woodpecker drum based on a diel scale (hour of the day) (A) and hours since sunrise (B). ....	20
Figure 2.5 Relationship of mean temperature and Pileated Woodpecker drumming detection probability as estimated by the smoothing term generated in the GAMM.....	22
Figure 3.1 The study area of Alberta, Canada. Black dots represent the approximate locations of deployed ARUs. Ecoregions, as defined by the Government of Canada (2016), are denoted by colour. ....	35
Figure 3.2 Conceptual model demonstrating the differences between occupancy and intensity of use described in this study. ....	37
Figure 3.3 Scatterplot showing the proportion of recordings where a Pileated Woodpecker (PIWO) was detected (out of 15 recordings). ....	51
Figure 6.1 Current species habitat associations in forested regions of Alberta for the Pileated Woodpecker derived by ABMI (Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2023). ....	79
Figure 6.2 Correlation matrix for variables examined in Chapter 2, objective 2: environmental factors influencing Pileated Woodpecker drumming. ....	80

Figure 6.4 Relationship of day length (hours) and Pileated Woodpecker drumming as estimated by the smoothing term generated via GAMM (Chapter 2).....	81
Figure 6.5 The relationship between the deviation from the expected normal temperature (Celsius) and the probability of detecting a Pileated Woodpecker drum .....	83
Figure 6.6 Sample trace plot. ....	84
Figure 6.7 Histogram showing the distribution of age values extracted from Beaudoin <i>et al.</i> (2017) at 565 meter buffer scale (used as a representative) for locations used in Chapter 3. ....	85
Figure 6.8 Histogram showing the distribution of age values extracted from NTEMS at 565 meter buffer scale (used as a representative) for locations used in Chapter 3.....	85
Figure 6.9 Histogram showing the distribution of deciduous percentage values extracted from Beaudoin <i>et al.</i> (2017) at 565 meter buffer scale (used as a representative) for locations used in Chapter 3.....	86
Figure 6.10 Histogram showing the distribution of deciduous percentage values extracted from NTEMS at 565 meter buffer scale (used as a representative) for locations used in Chapter 3. ...	86
Figure 6.11 Histogram showing the distribution of biomass values extracted from Beaudoin <i>et al.</i> (2017) at 565 meter buffer scale (used as a representative) for locations used in Chapter 3. ....	87
Figure 6.12 Histogram showing the distribution of biomass values extracted from NTEMS at 565 meter buffer scale (used as a representative) for locations used in Chapter 3.....	87

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# 1. Chapter 1. Introduction

The study of wildlife behaviour is vital to understanding the roles and niches a species occupies. It is also essential for researchers to understand how behaviour influences our ability to survey a species. A commonly studied behaviour in birds is song. Birds use singing for various purposes, ranging from mate selection to territorial defence (Kilham 1959, Kroodsma and Byers 1991, Catchpole and Slater 1995). Song also creates distinguishable auditory cues that researchers can use to identify and count species (Emlen 1972, Dodenhoff *et al.* 1998, Priyadarshani *et al.* 2018). Most bird species show distinct seasonal patterns in breeding behaviour and frequency of auditory cues over the breeding season (Perrins 1970, Catchpole and Slater 1995, Helm *et al.* 2006, Tremain *et al.* 2008, Avey *et al.* 2011, Harms and Dinsmore 2014, Agostino *et al.* 2020, Upham-Mills *et al.* 2020).

Most research on the temporal variation of bird behaviours focuses on migratory songbird singing patterns. However, some bird species, namely woodpeckers, produce unique auditory cues (drumming) that are believed to be important for mate selection, territorial defence, and pair communication (Kilham 1959). Establishing how the frequency of drumming changes over the course of a breeding season or year is important to better understand the role that drumming has in the breeding ecology of woodpeckers. Furthermore, woodpecker species are typically non-migratory. Breeding of non-migratory species usually occurs earlier in the season compared to the arrival of migratory species (von Haartman 1968, Samplonius *et al.* 2018). Therefore, we expect that resident species may not display the same temporal patterns in song or other auditory cues as migrants. How these unique features influence the frequencies and timings of behaviours is important to determine for researchers who wish to monitor and study these species.

Variation in the frequency of auditory cues can affect the likelihood of whether researchers will observe their target species. One standardized bird survey program, the Breeding Bird Survey (BBS), employs surveys at times that capture a wide variety of species but are not necessarily timed to capture the peak in many species' auditory cues. As species may react uniquely to environmental variables that trigger breeding season behaviours, it is necessary to establish how

the frequency of these auditory cues shifts across a temporal scale. In doing so, we can ensure that survey efforts have the highest probability of observing a target species. Additionally, by examining species-specific responses, we can increase the accuracy of data and limit the costs of sampling. Optimizing species-specific sampling designs will ultimately allow researchers to improve the predictive capabilities of species habitat models.

### *Wildlife Habitat Use and Modeling*

Habitat use models typically use counts of a species collected during a fixed period, often referred to as point counts for bird surveys. Biologists use these counts to understand the spatial distribution of species by regressing counts against various environmental variables. Numerous ways of using these counts have been developed, such as occupancy, habitat preference, intensity of use, and temporal occupancy, each of which attempts to describe how species are utilizing aspects of the environment. Occupancy is commonly used to describe habitat use relationships (Mackenzie *et al.* 2002, 2006, Royle 2006). As a binary measure, occupancy tells us whether a species is present in a particular area or not, accounting for detection probability (Mackenzie *et al.* 2002, 2006, Royle 2006). However, occupancy may not necessarily give an accurate estimation of habitat preference or importance. More detailed metrics have been developed to understand how a species interacts with its environment (i.e., intensity of use and temporal occupancy). However, the efficacy of these metrics is not well understood and are likely species-specific. Determining what measurements effectively explain and predict species' habitat use relationships is key to understanding how animals interact with the environment.

Habitat use models can exhibit variability in how the land cover/habitat (predictor) variables are measured or calculated. Typical approaches used to investigate the influence of predictor variables (measures, scales, etc.) often examine land cover data at different spatial scales (Savignac *et al.* 2000, Mayor *et al.* 2009, Baumgardt *et al.* 2014, McGarigal *et al.* 2016). With the rapidly advancing field of remote sensing technologies, most land cover data are measured through satellite imagery. Land cover datasets are approximations of the true environment, which may not be entirely accurate or representative of the true habitat. The importance of variation in remote

sensing layers in understanding species' habitat selection patterns is poorly understood in the boreal forest (e.g., Hedley *et al.* 2020).

### *The Pileated Woodpecker*

This thesis explored the optimization of sampling, habitat use metrics, and other model variations for the Pileated Woodpecker (*Dryocopus pileatus*). As North America's largest primary cavity excavator, the Pileated Woodpecker is a keystone species (Martin and Eadie 1999, Bonar 2000, 2001, Aubry and Raley 2002, Martin *et al.* 2004, Aitken and Martin 2007, Tarbill *et al.* 2015, Trzcinski *et al.* 2022). Keystone species are identified by fulfilling critical niches within an ecosystem, allowing additional species to inhabit the environment. Cavities excavated by Pileated Woodpeckers are used by various taxa, including other landbirds, waterfowl, bats, and weasels (Bonar 2000, 2001). Cavity nesting species, such as the diving ducks, only utilize cavities excavated by Pileated Woodpeckers and other large natural cavities due to their larger body size (Bonar 2000, 2001, Aubry and Raley 2002, Aitken and Martin 2007). The Pileated Woodpecker is an old-growth forest specialist relying on large-diameter trees to excavate these cavities (Bull *et al.* 1992, Renken and Wiggers 1993, Flemming *et al.* 1999, McClelland and McClelland 1999, Savignac 2000, Bonar 2001, Hartwig *et al.* 2004, Bull *et al.* 2007, Raley and Aubry 2010, Kremetz *et al.* 2012). As the forestry sector has prioritized the extraction of high-value forest products, old-growth forest ecosystems have become rarer in North America over the past century. Habitat loss threatens old-growth specialists and keystone species such as the Pileated Woodpecker.

Despite their ecological importance, little research has examined the Pileated Woodpecker's habitat use at the northern extent of its range, the western Canadian boreal forest. Understanding Pileated Woodpecker ecology is particularly important in this region due to increases in development and industrial activities. Current species-habitat models for Alberta using data collected by the Alberta Biodiversity Institute (ABMI) do not show strong associations with specific forest types using point count data (Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2023). This specialist species should have strong associations with specific age categories (old forests), structural stages (gap dynamic and old forest stand dynamic

stage), and forest types (deciduous/ mixed forest types) (Bull and Holthausen 1993, McClelland and McClelland 1999, Aubry and Raley 2002, Hartwig *et al.* 2004, Martin *et al.* 2004, Krementz *et al.* 2012, Hu and Tong 2022). It is possible that relationships are missing in these models because ABMI has not optimized the timing of surveys and modeling techniques for this specific species.

### *Thesis Objectives*

The core objective of this thesis was to improve our understanding of Pileated Woodpecker habitat relationships by optimizing sampling and modeling methods in the western Canadian boreal forest. In Chapter 2, I explored how temporal variation of Pileated Woodpecker drumming affects detectability and identified environmental variables that can predict Pileated Woodpecker behaviour. In Chapter 3, I applied the results from Chapter 2 to generate habitat use models using data from peak detectability periods. I then examined how altering the response variable, land cover dataset, and scale affects the results and accuracy of the Pileated Woodpecker habitat use models.



## **2. Chapter 2. Temporal variation in Pileated Woodpecker behaviour: ecological explanations and management implications**

### **2.1 Introduction**

Accurate and reliable data collection for wildlife species is essential for designing and implementing effective monitoring. Wildlife species differ in activity levels throughout the day, so researchers are tasked with assessing when they will most likely be able to observe the target species. While useful for determining occurrence and trend for hundreds of species, surveys like the Breeding Bird Survey (BBS) are not well suited for some species because the timing of the surveys is not aligned with peak periods of activity resulting in higher false negative rates and less accurate data status, trend, and habitat modeling. Thus, determining when a species is most likely to be detected is crucial for minimizing costs, avoiding additional surveys, and maximizing data quality.

Point counts, conducted through human observation and autonomous recording units (ARUs), primarily rely on each bird species to produce an auditory cue to detect a species' presence. The rationale for the timing of the BBS (late May to early July; Ziolkowski *et al.* 2023) is that the greatest number of species are audible at that time because it is the peak breeding period for most songbirds (Ziolkowski *et al.* 2023). Vocalization is vital to mate selection and territory defence for many species (Kilham 1959, Kroodsma and Byers 1991, Catchpole and Slater 1995); thus, acoustic signals ebb and flow with each stage of the breeding cycle (Catchpole and Slater 1995, Helm *et al.* 2006, Tremain *et al.* 2008, Avey *et al.* 2011, Harms and Dinsmore 2014, Upham-Mills *et al.* 2020). As such, peak auditory activity does not occur simultaneously across all avian fauna because of variability in the breeding cycle (e.g., different time periods for each stage of the breeding cycle and asynchrony in the timing of the breeding cycle) (Perrins 1970, Tremain *et al.*

2008, Harms and Dinsmore 2014, Agostino *et al.* 2020, Hannah *et al.* 2020, Edwards *et al.* 2022). Furthermore, whether auditory behaviours align with breeding activities should be established for all species. This is especially true for non-migratory species that do not have to travel to breeding grounds to begin the breeding season. Additionally, cryptic species (vocalize infrequently or quietly) may have a low probability of detection and are often of particular concern because of limited data (Harms and Dinsmore 2014). If survey timing does not coincide with peak detection times for such species, they may appear rare when, in fact, they are simply less detectable when most surveys are conducted (Harms and Dinsmore 2014, Hannah *et al.* 2020, Hedley *et al.* 2020, Jeliaskov *et al.* 2022).

One such species is the Pileated Woodpecker (*Dryocopus pileatus*), a species of conservation concern in Canada. As a primary cavity excavator, the Pileated Woodpecker plays a keystone role in forest ecosystems by creating cavities that are used by species across taxa (Martin and Eadie 1999, Bonar 2000, 2001, Aubry and Raley 2002, Martin *et al.* 2004, Aitken and Martin 2007). Thus, researchers and land managers have emphasized the importance of monitoring this species more effectively (Aubry and Raley 2002, Aitken and Martin 2007, Trzcinski *et al.* 2022). Pileated Woodpeckers use auditory cues to attract mates and establish a breeding territory (Kilham 1959, Tremain *et al.* 2008). The Pileated Woodpecker typically produces two types of auditory cues: calling and drumming (Kilham 1959). Pileated Woodpecker calling has been associated primarily with foraging but is also used to communicate between breeding pairs (Kilham 1959). Drumming is believed to occur primarily during mating displays and territorial defence but may also occur outside of the breeding season (Kilham 1959, Tremain *et al.* 2008). Foraging and excavation may sound like drumming in that the individual strikes a surface with their beak, but these taps do not produce the distinguishable rhythmic pattern of a drum (Kilham 1959). Thus, understanding temporal patterns of different acoustic cues may help inform us when and why Pileated Woodpeckers are using particular land-cover types.

Over the past decade, the use of autonomous recording units (ARUs) has increased (Shonfield and Bayne 2017). ARU sampling occurs at a larger temporal scale (both in frequency and length of the sampling periods) to detect species throughout a much larger part of the day and year than traditional point counts. Little research has been done to evaluate how ARUs might be used to monitor Pileated Woodpecker occurrence and behaviour. As a non-migratory species, it is

well established that you can hear Pileated Woodpeckers at many different times of the year, but whether there are distinct peaks in activity is important to establish. Tremain *et al.* (2008) suggested that Pileated Woodpecker drumming patterns in Florida follow a similar seasonal pattern to that of many passerines, peaking in March. In Oregon, activities associated with breeding (e.g., cavity excavation, mate selection, territory defence) have been observed to begin in March/April (Bull and Meslow 1988). However, due to the extensive latitudinal range of the Pileated Woodpecker, it is necessary to first understand if these patterns differ at the northern edge of the species' range where spring conditions are delayed. Furthermore, it is important to establish if Pileated Woodpeckers demonstrate behavioural patterns like other birds on a daily cycle (i.e., dawn chorus). With such an extensive range, the Pileated Woodpecker experiences a wide array of environmental conditions, so the timing of peak acoustic behaviour may vary considerably geographically (Tremain *et al.* 2008, Bull and Jackson 2020). Thus, evaluating the environmental cues that prompt a species to alter its acoustic behaviour is essential. Whether the Pileated Woodpecker uses photoperiod (Dawson 2008, Da Silva and Kempnaers 2017, Welklin *et al.* 2023), average temperature (Bruni *et al.* 2014, Boelman *et al.* 2017, de Zwaan 2022), snowpack (Boelman *et al.* 2017), or seasonal rainfall (Welklin *et al.* 2023) as cues to begin giving acoustic cues for breeding is unclear. Additionally, it is unknown if Pileated Woodpeckers alter their vocalization behaviour in response to daily changes in weather conditions (de Zwaan *et al.* 2022).

We address these knowledge gaps with the following three objectives:

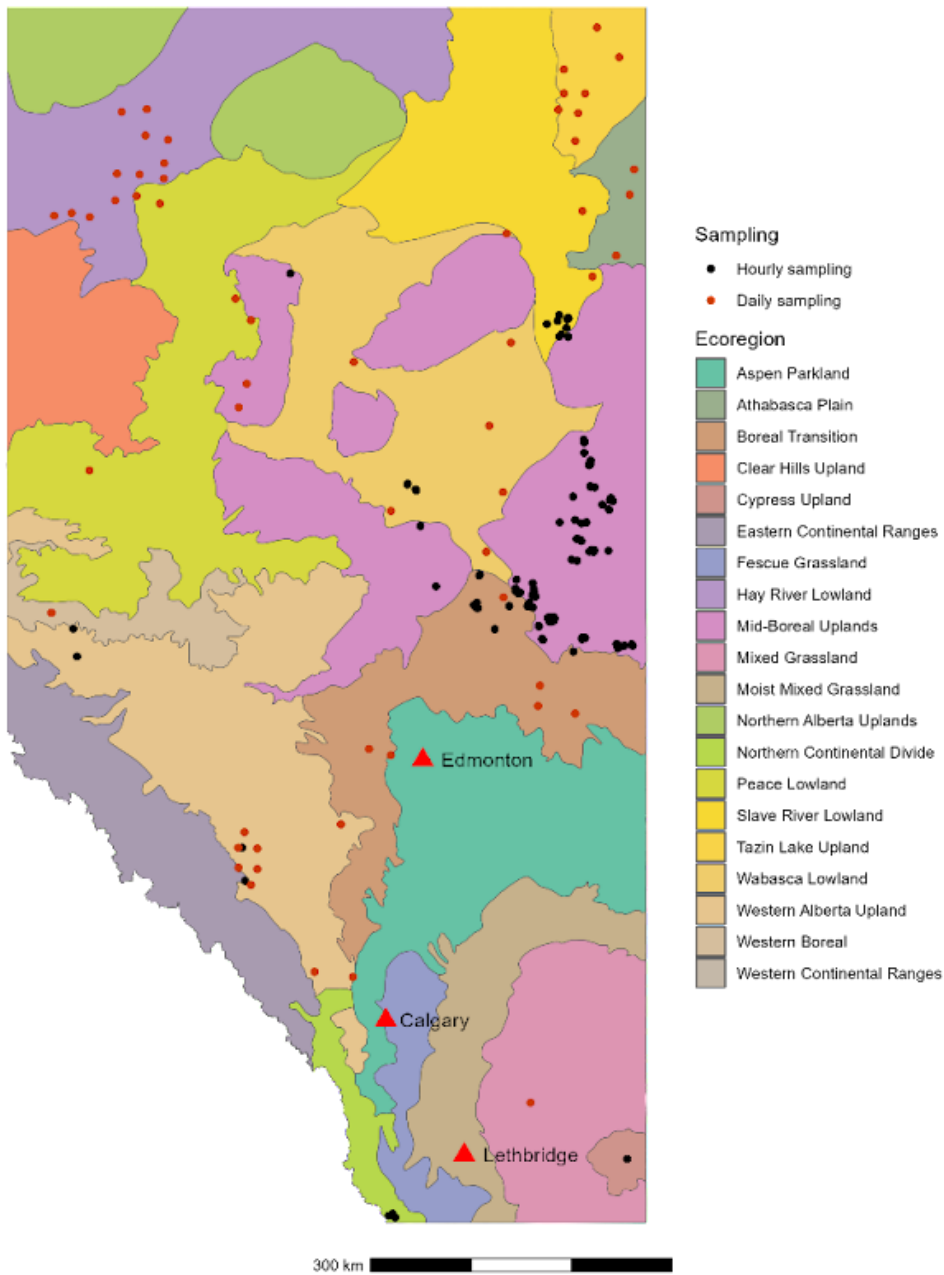
- (1) Evaluate how Pileated Woodpecker drumming behaviour changes on both daily and seasonal scales. To achieve this objective, we evaluated how drumming varies as a function of the hour of the day and day of the year. By doing this, we determined the effort required to detect a Pileated Woodpecker at different times of the day and different days of the year.
- (2) Identify the environmental variables that best predict variation in Pileated Woodpecker drumming behaviour on a seasonal/yearly basis. In doing so, we test if Pileated Woodpecker drumming frequency is best explained by (a) static variables (low interannual variation) like Julian date, day length, and expected mean daily temperature; (b) dynamic variables (strong interannual variation) like mean temperature, snow cover, and days from green up; or (c) a combination of static and dynamic variables.

(3) Explain the degree to which Pileated Woodpecker drumming behaviour is affected by daily variations in weather (i.e., precipitation and deviation from the expected normal mean temperature).

## 2.2 Methods

### *Study Area:*

Our study area includes sites across the western Canadian boreal forest and Rocky Mountains of Alberta, Canada. Upland boreal forest ecosystems in this area are generally made up of jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*; Larsen 1980, Krebs *et al.* 2001). Lowland boreal forests (i.e., muskegs, bogs, or fens) are dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*; Larsen 1980, Krebs *et al.* 2001, Chen and Popadiouk 2002). Areas in the Rocky Mountains and foothills are characterized by more elevational variation and include three distinct ecozones: montane, subalpine, and alpine. We examined locations in the montane ecozone within the Rocky Mountain and foothills regions. The montane ecozone is typically made up of upland pine (lodgepole pine; *Pinus contorta*), spruce (white spruce), or mixed wood (containing spruce/pine and trembling aspen) forests (Habeck 1987).



**Figure 2.1** Map of Alberta, Canada, showing the sites where Pileated Woodpeckers were surveyed. Black dots represent the sites where hourly data was collected and analyzed. Red dots represent sites where data was collected daily, over a seasonal time frame, for the day of year analysis. Black dots represent sites where data was collected hourly for the time-of-day analysis. Major ecoregions of Alberta are displayed (Government of Canada 2016). Red triangles represent major cities.

### *Acoustic Data Collection and Processing:*

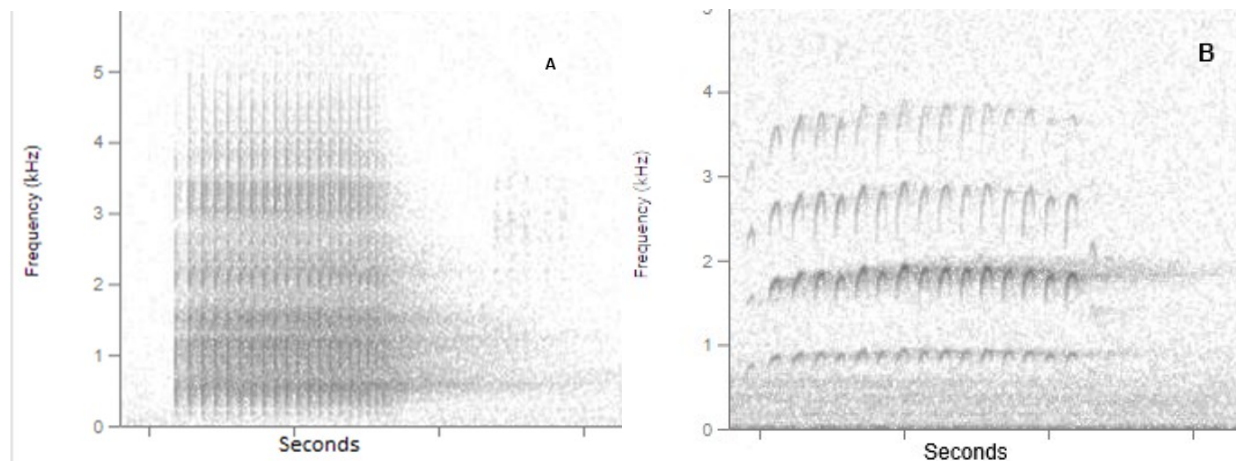
We deployed one ARU (model SM2, SM3, & SM4, Wildlife Acoustics Inc., Maynard, Massachusetts, USA) at each location in Figure 2.1. Each ARU was at least 600 meters from other ARUs at locations where community bird monitoring programs conducted by the Alberta Biodiversity Monitoring Institute (ABMI) previously detected Pileated Woodpeckers. In other words, we selected locations where Pileated Woodpeckers were known to be present.

Sites selected for the seasonal analysis had ARUs deployed in the late winter/early spring (February/March) and were retrieved in July or August. We programmed ARUs to record one-minute recordings around the approximate time of sunrise each day. We sampled these recordings by randomly selecting one recording per site per day. Recordings were all within two hours after sunrise to ensure consistency of the time of day for this subset of data.

We deployed locations for the analysis of daily patterns in late May/ early June and retrieved them within a few days of deployment. The units deployed at these locations had a more frequent recording schedule, recording one minute every half-hour during the morning (~03:00-10:00) and every other hour during the rest of the day. We took a subsample of these recordings to analyze one full day of recordings from each location. One full day included every recording that day (at least 20). We collected these recordings on the second day of the ARUs' deployment. A total of 165 locations were used across both analyses. Once samples were chosen, we uploaded them to WildTrax ([www.wildtrax.ca](http://www.wildtrax.ca)), where processing occurred.

We used two types of acoustic processing methods: visual scanning and manual listening. Within Wildtrax, expert observers tagged target species as they processed each recording using visual (via spectrogram) and auditory cues. Observers visually processed each recording's spectrogram to find the spectral signature of Pileated Woodpecker drumming and calling patterns (Figure 2.2). An observer could confirm correct identification when auditory cues align with the visual identification of the target spectral signatures (Figure 2.2). Observers tagged each instance where they could identify a Pileated Woodpecker and labelled whether it was a call or drum (Figure 2.2). Three observers processed a total of 8,077 one-minute recordings. A single observer verified

all tagged vocalizations to ensure consistency and accuracy among identification. Pileated Woodpecker drumming patterns are approximately 3 seconds long and consist of 10-30 knocks with decreasing amplitude (Kilham 1959; Figure 2.2). Although all types of Pileated Woodpecker auditory cues were identified and tagged, this study focused on the drumming cues due to the low frequency of calling behaviour (only 70 recordings with observations of calling). This study only used locations that recorded Pileated Woodpeckers presence at least once.



**Figure 2.2** Example spectrograms of a Pileated Woodpecker drum (A) and call (B) in Alberta, Canada. The spectrograms were generated from WildTrax ([www.wildtrax.ca](http://www.wildtrax.ca)).

### *Environmental and Ecological Predictor Variables*

We assessed how various ecological and environmental variables influenced Pileated Woodpecker drumming behaviour. Specific variables included: hours from sunrise, day length, mean temperature, normal expected mean temperature, snow cover, days from green-up, precipitation, and deviation from expected normal temperature. A full description of these variables and which analyses they were used for is available in Table 2.1.

We calculated time since sunrise for each recording with the *suncalc* package in the program R (Thieurmel and Elmarhraoui 2022). Sunrise is when the sun crests the horizon, while sunset is when the sun is entirely below the horizon (Thieurmel and Elmarhraoui 2022). Time

since sunrise is the difference between sunrise and recording time in hours. Day length was calculated as the time elapsed between sunrise and sunset.

We downloaded daily mean temperature values for each recording from Wildtrax. Wildtrax extracts weather data from the closest publicly available weather station from Environment and Climate Change Canada. In addition, we determined the normal expected mean temperature from the *weathercan* R package (LaZerte and Alberts 2018). We extracted daily expected normal temperatures from the nearest publicly accessible temperature station for each day of the year. The normal expected mean temperature is calculated by the average of the daily mean temperatures observed for at that weather station for a particular day of year across the years 1981-2010 (LaZerte and Alberts 2018). We calculated the deviation from the expected normal temperature to determine if the weather on that day was hotter or colder than average for that specific time of the year. To do this, we calculated the difference between the daily mean temperature and the normal expected mean temperature. These weather stations also measured daily precipitation (in millimeters).

We extracted snow cover values from the global snow cover dataset produced by Hengl (2021). This dataset uses MODIS imagery to create near-daily composites of snow cover at a 250-meter resolution. The values derived from this dataset represent the fractional snow cover, or the number of pixels determined to be covered by snow at a 1-kilometer resolution. With these data, we determined snow cover (within 1 kilometer) for the nearest available date for each recording.

We derived the green-up date from Friedl *et al.* (2019) for each site location. This dataset uses MODIS imagery to calculate the enhanced vegetation index (EVI) on a temporal frequency of approximately every other day (from 2000- 2020) and a spatial resolution of 500 meters. We determined the days since green-up by calculating the difference between the recording date and the date when EVI first crossed 15% of EVI amplitude (i.e., the green-up date). We calculated green-up dates for each location within a 500-meter buffer based on the year the location was sampled. The 500-meter buffer averages the green-up pixel values within the radius.



**Table 2.1** Predictor variables that describe the relationship between time and Pileated Woodpecker behaviour. Objective indicates the study objective the variable was used to achieve.

<i>Predictor variable</i>	<i>Description</i>	<i>Objective</i>
<i>Julian date</i>	Numeric index for the day of the year. January 1 equates to Julian date 1.	1,2
<i>Hour</i>	Hour of the day (1-24).	1
<i>Hours from sunrise</i>	The number of hours from the time the sun crosses the horizon.	1
<i>Day length</i>	The number of hours the sun position was above the horizon.	2
<i>Mean temperature</i>	Average observed daily temperature gathered from nearby weather station data.	2
<i>Normal expected mean temperature</i>	The expected mean temperature for a given date based on historical temperature data.	2
<i>Snow cover</i>	Estimated average snow cover (% of ground covered within approximately 1 km).	2
<i>Days from green-up</i>	The number of days from the green-up date of that location.	2
<i>Precipitation</i>	Amount of daily precipitation (mm) occurring at the nearest weather station.	3
<i>Deviation from the expected mean temperature</i>	The difference in observed temperature and normal expected temperature.	3

### *Seasonal and Daily Patterns*

We utilized generalized additive mixed effect models (GAMMs) to determine the relationship between temporal variables and Pileated Woodpecker drumming behaviour. These models apply smoothing parameters to relationships, allowing non-linear relationships between predictor and response variables (Pedersen *et al.* 2019). We treated location as a random effect because each observation at a specific location was not independent. Using a circular spline transformation, we fit the smoothing terms used for the variables, hour since sunrise and hour of the day (Pedersen *et al.* 2019). We implemented a circular spline for these models because the values at the beginning and end of the distribution were equally close to the value minus one (i.e., hour 23 is equally close to hour 0 as it is to hour 22). We used a thin-plate spline for the Julian date model (Pedersen *et al.* 2019). These models are further described in Table 2.2. We predicted the peak detection windows from these models by finding the maximum drumming rate. To observe how latitude influenced these relationships, we created additional models that contained an interaction spline (Pederson *et al.* 2019) between the model's main effect variable and latitude. We did not include the interaction in further models if there was no significant relationship between latitude and the corresponding variable. Significant p-values were used to determine how drumming rate could be predicted by time of day, time since sunrise, and day of year (objective 1).

**Table 2.2** The model set used to examine how Pileated Woodpecker (PIWO) drumming patterns change on a seasonal and daily scale. All models are GAMMs, and notation is described in the “mgcv” R package (Wood 2017). The notation “bs” indicates the base spline smoothing function used, “cc” indicates a circular spline and “re” indicates a random effect spline. The default thin-plate spline (“tp”) was used if no base spline was specified.

<i>Model Set 1. Seasonal and Daily Patterns</i>		
<i>Model Input</i>	<i>Variable</i>	<i>Pattern Described</i>
gam(PIWO drum~ s(Julian Date, bs= “cc” )+ s(Location, bs= “re”))	Julian Date	Seasonal
gam(PIWO drum~ s(Hour, bs= “cc”)+ s(Location, bs= “re”))	Hour	Daily
gam(PIWO drum~ s(Time Since Sunrise, bs= “cc”)+ s(Location, bs= “re”))	Time Since Sunrise	Daily

*Surveys until detection confidence calculation*

A key question in monitoring is how much effort is needed to demonstrate whether a species is present or absent from a location. Thus, we calculated the detection probability for Pileated Woodpeckers. Detection probability is the likelihood of observing an individual during a survey and can be calculated by  $\frac{\# \text{ of observations}}{\text{survey effort}}$ .

We used Equation 2.1 to estimate how many surveys ( $x$ ) were required to obtain high confidence (90%  $d=0.1$  and 99%  $d=0.01$ ) if a Pileated Woodpecker was not detected at a site that the species would not use that site over the course of the breeding season. We calculated the probability of detection and the number of surveys for the peak detection intervals for the hour of the day, hour from sunrise, and Julian date. Additionally, we conducted these calculations for the standard BBS survey periods in June.

**Equation 2.1** Sliwinski *et al.* (2015) estimated the number of surveys required ( $x$ ) to obtain a given confidence level ( $d$ ) to detect a Pileated Woodpecker during the breeding season if an individual occupied the site.  $P$  represents the probability of detecting a Pileated Woodpecker within the peak detection times.

$$\text{Equation 2.1: } x \geq \ln(d) * \ln(1 - P) - 1$$

### *Variables influencing acoustic behaviour*

We created six GAMMs (Table 2.3), containing one predictor variable, as well as the random effect of location. We used these GAMMs to evaluate what environmental variables best predicted variation in Pileated Woodpecker drumming. We used the Akaike information criterion (AIC) score to select the model that best explained the data using these univariable models. From this comparison, we determined the most influential static versus dynamic variables that affected Pileated Woodpecker drumming behaviour on seasonal/yearly scales. Based on p-values, we determined that static variables that were important predictors of drumming were Julian date, day length, and normal expected mean temperature. The significant dynamic variables were mean temperature, snow cover, and days from green up. These variables are expected to shift yearly based on local conditions. To test the importance of static versus dynamic variables, we determined which static and which dynamic variable best explained variation in drumming behaviour via AIC comparisons of the univariable GAMMs (Table 2.3). Then we compared AIC scores of multivariable models which included the best static variable and the best dynamic variable. Ridge regression models were considered in the case of collinearity between the best static and dynamic variable. A correlation matrix can be found in the Appendix. Results generated via ridge regression and multivariable GAMMs were not noticeably different; therefore, the GAMMs were used for consistency and simplicity in analysis. The results of the ridge regression analysis can be found in the Appendix.

**Table 2.3** The model set used to examine what environmental factors drive Pileated Woodpecker (PIWO) drumming patterns to change over a seasonal scale. All models are GAMMs, and notation is described in the “mgcv” R package (Wood 2017). The notation “bs” indicates the base spline in which the smoothing function should be used, “cc” is a type of circular spline and “re” indicates a random effect spline. A thin-plate spline (“tp”) is used if no base spline is specified.

<i>Model Set 2. Ecological Mechanisms</i>	
<i>Model Input</i>	<i>Variable</i>
gam(PIWO drum~ s(Julian Date, bs= “cc” )+ s(Location, bs= “re”))	Julian Date
gam(PIWO drum~ s(Day length)+ s(Location, bs= “re”))	Day length
gam(PIWO drum~ s(Mean Temperature)+ s(Location, bs= “re”))	Daily Mean Temperature
gam(PIWO drum~ s(Normal Temperature)+ s(Location, bs= “re”))	Daily Normal Expected Mean Temperature
gam(PIWO drum~ s(Snow Cover)+ s(Location, bs= “re”))	Snow Cover
gam(PIWO drum~ s(Days from Green-up)+ s(Location, bs= “re”))	Days from Green-up

### *The Effects of Daily Variation in Weather*

To determine the effects of daily variations in weather (objective 3), we created two generalized linear mixed models, including location as a random effect (Table 2.4). One model contained the predictor variable of deviation from the normal expected mean temperature, while

the other contained precipitation (Table 2.4). We evaluated the p-values from this generalized linear mixed model to determine if these weather variables influence Pileated Woodpecker drumming behaviour. Additionally, we compared AIC values to a null model to further investigate how these models performed. For this analysis, we used generalized linear models because we were not as concerned with model fit as we were in the previous analyses. Rather, we were more interested in detecting a signal (i.e., if the variables influenced drumming behaviour). We fit these models following the binomial distribution.

**Table 2.4** The model set of generalized linear models used to examine how daily variations in weather affect Pileated Woodpecker drumming patterns.

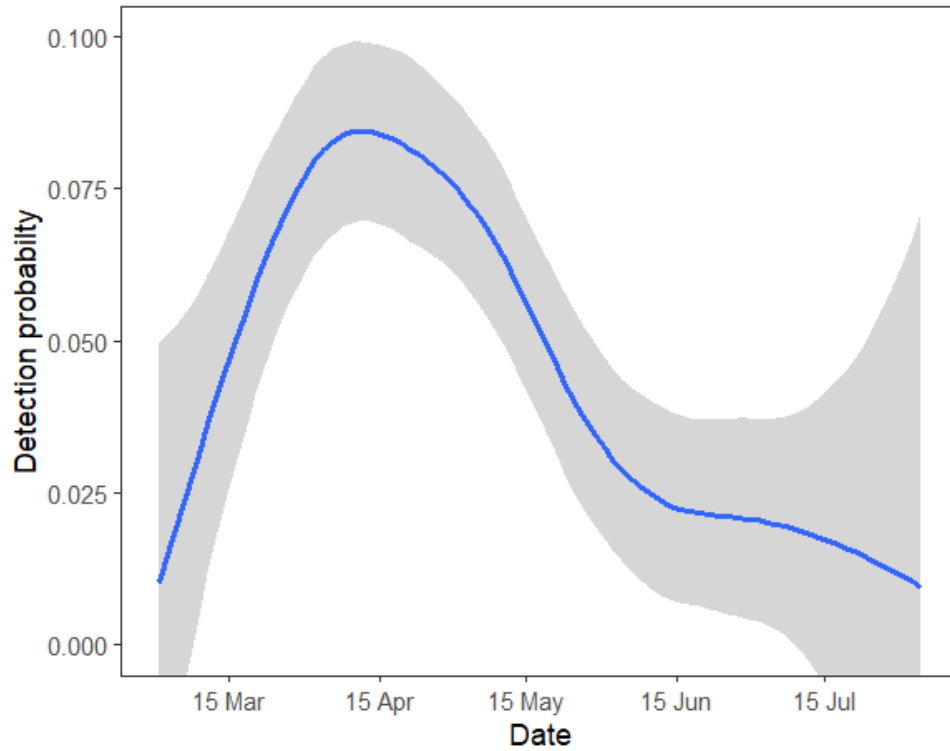
<i>Model Set 3. Daily Variation Effects</i>	
<i>Model Input</i>	<i>Variable</i>
$\beta_{\text{Normal Temperature Deviation}} + \epsilon_{\text{Location}}$	Deviation from Normal Expected Mean Temperature
$\beta_{\text{Precipitation}} + \epsilon_{\text{Location}}$	Precipitation

## 2.3 Results

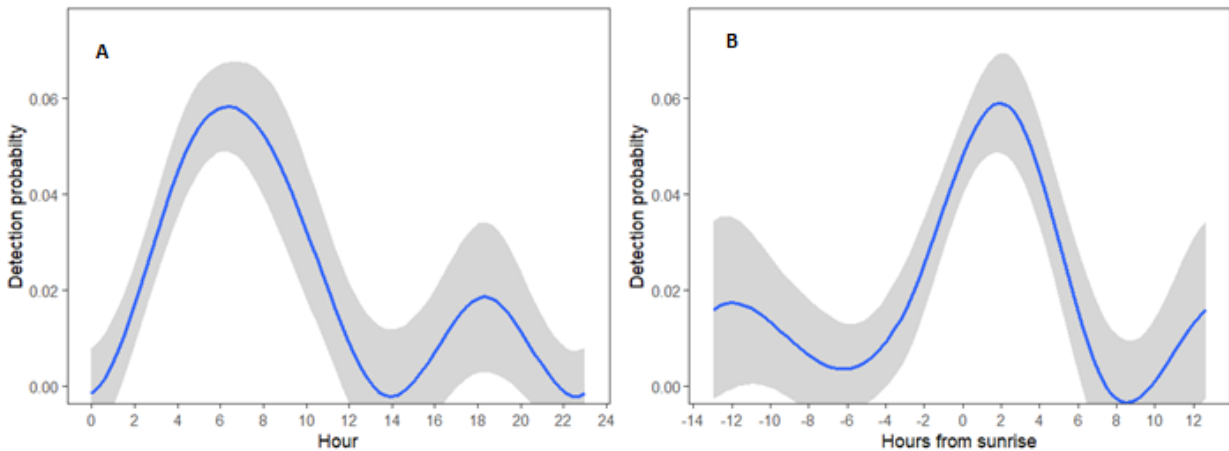
We identified a total of 133 acoustic recordings that contained a Pileated Woodpecker drum during our time-of-year sampling across 42 locations. Across our time-of-year sampling design we detected a Pileated Woodpecker between 1-14 times at a site. In the time-of-day sampling, we identified 116 acoustic recordings with a Pileated Woodpecker drum across 68 locations. Across our time-of-day sampling design we detected a Pileated Woodpecker between 1-4 times at a site. Locations where Pileated Woodpeckers were not observed in this study were either sites where Pileated Woodpeckers had been observed in a previous year or locations outside of our sampling period. We found a significant relationship between the day of the year (Julian date) and Pileated Woodpecker drumming ( $p < 0.05$ ) (Figure 2.3). Both the hour from sunrise and the hour of the day ( $p < 0.05$ ) significantly affected Pileated Woodpecker drumming behaviour ( $p < 0.05$ ) (Figure 2.4).

Peak detection of Pileated Woodpecker drums occurred on April 2 (Julian date 92) (Figure 2.3) and during hours 06:00 or 1 hour since sunrise (Figure 2.4). The probability of detecting a Pileated Woodpecker drum on April 2 was approximately 9.00% (Figure 2.3). The probability of detecting a Pileated Woodpecker drum at hour 06:00 was 7.76%. The probability of detecting a Pileated Woodpecker drum 1 hour since sunrise was 7.01% (based on an average day of the year in the data set, June 4). There was no significant effect of an interaction with latitude on Pileated Woodpecker drumming, so we did not include this interaction in the models described below.

With these estimated probabilities, we calculated the number of on-minute surveys required to be 90% and 99% confident that a Pileated Woodpecker would or would not use a site. During the peak detection window of April 2, we calculated that a minimum of 22 one-minute surveys were required for 90% confidence and 239 surveys for 99% confidence that a Pileated Woodpecker would or would not use a location. For the peak detection window of 06:00 AM, we calculated a minimum of 25 surveys for 90% confidence and 264 surveys for 99% confidence to ensure that a Pileated Woodpecker is not using a particular location. By combining peak detection dates (+/-5 days) and hours (+/- 2 hours), we obtained a detection probability of ~20%. At this detection probability, we calculated a minimum of 10 one-minute surveys at 90% confidence and 20 one-minute surveys at 99% confidence are required to ensure that you can be confident that a Pileated Woodpecker is or is not using a particular location. Approximately 32 one-minute surveys are required during typical BBS survey timings (near sunrise in June) to obtain a 90% confidence, or 334 one-minute surveys at 99% confidence.



**Figure 2.3** The predicted probability of detecting a Pileated Woodpecker drum on a seasonal scale. Predictions generated from the generalized additive model are described in Table 2. The shaded area represents the standard error.



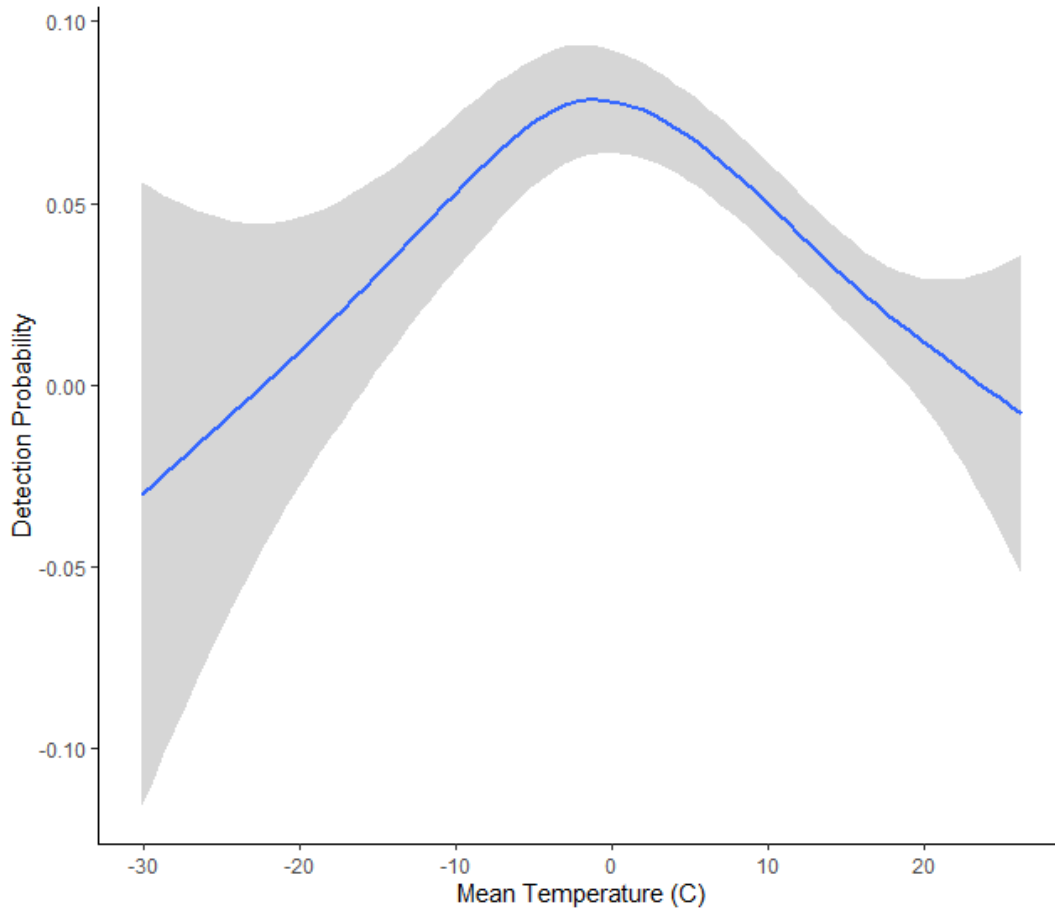
**Figure 2.4** The predicted probability of detecting a Pileated Woodpecker drum based on a diel scale (hour of the day) (A) and hours since sunrise (B). Predictions generated from a generalized additive model are described in Table 2.2. The shaded area represents the standard error.



All models that contained environmental variables were significant and explained more variation in the data than the null model (Table 2.5). The models that explained the most variation in seasonal Pileated Woodpecker drum detection were the mean observed temperature (dynamic variable) and Julian date (static variable) (Table 2.5). The model, which contained the static variable day length, also explained a comparable amount of variation to the Julian date model (<1 AIC score difference; Table 2.5). Therefore, both the Julian date and day length variables were used to test the static and dynamic variable hypotheses (Table 2.6). The snow cover model explained the least variation (Table 2.5). Peak drum detection occurred at approximately 0°C (Figure 2.5).

**Table 2.5** Model results and Akaike information criterion (AIC) scores for models describing the relationship between Pileated Woodpecker drumming and seasonal predictor variables. Models were produced through a generalized additive mixed effect model, including location as a random effect.

<b>Seasonal predictor model</b>	<b>p-value</b>	<b>Effective degrees of freedom</b>	<b>Degrees of freedom</b>	<b>AIC</b>
NULL	N/A	18.82	19.81	1061.26
Julian date	<0.005	4.19	24.74	1024.55
Day length	<0.005	3.21	26.15	1025.01
Mean temperature	<0.005	4.06	24.42	1018.62
Normal expected mean temperature	<0.005	3.68	22.49	1030.29
Snow cover	<0.005	1.11	24.531	1036.73
Days from green up	<0.005	2.61	22.285	1036.55



**Figure 2.5** Relationship of mean temperature and Pileated Woodpecker drumming detection probability as estimated by the smoothing term generated in the GAMM. The shaded area represents the bounds of the 95% confidence intervals.

The multivariate GAMM containing day length and mean temperature explained the most variation via AIC scores (Table 2.6). Both multivariable models outperformed single variable GAMMs described in Table 2.5. All variables within the multivariable models were described nonlinearly (effective degrees of freedom >1; Table 2.6).

**Table 2.6** Model results for multivariate GAMMs that include the most predictive static (Julian date and day length) and dynamic (mean temperature) interannual environmental variables.

<b>Model</b>	<b>Variable</b>	<b>Effective degrees of freedom</b>	<b>p-value</b>	<b>AIC</b>
<i>Julian date + mean temperature</i>	Julian date	2.96	0.015	1012.92
	Mean temperature	3.76	0.037	
<i>Day length + mean temperature</i>	Day length	2.61	0.014	1010.06
	Mean temperature	2.83	0.003	

Results from the generalized linear mixed effects model with location as a random effect found failed to find a significant relationship with daily precipitation ( $p = 0.650$ ) on Pileated Woodpecker drumming (Table 2.7). However, we did identify a significant relationship of the deviation from the normal expected mean temperature ( $p = 0.021$ ; Table 2.7). Furthermore, the model containing daily precipitation did not explain more variation than the null model. However, the model containing the deviation from normal expected temperature did explain more variation than the null model. The beta coefficient for the deviation from the normal expected mean temperature model demonstrated a positive relationship with Pileated Woodpecker drumming (Table 2.7).

**Table 2.7** Table showing the results of the generalized mixed effects models describing the relationship between Pileated Woodpecker drumming behaviour and daily fluctuations in weather described by the model variable.

<b>Model Variable</b>	<b>Beta coefficient</b>	<b>p-value</b>	<b>AIC</b>
NULL	N/A	N/A	1130.32
Precipitation	-0.013	0.650	1132.10
Deviation from the normal expected mean temperature	0.037	0.021	1127.03

## 2.4 Discussion

Our results not only provide baseline information for Pileated Woodpecker ecology, in terms of behavioural timings and environmental influences on behaviour, but also provide guidelines for optimizing detection in Pileated Woodpecker surveys. We demonstrated how best to use existing non-optimized surveys to obtain a high confidence in the accuracy of Pileated Woodpecker habitat use.

The observed pattern of seasonal drumming variation of the Pileated Woodpecker supports the idea that Pileated Woodpeckers use drumming to attract mates (Kilham 1959). Similar relationships are supported by Tremian *et al.* (2008), who demonstrated a seasonal relationship between Floridian Pileated Woodpeckers' drumming and calling behaviours with drumming peaks in late March. However, Pileated Woodpecker drumming occurred throughout our sampling period, suggesting that the species also use drumming for purposes unrelated to mate attraction or breeding.

We found that the peak drumming occurred on April 6 in the boreal forest at the northern edge of the species' range. This peak drumming timing differs between Florida and Alberta, suggesting that latitudinal variation and potentially different cues may trigger changes in Pileated Woodpecker drumming behaviour. These results provide key information to optimize survey timing for future Pileated Woodpecker surveys. However, we did not demonstrate latitudinal

effects in our study. This could be due to our study's relatively small extent compared to the global range of the Pileated Woodpecker. It is likely that data from across the species' range would be required to observe this latitudinal effect on Pileated Woodpecker drumming patterns.

We also found a relationship between Pileated Woodpecker drumming and time of day. We observed that Pileated Woodpeckers were more likely detected by drumming during the morning, around sunrise. Most songbird species follow a similar daily pattern to what we observed with Pileated Woodpecker drums (Kacelnik and Krebs 1983, Stacier *et al.* 1996, Bruni *et al.* 2014), suggesting that the woodpecker drum is analogous to birdsong. Additionally, we observed a secondary peak in drumming activity near dusk; many avian species demonstrate a similar pattern of crepuscular activity (Catchpole and Slater 1995, Stacier *et al.* 1996, Hannah *et al.* 2020). A possible explanation for this change in drumming activity is that the sunlight, visibility, and temperature in midday hours may be more conducive for activities such as foraging. The Pileated Woodpecker specializes in consuming ectotherm invertebrates, mainly carpenter ants (McClelland and McClelland 1999), which rely on temperature for mobility. Therefore, the more active the carpenter ants are, the more likely Pileated Woodpeckers may be successful in hunting and capturing their prey.

Our findings suggest that standard BBS procedures focused in June do not adequately capture the peak detection windows for Pileated Woodpeckers. During typical BBS timings (near sunrise in June), a minimum of 32 surveys should be conducted to obtain high confidence about Pileated Woodpecker use of a site. This survey requirement is rarely met due to the BBS protocol's design and temporal constraints (Ziolkowski *et al.* 2023). However, this guideline will be helpful for other projects that follow similar protocols to the BBS and have repeat surveys at a single site (e.g., ABMI). The optimal daily timing of Pileated Woodpecker drums occurs simultaneously with typical songbirds (Kacelnik and Krebs 1983, Stacier *et al.* 1996, Bruni *et al.* 2014). Therefore, the daily timing of BBS surveys maximizes the likelihood of detecting a Pileated Woodpecker drum. We recommend that surveys of Pileated Woodpeckers in Alberta, Canada (or locales within similar latitudinal/environmental boundaries) begin in the first week of April to ensure the greatest likelihood of detection. It is most beneficial to focus sampling near sunrise to increase the likelihood of detecting Pileated Woodpeckers. Specifically, one hour from sunrise is the optimal time for detecting Pileated Woodpecker drums. Combining the seasonal and daily optima requires

at least ten 1-minute recordings to ensure with 90% confidence that the Pileated Woodpecker is or is not using a location. A caveat of this recommendation is that the Pileated Woodpecker may not be using a particular location on a given day, so distributing these recordings across multiple days will increase the probability of detecting the species. Additionally, we emphasize that these survey requirements are a minimum requirement. Because we calculated our detection probability only from sites where we observed Pileated Woodpeckers, we established the ‘best case’ for Pileated Woodpecker survey requirements based off locations where we established their presence.

These recommendations highlight the utility of ARUs for sampling Pileated Woodpeckers. It is costly in terms of time and money to send human observers to a single location upwards of ten times to conduct point count surveys. ARUs allow researchers the ability to survey a site numerous times and technicians only need to access a site twice, once on deployment and once on retrieval of the ARU. In this study we essentially established optimal ARU deployment/retrieval timings (day of year) and optimal ARU recording schedule timings (time of day) for Pileated Woodpecker surveys.

Although there is significant variation in Pileated Woodpecker seasonal drumming detection, it is important to note that we were able to detect drums throughout the sampling period. Financial and institutional constraints, along with more inclement weather in many parts of the world, make sampling difficult during March/April. Challenging weather conditions can often result in suboptimal sampling via reduced ability for observers to hear or see their surroundings. How often poor weather influences the ability to detect Pileated Woodpeckers in March/April should be compared to May/June.

The single-variable model mean temperature explained the most variation in the seasonal detection of Pileated Woodpecker drums, suggesting that the initiation of the Pileated Woodpecker breeding season is linked to conditions that may change yearly. This finding suggests that this species may be more flexible to changes in phenology caused by climate change (Stenseth *et al.* 2002, Visser *et al.* 2012, Samplonius *et al.* 2018). However, as we further investigated this relationship, we discovered that static variables such as Julian date and day length, in addition, to mean temperature, better explain variation in seasonal Pileated Woodpecker drumming patterns. This suggests that Pileated Woodpeckers are both hard-wired to begin breeding behaviours

(increased frequency of drumming) based on a combination of the local environmental conditions and the static patterns of seasonal change. These relationships are nonlinear in nature which suggests Pileated Woodpeckers prefer conditions that are not too late in the season and not too hot or cold temperature for drumming. We observed that the peak detection of Pileated Woodpecker drums occurred when the daily mean temperature was approximately 0 °C, and detection was highest in April. It is probable that the early onset of warmer conditions (above freezing) may be more conducive for Pileated Woodpecker drumming.

Since Pileated Woodpeckers utilize dynamic environmental variables such as the observed temperature as a cue to start breeding, they are less at risk of initiating nesting during unfavourable breeding conditions. Food availability is a limiting factor in reproductive success and survival for all birds. The timing of peak invertebrate egg hatching, and therefore prey abundance, is often linked to temperature (Powell and Logan 2005, Dunn *et al.* 2011, Nadolski *et al.* 2021). Thus, warmer spring temperatures could create a timing or phenological mismatch between invertebrate phenology and avian nest initiation. The combination of static and dynamic interannual variables which influence Pileated Woodpecker drumming suggests that this species may be less susceptible to phenological mismatches created by climatic change than migratory species. Although, additional research should examine how Pileated Woodpeckers react if the optimal conditions are not met. Additionally, limited research has been conducted on the seasonality of the Pileated Woodpecker's primary food source, carpenter ants (McClelland and McClelland 1999, Powell and Logan 2005, Bull and Jackson 2020). We suggest further research to investigate the environmental triggers influencing carpenter ant egg hatch timing and whether these factors correlate with drumming frequency or nest initiation. Additionally, it is important to note that all the environmental variables explored in this analysis (mean temperature, normal expected mean temperature, snow cover, and days from green up) proved to influence the Pileated Woodpecker drumming. Therefore, it is likely multiple static and dynamic interannual variables could influence Pileated Woodpecker behaviour.

We found a relationship between the deviation from the expected normal temperature and Pileated Woodpecker drums, suggesting that the daily weather can influence Pileated Woodpecker drumming behaviour. This result further supports our findings that temperature influences the seasonal/interannual variation in drumming. The positive relationship observed suggests that

Pileated Woodpeckers are more likely to drum on warmer than average days. Furthermore, we found no relationship with precipitation. However, weather is often variable across the landscape. Weather stations used in this study were occasionally >10 kilometers from the site, and even stations as close as 1 kilometer away from the survey site may not accurately represent the local weather conditions.

Prior to this study, there had been no formal attempt to standardize acoustic sampling for Pileated Woodpeckers in Alberta. Current survey standards employ data collection during the songbird breeding season, but our results demonstrate that Pileated Woodpecker drumming activity and detection are non-optimal during this period. Modeling attempts using this sub-optimal period may only partially capture how the species uses the landscape, especially for breeding purposes. We recommend that future modeling and survey efforts for Pileated Woodpeckers in Alberta be focused during the optimal periods of March/April. From our calculated detection probabilities, land managers can reliably assess whether potential suitable Pileated Woodpecker habitat occurs within their operating areas. This is increasingly important for land managers due to regulations put in place by the Government of Canada's Section 70 of the Migratory Birds Regulations (2022), stating that Pileated Woodpecker nesting cavities may not be disturbed for 36 months after being deemed unoccupied. This regulation affects industries such as the forestry and energy sectors, which are prevalent in Alberta and have competing interests with the Pileated Woodpecker's associated habitats of old-growth forests (Bull and Holthausen 1993, McClelland and McClelland 1999, Aubry and Raley 2002, Hartwig *et al.* 2004, Kremetz *et al.* 2012). Following this study's temporal survey guidelines and minimum survey effort requirements, these industries can adequately detect a Pileated Woodpecker and make informed adjustments when operating.



# **3. Chapter 3. Pileated Woodpecker habitat use in the boreal forest of Alberta: The relative importance of response variables, land cover, and scale**

## **3.1 Introduction**

The study of species distribution and habitat preference is fundamental to understanding ecology and informing conservation and management strategies. Traditional species occupancy models (MacKenzie *et al.* 2002, 2006) have become a common tool to provide insights into the relationships between species and their habitats. Occupancy modeling advanced species-habitat modeling by accounting for detection error. Detection error is the probability that a species is present at a location but not observed by the researcher during the observation period. This modeling approach provides many benefits, such as the simplicity of data collection and the ability to give an absolute estimate of the proportion of locations where a species is present. However, population closure is a critical assumption of traditional occupancy models. Thus, occupancy may misinform our understanding of habitat use patterns if animals move in and out of the sampling area. Because mobile wildlife species typically violate the closure assumption, the interpretation of occupancy shifts from an absolute probability of a site being occupied to a probability of observing the species at least once throughout the survey or study period (Otto *et al.* 2013, Hayes and Monfils 2015). Various approaches have been developed to correct violations of the closure assumption through modified study designs or adjustments to the temporal resolution at which detection rates are estimated (Otto *et al.* 2013, Hayes and Monfils 2015, DiRenzo *et al.* 2022).

Sedentary species or species with small home ranges can more easily meet the closure assumption than large-ranging species due to their lack of extensive movement. How temporary migration, where individuals leave or enter the sampling area, is affected by environmental conditions that change throughout the survey period is an important part of understanding habitat preference. Environmental variables like temperature can affect species' activity levels, and

predator abundance or presence can affect species' movement patterns (Cuddington and Yodzis 2004, Berger-Tal and Bar-David 2015). Such patterns cause mobile species to occupy habitats of various qualities at any given time and for different durations. As occupancy requires only a single detection to determine use, this can lead to an inflation of the perceived importance of habitat quality that is less preferred. Snell Taylor *et al.* (2021) demonstrated how different measures of temporal occupancy (proportion of years where researchers observed a species at the same location) improved species distribution models relative to traditional occupancy models based on a single year of data. Temporal occupancy gives greater weight to sites visited more regularly. Whether temporal occupancy provides a better estimation of habitat importance or preference than traditional occupancy models warrant further study as a result.

Like temporal occupancy, remote camera analysis has developed the response metric of intensity of use as an alternative to occupancy (Keim *et al.* 2019). The intensity of use is the number of use events (when the target species triggers a camera trap photo) occurring over a sampling period (Keim *et al.* 2019). The same concept can be applied to acoustic data collected by autonomous recording units (ARUs). However, ARUs are subject to detection error when animals are present but not vocalizing. When applied to acoustic data, intensity of use is typically used to assess if the detection rate influences standard occupancy estimates. In an occupancy model where the closure assumptions are met, a change in detection rate as a function of environmental variables means that auditory cues are less/more frequent in particular habitats or that sound travels a shorter/longer distance. However, when animals move in and out of the sampling area, there are two processes at play: imperfect detection and movement. Ideally, we would separate these processes, but even if separation is impossible, evaluating how the importance of habitat variables changes depending on whether you model them in an occupancy versus intensity of use context is crucial. The intensity of use at an ARU site may increase with more sampling, while occupancy rates may plateau after relatively few surveys and remain static. Thus, evaluating both occupancy and intensity of use is essential for understanding habitat preference or importance for a species, especially those with home ranges larger than the sampling area as movement within the home range will likely violate the closure assumption of standard occupancy.

While the estimation of occupancy/intensity of use is often debated as the most influential factor influencing species-habitat model accuracy, variation in habitat covariates can cause

discrepancies in estimating species-habitat relationships. Land cover data, primarily from satellite imagery, are often modelled as if they are the truth. However, there is often considerable variation in the same variable measured using different satellites or created using different processing methods (Barry and Elith 2006, Hedley *et al.* 2020). Error in habitat covariate values can lead to changes in the beta coefficients and, thus, the relative importance of habitat variables in models (Barry and Elith 2006). With imperfect information relating to habitat conditions, evaluating which products are most reliable is important. Thus, we explored how differences in the variables affect the overall model outputs. In doing so, we assessed whether there was a difference in the modeling outputs using one measurement versus another.

In addition to the data source of landscape variables, the scale at which the land cover data is extracted can influence model output (Savignac *et al.* 2000, Mayor *et al.* 2009, Baumgardt *et al.* 2014, DiRenzo *et al.* 2022). With the improvement of remote sensing technology, researchers have access to high-resolution land cover data. However, higher resolution land cover data may not necessarily improve modeling attempts for many species, primarily if the species responds to larger landscape-level changes or features that fine-resolution land cover data may not capture. A standard method to solve this issue is to apply a buffer around a given point, averaging the surrounding pixels and increasing extent. There is no silver bullet for the correct resolution to assess species-habitat relationships, as they are dependent on species and habitat attributes (McGarigal *et al.* 2016). Species-habitat relationships do not necessarily translate across spatial scales, creating challenges in species distribution modeling (Mayor *et al.* 2009). To improve these models, assessing species-habitat relationships across multiple scales is needed to provide insight into the ecological processes driving species' distributions across a landscape (McGarigal *et al.* 2016, Hallman and Robinson 2020).

The Pileated Woodpecker (*Dryocopus pileatus*) is a suitable study species for testing how different response measures, remote sensing layers, and scales influence species-habitat models. They are a large-bodied species that regularly violate the closure assumption due to their extensive home range size (Mellen *et al.* 1992). Home range size estimates for Pileated Woodpeckers are 250-1,500 hectares (Renken and Wiggers 1989, Mellen *et al.* 1992, Bull and Holthausen 1993, Bonar 2001). Pileated Woodpeckers use various habitat types to meet their life requisites across their home range. For example, Pileated Woodpeckers require (1) large trees for nesting and

roosting (Bull *et al.* 1992, McClelland and McClelland 1999, Hartwig *et al.* 2004, Tomasevic and Marzluff 2020), (2) foraging sites containing carpenter ants or bark beetles (McClelland and McClelland 1999, Raley and Aubry 2010), and (3) drumming posts (places in which a woodpecker repeatedly visits to establish territory and attract mates) located on specific trees (e.g., typically dead trees with a particular sound resonance) and in specific locations within their home range (e.g., typically near the boundary) (Lawrence 1967, Tomasevic and Marzluff 2018). Areas in which Pileated Woodpeckers conduct these activities are not contained within a single area. In our study area, current habitat models using an occupancy model framework explained limited variation in ecological relationships for the Pileated Woodpecker despite over ten years of data (Alberta Biodiversity Monitoring Institute 2019). Two possible explanations for this outcome are that (1) current surveys do not sample at optimal time periods to detect most Pileated Woodpeckers (Chapter 2) or (2) current modeling frameworks that emphasize presence over intensity of use may misrepresent the actual use of key resources.

The need to improve existing habitat models for this species is needed to meet conservation and management objectives. Pileated Woodpeckers are often referred to as ecosystem engineers due to their role as excavators of the largest tree cavities in North America (Martin and Eadie 1999, Bonar 2000, 2001 Aubry and Raley 2002, Hartwig *et al.* 2004). Ecosystem engineers are vital to ecosystems as they provide crucial structural modifications to their habitat which has a cascading effect throughout the ecosystem. Many species across taxa (e.g., waterbirds, bats, rodents, weasels and owls) rely on the cavities excavated by Pileated Woodpeckers for different life stages, including nesting and roosting (Bull *et al.* 1992, Bonar 2000, 2001, Aubry and Raley 2002). As the largest extant woodpecker in North America, the Pileated Woodpecker is vital to a variety of ecosystems, including western temperate coastal forests (Hartwig *et al.* 2004), the boreal forest (Bonar 2000), interior mixed wood forests (Martin *et al.* 2004), southern United States pine forests (Saenz *et al.* 1998), southeastern United States bottomland hardwood forests (Krementz *et al.* 2012), forested Floridian wetlands (Leonard and Stout 2006), and many more. Furthermore, in 2022, the Government of Canada highlighted the importance of Pileated Woodpecker nest cavities, protecting them for up to three years after they are deemed vacated (Government of Canada 2022). This legislation creates several challenges in mature forests containing large-diameter trees that provide crucial habitat for Pileated Woodpeckers because they are also high-value forest types for

harvesting (Savignac *et al.* 2000, Bonar 2001, Hartwig *et al.* 2004, Hu and Tong 2022). Therefore, it is a top priority for industries such as the forestry and the energy sectors that operate in the boreal forest to identify areas where Pileated Woodpeckers are more likely to create nesting cavities.

This study investigated the influence of occupancy and intensity of use, different land cover datasets, and spatial scale on the variables incorporated into habitat models for the Pileated Woodpecker in forested areas of Alberta, Canada. In doing so, we explored the following objectives:

- (1) Determine the most important habitat variables for characterizing Pileated Woodpecker response variables (occupancy and intensity of use) and compare model results generated from these metrics.
- (2) Evaluate how differences across land cover data sources affect the predictive accuracy of the occupancy and intensity of use models.
- (3) Assess how the scale at which land cover data is extracted and summarized affects the predictive accuracy of the occupancy and intensity of use models, thereby assessing the scale in which Pileated Woodpeckers respond to environmental characteristics.

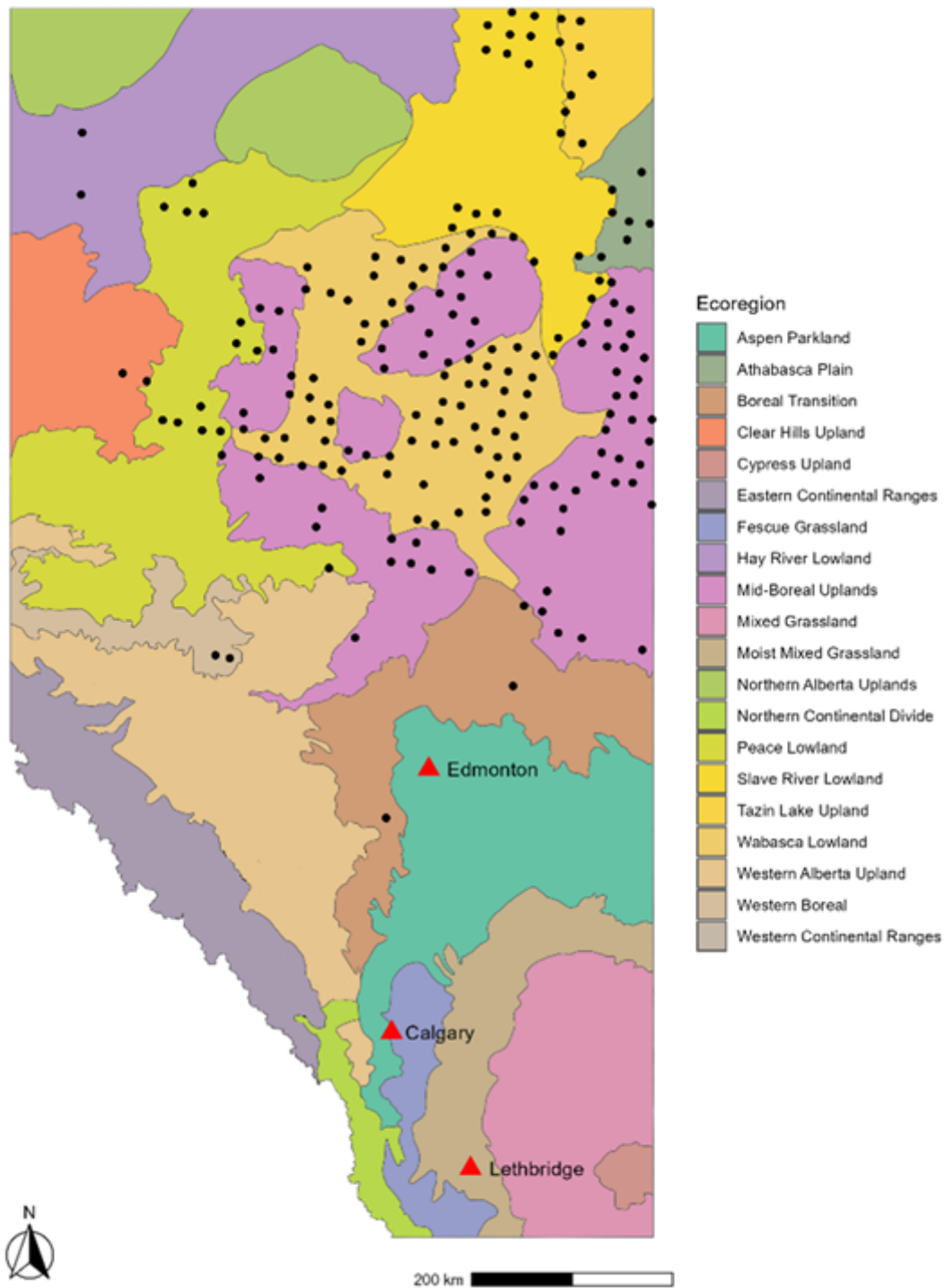
By achieving these objectives, we created a set of guidelines that demonstrate the most effective way to measure, model, and evaluate how Pileated Woodpeckers use the landscape.

## 3.2 Methods

### *Site selection*

The Alberta Biodiversity Monitoring Institute's (ABMI) maintains a province-wide systematic grid known as the Ecosystem Health Program. The grid consists of over 1,000 sites, separated by 20 km each. From the +1,000 ABMI locations, we selected sites within the boreal forest ecosystem with at least 60% tree cover within a 565-meter radius of the site, according to Beaudoin *et al.* (2017). This left us with 258 sites for the current study. One ARU was deployed at each site to record audio from March to July. We scheduled ARUs to record audio at set time

intervals each day. From each ARU, 15 one-minute recordings from the first week of April and within a window of 3 hours from sunrise were randomly selected. As described in Chapter 2, we calculated *a priori* how many recordings were needed to ensure greater than 90% confidence that a Pileated Woodpecker did not use that location within the desired time frame (during the first week of April within two hours from sunrise). In so doing, we can be more confident that we observed all the locations where Pileated Woodpecker occurred. The recordings were uploaded to the open data platform WildTrax ([www.wildtrax.ca](http://www.wildtrax.ca)).



**Figure 3.1** The study area of Alberta, Canada. Black dots represent the approximate locations of deployed ARUs. Ecoregions, as defined by the Government of Canada (2016), are denoted by colour. Red triangles represent major cities.

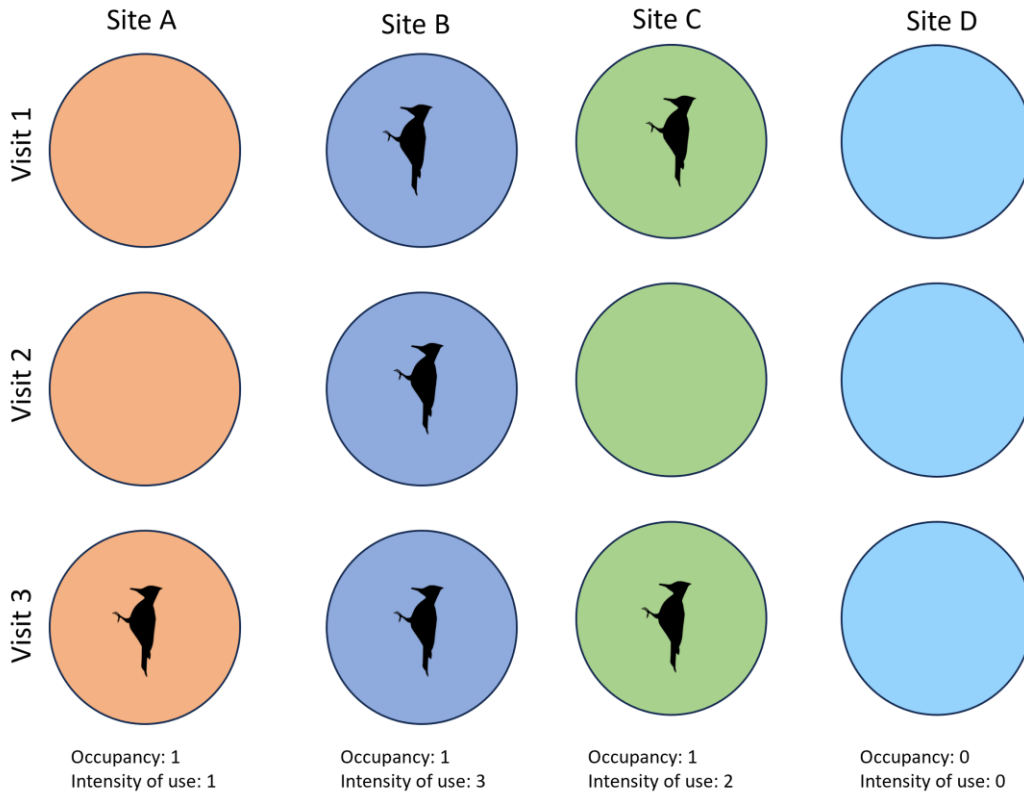
### *Data processing*

In Wildtrax ([www.wildtrax.ca](http://www.wildtrax.ca)), spectrograms were produced, and expert observers used visual scanning to identify a Pileated Woodpecker auditory cue (calls, drums) and tag the associated spectrogram. As described in Chapter 2, we utilized visual scanning processing techniques to identify auditory cues. We identified calls and drums because we were interested in any behavioural auditory cue associated with Pileated Woodpeckers.

### *Occupancy and Intensity of Use*

A site was considered occupied if a Pileated Woodpecker was detected at least once during our sampling period. As we sampled during the peak detection window described in Chapter 2 (the first week of April, between sunrise and 2 hours after), we expected to detect a Pileated Woodpecker as present with 90% confidence, given the sampling effort of fifteen one-minute-long recordings. Therefore, by design, we eliminated the probability of the detection side of the occupancy equation described in MacKenzie *et al.* (2002, 2006). We defined the intensity of use variable as the number of recordings where a Pileated Woodpecker was observed at a site. We defined the occupancy variable as a binary measure of whether a Pileated Woodpecker was detected during sampling at a given site (yes = 1 / no = 0). The differences between variables are illustrated in Figure 3.2.





**Figure 3.2** Conceptual model demonstrating the differences between occupancy and intensity of use described in this study. Circles represent a sampling site across the number of visits (or surveys), and the colours indicate unique sites. The Pileated Woodpecker silhouettes represent a detection of the target species during that visit. The output for each site’s occupancy and intensity of use are summarized below the corresponding site.

### *Land Cover*

We collected habitat covariates from Canada-wide publicly available data sources, Beaudoin *et al.* (2017) and the National Terrestrial Ecosystem Monitoring System for Canada (NTEMS) datasets. These land cover datasets are publicly accessible Canada-wide datasets; therefore, studies throughout the western boreal forest can use and adapt these models to fit their specific study locations. These datasets differ in modeling technique, year in which data was sampled, resolution, and equipment used to generate values. Beaudoin *et al.* (2017) apply a *k*-nearest neighbour statistical approach to coarser grain MODIS satellite imagery to generate a 250-meter resolution map of land cover in Canada. Specifically, this approach used satellite imagery

from 2001 and 2011 to predict land cover as influenced by the surrounding pixel values. In contrast, the NTEMS dataset applies a Random Forest machine learning algorithm to Landsat satellite imagery from 2019 (age and deciduous composition) and 2015 (biomass) to predict land cover at a finer-grain resolution of 30-meter (Matasci *et al.* 2018).

The habitat covariates we examined in this study reflected ecologically important variables for Pileated Woodpeckers, as established by previous studies. The variables examined in the Beaudoin *et al.* (2017) land cover dataset (250-meter resolution) included forest age, percentage of forest composition that is deciduous, aboveground biomass, canopy closure, and forest composition identified as deadwood (in biomass) (Table 3.1). The variables within the NTEMS dataset (30-meter resolution) included forest age (Maltman *et al.* 2023), percentage of forest composition that is deciduous (Hermosilla *et al.* 2022), and total aboveground biomass (Matasci *et al.* 2018) (Table 3.2). As Pileated Woodpeckers are often associated with old growth forests, forest age is often described as the best predictor across various Pileated Woodpecker habitat studies (Bull *et al.* 1992, Renken and Wiggers 1993, Flemming *et al.* 1999, McClelland and McClelland 1999, Savignac 2000, Hartwig *et al.* 2004, Bull *et al.* 2007, Raley and Aubry 2010, Krementz *et al.* 2012, Hu and Tong 2022). Therefore, we included forest stand age in our models. Deciduous trees are essential habitat resources for many cavity-nesting species like the Pileated Woodpecker, so we included the percentage of deciduous trees in our models (Martin 2002, Martin *et al.* 2004, Cockle *et al.* 2019). Finally, we included aboveground biomass because it indicates tree size (tree diameter/stem thickness), often a limiting factor for Pileated Woodpecker roosting and nesting habitat (Bull *et al.* 1992, Renken and Wiggers 1993, McClelland and McClelland 1999, Bonar 2000, Aubry and Raley 2002, Krementz *et al.* 2012). Aboveground biomass has also indicated structural features necessary for Pileated Woodpecker foraging activities (Renken and Wiggers 1993, McClelland and McClelland 1999, Aubry and Raley 2002, Finley *et al.* 2009, Tremblay *et al.* 2015, Dufour-Pelletier 2020, Martin *et al.* 2021, Hu and Tong 2022). Furthermore, biomass is a good measure of the productivity of an environment, which can affect species composition (Finley *et al.* 2009). Both latitude and longitude were included in the models so that we could examine if there were spatial differences in the Pileated Woodpecker habitat use within our study area. Latitude is especially relevant as our study takes place at the northern edge of the estimated Pileated Woodpecker range. As there has not been a formal attempt to establish the range

edge in Northern Alberta/the western boreal forest, latitude was used to examine how Pileated Woodpecker habitat use may change with distance from the species' northern range edge.

Beaudoin *et al.* (2017) examined two covariates not found within the NTEMS dataset: deadwood and canopy closure. Both variables are effective predictors for Pileated Woodpeckers in prior studies (Savignac *et al.* 2000, Hartwig *et al.* 2004, Nappi *et al.* 2015, Dufour-Pelletier 2020, Hu and Tong 2022). With the Beaudoin *et al.* (2017) land cover data, we created model sets that contained only these variables (deadwood and canopy closure), but also created model sets that only contained variables found in both NTEMS and Beaudoin *et al.* (2017) (i.e., excluded deadwood and canopy closure) so that we could examine how measurements of the same land cover variable (e.g., forest age) affect model predictive accuracy. We examined correlations via the Pearson correlation coefficient across all variables within a dataset. If variables were considered highly correlated (coefficient greater than  $|0.75|$ ), we removed one of the variables to ensure that variance inflation did not occur in our dataset.

The Beaudoin *et al.* (2017) dataset used land cover data extracted in 2011, while NTEMS used land cover data extracted in 2019 (age and deciduous percentage) and 2015 (biomass). We calculated the age of stands relative to the year in which the location was visited. After assessing the sampling design, we concluded that most of our forest age values lay within the range of 20-80 years old; therefore, we assigned age values over 150 (about five sites) a value of 150 to ensure that outliers in the dataset would not skew results. We examined the correlation of values for variables across the two datasets to assess the similarity of the two land cover datasets (i.e., are they measuring the same thing). We calculated Pearson's correlation coefficient between variables measuring the same habitat variable at all scales (150, 565, and 1000 meter) and land cover dataset.

**Table 3.1** Variables selected from the Beaudoin *et al.* (2017) dataset (250-meter resolution). Italicized variables are exclusive to this dataset.

<i>Variable Name</i>	<i>Description</i>
Forest Age	Derived age of forest in 2011
Forest % Deciduous	Percentage of the area (250 m) classified as containing deciduous tree species
Aboveground Biomass	Calculated biomass as a function of tree species, tree height, DBH and stand volume within an area
Latitude	Site location in decimal degrees
Longitude	Site location in decimal degrees
<i>Forest Deadwood</i>	Calculated biomass of standing dead trees (Boudewyn <i>et al.</i> 2007)
<i>Canopy Closure</i>	Amount of area that is not covered by forest canopy

**Table 3.2** Variables selected from the NTEMS dataset (30-meter resolution) Italicized variables are exclusive to this dataset.

<i>Variable Name</i>	<i>Description</i>
Forest Age	Derived age of forest in 2019
Forest % Deciduous	Percentage of the area (30m) classified as containing deciduous tree species
Aboveground Biomass	Calculated biomass as a function of tree species, tree height, DBH and stand volume within an area
Latitude	Site location in degrees
Longitude	Site location in degrees

### *Land cover extraction scale*

We calculated the average value of each habitat variable within a 150, 565, and 1000-meter buffer radii for comparisons of spatial scale. These buffers take the average value of each variable in the specified buffer radius around the location. Buffer scales were chosen to demonstrate a noticeable difference between covariate values and represent a gradient from the local to landscape scales. The smallest scale (150 meters) was slightly larger than the Pileated Woodpecker's effective detection radius (Edwards *et al.* 2022) and represents the local environment immediately surrounding the ARU. The 565-meter scale was used to examine a gradient of scale sizes that may represent an area within an individual's home range (i.e., foraging or nesting site). We investigated the effects of the macrohabitat by estimating landscape variables within 1000-meter buffers. As the 1000-meter scale is slightly larger than the maximum distance a Pileated Woodpecker will respond to playback calls (Savignac *et al.* 2000), we decided that this scale would appropriately capture the broader environmental characteristics which are present at a home range scale.

### *Model structure*

We used the logit link function to fit the mean response within a binomial distribution and for ease of comparison in occupancy models. We used the log link function for the intensity of use models and the count distribution. Generalized linear models were created for each combination of scale (150, 565, and 1000-m buffers), data source (Beaudoin *et al.* 2017 and NTEMS), and response variable (occupancy and intensity of use) (total 12 combinations) (Table 3.3, Table 3.4). We implemented a binomial distribution for occupancy models and a Poisson distribution for intensity of use models to predict the relationships of Pileated Woodpeckers with our habitat variables of interest. Due to repeated use events occurring within our sampling period (15 recordings), the Poisson distribution fit our count data the best. We tested the negative binomial distribution, and it did not have a noticeable effect on the model's beta coefficients.

Predictor variables in models varied according to the scale and data source. Each model was multivariable and contained a measure of the following non-correlated variables: forest age, forest composition that is deciduous, above-ground biomass, latitude, and longitude. If variables

were found to have an unreliable impact (explained further in *Bayesian Modeling*) across simulations, then the variable was not included in the final model.

**Table 3.3** Model Set 1 describes variables in the base occupancy models (binomial). Variables were extracted through the land cover data source, and scale is denoted for each model. The final predictive models included only reliable variables (they did not cross the threshold of 0 across 95% of their simulated beta coefficients).

***Model Set 1. Occupancy***

<i>Variables</i>	<i>Data source</i>	<i>Scale</i>
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	1000 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	1000 meter

**Table 3.4** Model Set 2 describes variables included in the base intensity of use models (Poisson). Variables were extracted through the land cover data source, and scale is denoted for each model. The final predictive models included only reliable variables (they did not cross the threshold of 0 across 95% of their simulated beta coefficients).

***Model Set 2. Intensity of Use***

<i>Variables</i>	<i>Data source</i>	<i>Scale</i>
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	Beaudoin <i>et al.</i> 2017	1000 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}} + \beta_{\text{Longitude}}$	NTEMS	1000 meter



**Table 3.5** Model Set 3 describes variables scale and response metrics used in creating models exclusively in the Beaudoin *et al.* 2017 dataset. Each model's response metric (occupancy and intensity of use) and scale are denoted. The final predictive models included only reliable variables (they did not cross the threshold of 0 across 95% of their simulated beta coefficients).

***Model Set 3. Beaudoin exclusive***

<i>Variables</i>	<i>Response Metric</i>	<i>Scale</i>
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Occupancy	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Occupancy	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Occupancy	1000 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Intensity of use	150 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Intensity of use	565 meter
$\beta_{\text{Age}} + \beta_{\text{Deciduous}} + \beta_{\text{Biomass}} + \beta_{\text{Latitude}}$ $+ \beta_{\text{Longitude}} + \beta_{\text{Deadwood}} + \beta_{\text{Canopy}}$ Closure	Intensity of use	1000 meter

## *Bayesian modeling*

We estimated the extent to which habitat covariates contribute to describing occupancy or intensity of use using a Bayesian approach through JAGS (Plummer 2003) that we called from the R environment using the *rjags* and *coda* packages (Plummer et al. 2023). Using a Bayesian approach allowed us to identify variables that reliably predict Pileated Woodpecker habitat use without relying on arbitrarily assigned significance thresholds. Furthermore, the Bayesian method of modeling produces full probability distributions, rather than point estimate with confidence intervals as produced via frequentist approaches. This probability distribution clearly identifies the magnitude and uncertainty of the estimated beta coefficients. Finally, Bayesian inference allowed us to specify complex hierarchical structures to explore potential interactions of variables without altering the base model (methods used to identify interactions explained further below).

We calculated beta coefficients for each habitat variable across iterations and determined a distribution of values for beta coefficients (posterior distribution). We define a reliable predictor as one in which the calculated beta coefficients are consistently (in 95% of iterations), either positively or negatively, associated with the response variable. Parallel to frequentist statistics, these consistently associated predictive variables significantly impact the response variable. Furthermore, variables that have a posterior distribution that crosses zero (i.e., inconsistently associated with the response variable) do not significantly affect the response variable or the rest of the simulated beta coefficients. Thus, post-hoc model selection is not required in a Bayesian modeling (Gelman *et al.* 2013). If no variable proved to be consistently associated, then no meaningful predictive model could be created for that specific combination of response variable, land cover data source, and scale.

Each model ran 400,000 iterations across four chains after an equally long burn-in phase (400,000 iterations). The burn-in phase allows the independent chains to explore the probability space of each variable and to converge to the value that satisfies the relationships specified in the model and is thus discarded. The computational Bayesian statistics we used are based off Markov Chain Monte Carlo (MCMC) processes. Markov Chains are memoryless; therefore, they simulate

values based only on the previous iteration. Complex models (e.g. non normally distributed, hierarchical, interactions, etc.) may require a larger gap between retained values to prevent autocorrelation (Gelman *et al.* 2013). Given the complexity of our models we deemed it appropriate to retain one of every 40 simulated between estimates (see below for details on model validation) (Gelman *et al.* 2013). Models using the metric of intensity of use were fitted using the Poisson probability distribution to describe the response variable. Models using the occupancy metric followed a specific case of the binomial probability distribution, known as the Bernoulli distribution, where the number of attempts equals one. For the occupancy model (binomial), we used a logit link function for our linear expression to ensure relatability with the values chosen for each response variable (i.e., a real number between zero and one). Alternatively, we used a log link function for the intensity of use model (Poisson).

We compared model performance through a five-fold cross-validation. We subsampled one-fifth of our data and predicted the occupancy and intensity of use using each model, thus effectively covering the entire distribution of our data. We combined the results of these five cross-validation sets to compare predictive accuracy. We observed the results of each model, which is used to establish the best predictive model for each response variable (occupancy and intensity of use). We calculated the accuracy of the occupancy models by dividing the expected occupancy produced by the model's median beta value by the total observed occupancy. We decided that there were few ecological differences between certain intensity of use values (i.e., the difference between 4 and 5 use events ecologically means about the same thing). To account for this, we created categories of not used (0 use events), low (1 use event), medium (2-3 use events), and high (4+ use events) intensity of use per location when doing the cross-validation. Furthermore, we also analyzed the data using the raw estimated intensity of use values (i.e., no binning) and found no notable differences in accuracies. We considered accurate predictions as ones for which the predicted intensity of use category fell within the observed intensity of use categories per location. From these calculations, we calculated the total number of locations where the estimated intensity of use was accurately described and divided by the total number of sites.

Equation 3.1 exemplifies the modeling framework used for the intensity of use models. The prior distribution values specified influence the range of values the simulations explored for the specified coefficients. By specifying uninformative (broad and zero-centered) prior

distributions for all parameters, we ensure unbiased simulated values (i.e., we are not limiting them to be very small or centered around positive or negative numbers) at the cost of slower simulations. This allows for confident (because of the width) and fair (because of the zero-centering) comparisons of posterior (after the simulation) and prior (before the simulation) distributions for all variables.

**Equation 3.1** Modeling framework used in the estimation of posterior coefficients for a Poisson distribution of intensity of use ( $y$ ) across a site ( $q$ ) with habitat covariates ( $cov$ ). This model demonstrates the intensity of use through the likelihood estimation of the Poisson distribution. Here, the observations are indexed with “ $q$ ”, whereas the covariates are with “ $w$ ”. Note that we are describing normal distributions using precision ( $\tau$ ) instead of variance, as required by JAGS. To clarify, the smaller the precision, the bigger the variance, as these are reciprocal functions. Thus, we are opting for uninformative priors that require longer times to converge but usually allow for more objective inference (Gelman et al. 2014).

$$y[q] \text{Poisson}(\lambda_{[q]})$$

$$\log(\lambda_{[q]}) = \beta_0 + \beta_1 * cov_q 1 \dots + cov_q n * \beta_w$$

$$\beta_0 \text{Norm}(\mu = 0, \tau = 10^{-3})$$

$$\beta_w \text{Norm}(\mu = 0, \tau = 10^{-3})$$

After the models from Model Set 1 and 2 (Table 3.3, Table 3.4) were created, we explored whether the relationships between the habitat covariates included interactions or followed a non-linear relationship with all the response variables. In doing so, this ensured we identified all important habitat variables this dataset allows. We created a flexible interaction term within our models to explore non-linearity and interactions between variables. We ran these models through simulations using the same parameters as previous models (as described in Equation 3.2). From the model posterior, we identified variables with interactions and non-linear relationships. If the posterior distribution generated by running simulations with Equation 3.2 signalled that approximately 50% of the simulations contained an interaction/nonlinear term, we included this as a fixed effect within our model. These new models were run using the same priors, iterations

and thinning as stated previously. If no interactions or non-linear effects were identified through the posterior distribution, they were not added as a fixed effect to the model. In this case, we used the models derived from Model Sets 1 and 2 (Table 3.3, Table 3.4) to determine predictive accuracy.

**Equation 3.2** Example modeling framework where interaction and non-linearity are examined. Here, we describe the “*inter*” parameter to allow for flexible interaction between variables by taking advantage of the multiplicative effect of summing exponents, allowing us to use a binary switch (Bernoulli) variable “*ind $\beta$* ” to include (or not) each covariate to participate (or not) in the interaction. The success probability of each binary switch variable is hierarchically modelled by a Beta prior (*bp*) with scale and shape equal to 1. This use of the conjugate Beta prior is equivalent to a uniform distribution to start with, but it allows for very high flexibility as the parameters vary. Finally, we allow for non-linear relationships by raising each covariate to the power of a dedicated exponent variable (*expo*), which follows a uniform distribution between -3 and 3. Note that different models (occupancy /intensity of use) have different likelihoods for the response variable (i.e., Bernoulli).

$$y_{[q]} \text{Poisson}(\lambda_{[q]})$$

$$\log(\lambda_{[q]}) = \beta_0 + \beta_1 * cov_q 1 \dots + cov_q n * \beta_w + \ln(inter)$$

$$inter = e^{(ind\beta_{[1]}*\beta_{[1]}^{expo_{[1]}} + ind\beta_{[2]}*\beta_{[2]}^{expo_{[2]}} + \dots + ind\beta_{[n]}*\beta_{[n]}^{expo_{[n]}})}$$

$$ind\beta_w \sim \text{Bernoulli}(bp_w)$$

$$bp_w \text{Beta}(1,1)$$

$$expo \text{Uniform}(-3,3)$$

After exploring how the land cover variables found mutually in the Beaudoin *et al.* (2017) and the NTEMS datasets predicted woodpecker occupancy/use, we investigated model performance using covariates exclusive to each dataset. We evaluated deadwood and canopy closure from the Beaudoin *et al.* (2017) land cover dataset and evaluated their reliability in predicting Pileated Woodpecker occupancy and intensity of use across the three spatial scales. We also explored any interactions or non-linear relationships for these variables.

We visually inspected trace plots to ensure convergence across chains and conducted three diagnostic tests. These tests included the Gelman-Ruban, Heildberger and Welch, and effective size tests in the *coda* R package (Gelman *et al.* 2013, Plummer *et al.* 2023). The Gelman-Ruban test is designed to determine the reliability of the simulated beta coefficients. The Heidelberg and Welch test tells us whether the simulations were run for an appropriate number of iterations (Gelman *et al.* 2013). The effective size test determines whether the retained simulated values correlate, essentially determining whether the thinning processes are sufficient for the simulation (Gelman *et al.* 2013). After the models passed these tests, we ran a 5-fold cross-validation to validate our results and determine model prediction accuracy.

### 3.3 Results

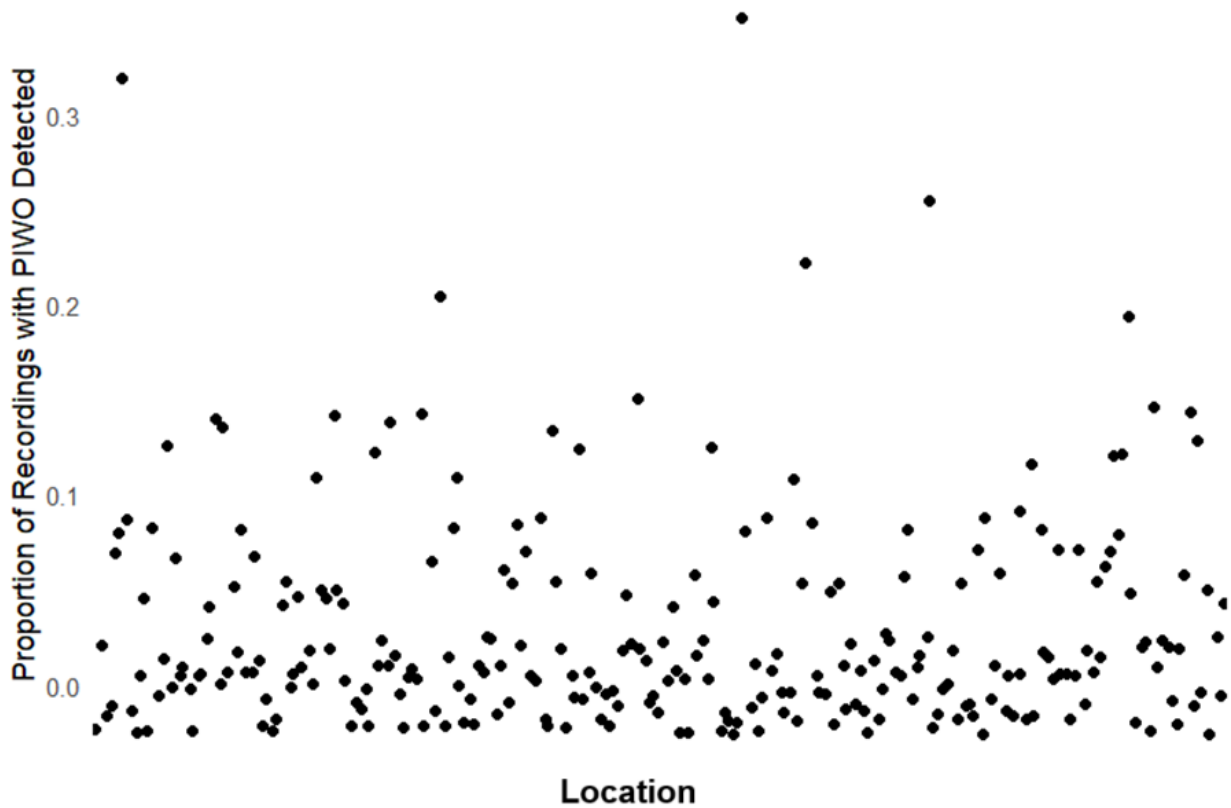
While attempting to measure similar forest stand characteristics, the variables found in the Beaudoin *et al.* (2017) and the NTEMS dataset were not always highly correlated (Table 3.6). The least correlated variable between datasets was age (0.611), and the most correlated variable was the amount of deciduous (0.877).

**Table 3.6** Pearson’s correlation coefficients for variables extracted from the Beaudoin *et al.* (2017) and NTEMS datasets at 565 meters (used as a representative scale).

Variable	Pearson’s correlation coefficient
Age	0.611
Deciduous Composition	0.877
Biomass	0.762

Pileated Woodpeckers were detected at 80 out of 258 (~33%) of the ABMI sites sampled. At any specific location, the maximum number of times a Pileated Woodpecker was detected was five out of fifteen recordings (Figure 3.3). Therefore, the highest detection probability at any given

location was approximately 33% (Figure 3.3). The mean detection probability is approximately 3% (Figure 3.3).



**Figure 3.3** Scatterplot showing the proportion of recordings where a Pileated Woodpecker (PIWO) was detected (out of 15 recordings). A jitter was applied to the points to illustrate the amount of approximate number of locations represented with certain proportions of recordings where Pileated Woodpeckers were detected. Locations assorted x-axis randomly.

Visual inspection of the trace functions for all models resulted in good convergence, and models passed all diagnostic and validation tests. The results of the Gelman-Ruban scale reduction factors ( $\hat{R}$ ) demonstrated the scale at which estimated coefficients would have reduced if the simulation approaches infinity iterations. All  $\hat{R}$  values were between 1 and 1.01, confirming good convergence across chains and reliability in the estimated coefficients. The Heidelberg diagnostics

results showed that the vast majority of variables passed the half-width test, and the ones which did not pass the stationarity test stated that the number of iterations to keep/discard was appropriate. Retained simulated values also passed the effective size test. These diagnostic tests allow us to be confident that the models generated accurately represent the relationships found within the data. Furthermore, we found no interactions or signs of non-linearity across all variables in occupancy and intensity of use models via our flexible *inter* term (Equation 3.2). Therefore, we did not include interactions or non-linear variables as fixed effects within our models.

### *Occupancy Results*

Two occupancy models containing consistently associated variables were produced (Table 3.7). The predictive accuracy determined through the cross-validation of these models was approximately 70%. Biomass from land cover Beaudoin *et al.* (2017; 250-meter resolution) was a reliable predictor at the 565 and 1000-meter scales. Biomass was the only variable found to be a reliable predictor of Pileated Woodpecker occupancy across land cover sources and scales. No reliable variables were found at a 150-meter scale using both datasets.



**Table 3.7** Occupancy model’s reliable variables with the calculated posterior distribution of beta values and model accuracy based on cross-validation results. If more than one variable is identified as reliable per model, the beta values are listed in order of appearance in the reliable variable column. Models are identified by response metric (occupancy or intensity of use), dataset (Beaudoin et al. 2017 or NTEMS), and scale (150, 565, 1000 m).

<i>Beaudoin et al. 2017</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross- validation accuracy</i>
150 m:	No reliable variables	N/A	N/A	N/A	N/A
565 m:	Biomass	0.233	0.754	1.287	68.63%
1000 m:	Biomass	0.179	0.732	1.292	68.63%
<i>NTEMS</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross- validation accuracy</i>
150 m:	No reliable variables	N/A	N/A	N/A	N/A
565 m:	No reliable variables	N/A	N/A	N/A	N/A
1000 m:	No reliable variables	N/A	N/A	N/A	N/A

### *Intensity of use results*

Three intensity of use models contained consistently associated variables (Table 3.8). The predictive accuracy determined through the cross-validation of these models was approximately 70%. Biomass from land cover Beaudoin et al. (2017; 250-meter resolution) was a reliable predictor at 565 and 1000-meter scales, and latitude was a reliable predictor at all three scales: 150, 565, and 1000 meter. The most accurate intensity of use model contained the Beaudoin *et al.* (2017) land cover data at the 565 or 1000-meter scale.

**Table 3.8** Intensity of use model’s reliable variables with the calculated posterior distribution of beta values and model accuracy based on cross-validation results. If more than one variable is identified as reliable per model, the beta values are listed in order of appearance in the reliable variable column. Models are identified by response metric (occupancy or intensity of use), dataset (Beaudoin *et al.* 2017 or NTEMS), and scale (150, 565, 1000 m).

<i>Beaudoin et al. 2017</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross-validation accuracy</i>
150 m:	Latitude	0.001	0.125	0.190	65.09%
565 m:	Latitude	0.025	0.216	0.408	67.05%
	Biomass	2.626	0.494	0.802	
1000 m:	Latitude	0.035	0.226	0.420	67.05%
	Biomass	0.083	0.436	0.772	
<i>NTEMS</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross-validation accuracy</i>
150 m:	No reliable variables	N/A	N/A	N/A	N/A
565 m:	No reliable variables	N/A	N/A	N/A	N/A
1000 m:	No reliable variables	N/A	N/A	N/A	N/A

*Models containing Beaudoin exclusive variables*

Including the two Beaudoin exclusive variables, deadwood and canopy closure, we produced two reliable occupancy models and three reliable intensity of use predictive models across all scales. Deadwood was not a reliable predictor in any model across response variables (occupancy, intensity of use) or scale. Canopy closure was found to be a reliable variable and had a negative relationship with both occupancy and intensity of use. Latitude and biomass were reliable predictive variables, demonstrating a positive relationship with occupancy and intensity of use. The most accurate predictive occupancy model from this model set included latitude, biomass and canopy closure at the 1000-meter scale. The intensity of use models at the 565 and 1000-meter scale had approximately the same predictive accuracy (~60%).

**Table 3.9** Table of habitat covariates that consistently influence Pileated Woodpecker occupancy. Models included deadwood and canopy closure only found within the Beaudoin *et al.* (2017) dataset. Quantiles describe the beta coefficient value at each percentile of their distribution across the simulations.

<i>Occupancy (Beaudoin exclusive)</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross- validation accuracy</i>
150 m:	No reliable variables	N/A	N/A	N/A	N/A
565 m:	Latitude	0.010	0.318	0.634	67.45%
	Biomass	0.519	1.205	1.916	
	Canopy Closure	-0.998	-0.494	-0.004	
1000 m:	Latitude	0.053	0.368	0.280	69.80%
	Biomass	0.511	1.238	1.983	
	Canopy Closure	-1.105	-0.599	-0.051	

**Table 3.10** Table of habitat covariates that consistently influence Pileated Woodpecker intensity of use. Models included deadwood and canopy closure only found within the Beaudoin *et al.* (2017) dataset. Quantiles describe the beta coefficient value at each percentile of their distribution across the simulations.

<i>Intensity of use (Beaudoin exclusive)</i>					
<i>Scale</i>	<i>Reliable Variables</i>	<i>2.5% quantile beta values</i>	<i>50% quantile beta values</i>	<i>97.5% quantile beta values</i>	<i>Cross- validation accuracy</i>
150 m:	Latitude	0.407	0.951	3.770	46.77%
	Biomass	0.985	1.093	10.823	
	Canopy Closure	-6.983	-0.811	-0.002	
565 m:	Latitude	0.407	1.080	2.140	60.39%
	Biomass	0.965	2.226	4.301	
	Canopy Closure	-1.688	-0.829	-0.132	
1000 m:	Latitude	0.474	0.890	2.069	60.39%
	Biomass	0.910	2.165	4.213	
	Canopy Closure	-2.103	-1.140	-0.371	

### 3.4 Discussion

#### *Occupancy versus intensity of use*

Both occupancy and intensity of use were only 65-70% accurate in predicting Pileated Woodpecker habitat use based on cross-validation. Thus, none of our models were highly predictive. We expected intensity of use models would provide more information to resolve important predictor variables than occupancy models. This expectation assumed that detecting more drumming at a location would reveal areas where Pileated Woodpeckers were spending more time and thus had more suitable resources. However, both occupancy and intensity of use models identified (across all models using the same response variables) the same relationships with habitat variables (biomass, latitude and canopy closure). One explanation for this result could be that the factors which influence complex measures, such as intensity of use are more complicated or nuanced (Nielsen *et al.* 2005). Once detectability is accounted for, occupancy may be sufficient for creating predictive habitat models for species management. Importantly, our measure of occupancy used a multiple-visit approach during the optimal time of the year for detecting Pileated Woodpecker. How models that use a single visit to a location are predicted by these covariates should be evaluated. Hundreds of thousands of single-visit ARU and point count data locations are available in Alberta ([www.wildtrax.ca](http://www.wildtrax.ca)) to build Pileated Woodpecker models, but most of that data is collected in June. Given the effort required to collect multiple visit data, it is important that future work compare different model structures.

The maximum number of times a Pileated Woodpecker was detected at any given location across fifteen one-minute surveys on different days was five (~33% of surveys). This suggests that Pileated Woodpeckers are either highly mobile animals and/or the sampling effort and coverage were insufficient to detect specific patterns of habitat use within large home ranges. We speculate that we observed the low detection probability because Pileated Woodpeckers are highly mobile. Our sampling design was fully random in areas that were forested. While our sample size was relatively large, the probability that an ARU was located near a particularly important resource like a nest or foraging tree was low. Explanations could be that the availability of such resources might be relatively low or, more likely, that the spatial coverage of ARUs was too coarse to detect high-use activity areas like drumming posts or foraging areas. Clearer signals may be observed if

many ARUs were placed within an individual's home range. This assumes that Pileated Woodpeckers are more likely to drum in areas with key resources. We are currently using and collecting additional data using two different approaches to answer this question: (1) we are placing ARUs at known nest and foraging trees; (2) we are using varying sized grids of ARUs to assess how an individual or pair of Pileated Woodpeckers may use habitat over the entire home range. The models in this paper give us a glimpse into second-order selection (i.e., where a home range might be located). These future data will help uncover whether greater detail in third-order selection (i.e., where specific habitats are used within a home range) can be revealed using ARU data. The Pileated Woodpecker can be heard by human observers (and ARUs) at distances between 100-150 meters (Edwards *et al.* 2022), meaning grids of ARUs spaced at approximately a 200-meter distance would be required to understand third-order selection within a typical Pileated Woodpecker >250-hectare home range (Renken and Wiggers 1989, Mellen *et al.* 1992, Bull and Holthausen 1993, Bonar 2001). This contrasts the ARU spacing distance used within our study of >20 kilometers.

We speculate our model would be more predictive if we had included areas that are likely less suitable, as the models would have likely accurately confirmed null use in unsuitable environments, but this should be confirmed. Our models examined how fine scale differences in one ecosystem type, the boreal forest, affect Pileated Woodpecker habitat use. By including Pileated Woodpecker non-habitat, such as grasslands, our models should be able to identify a negative relationship, both in occupancy and intensity of use, for these environments. Due to the life history requirements of nesting, foraging, and roosting in trees, we speculate that non-forested environments would be easily classified as non-habitat (null occupancy and null intensity of use) for Pileated Woodpeckers. However, the utility of adding non-habitat ecosystem types is negligible because researchers do not survey for Pileated Woodpeckers in these ecosystem types.

### *Land cover*

An alternative explanation for the limited predictive accuracy of our models is the limited number of land cover variables we examined. While these remote sensing layers had other variables that could be used, they were highly correlated with variables we did include. Correlation

analysis suggests that the same variable derived by different remote-sensing layers is only weakly correlated. This phenomenon is more common than many ecologists recognize (i.e., Hedley *et al.* 2020) and demonstrates the importance of evaluating different ways of describing vegetation conditions and land use when building habitat models for managers to use. Land cover data collected on the ground might produce more accurate and informative models but can not be mapped easily and are very expensive to collect. Additionally, smaller regional land cover datasets, such as the Alberta Vegetation Inventory or a growing LiDAR inventory, may be more representative of the local environment and produce better models. However, these products do not allow us to build models to the large extent that managers desire. Future work should evaluate how predictions from models built using different remote sensing products overlap in space and then use that information to study further areas consistently identified as important. Such an approach was used by Hedley *et al.* (2020) for the Yellow Rail (*Coturnicops noveboracensis*) in Alberta, whereby predictions of models from three different remote sensing products were used to find areas that were consistently identified as important across all layers rather than one. External validation demonstrated that the fused map of all three products was more accurate in finding the species than any of the individual remote sensing products.

We were surprised that the models produced using the Beaudoin *et al.* (2017) land cover dataset (250-meter resolution) were more likely to include reliable predictive variables. The NTEMS land cover dataset has a much finer resolution (30 meters), which often improves prediction accuracy. One explanation of why these datasets performed differently could relate to how they estimated biomass (the most predictive variable). The Beaudoin *et al.* (2017) dataset used the approach developed by Boudewyn *et al.* (2007), whereby ground measurements of DBH, stand volume, and tree species were recorded at sample locations and then using *k*-nearest neighbour clustering were correlated with remote sensing data. The NTEMS land cover dataset calculated biomass values using LiDAR data from a sample of locations to extract height, volume, and canopy cover (Matasci *et al.* 2018). They then estimated biomass through machine learning algorithms at a national extent. While LiDAR can have comparable accuracy to ground-based validation (Zellweger *et al.* 2013), the limited predictive ability of our models suggests that this approach to measuring biomass may be limited. Our current results indicate that the Beaudoin *et*

*al.* (2017) land cover dataset will provide more reliable predictions for those interested in developing Pileated Woodpecker habitat selection models.

### *Scale*

We did not produce meaningful predictive models at our finest scale (150 meters). A likely explanation is that Beaudoin *et al.* (2017) dataset pixel size (250m × 250m) is greater than this buffer size. When the resolution of the dataset is less than the scale at which the land cover is extracted, you are effectively taking the pixel value within which the sampling point occurs. This may be problematic with coarse resolution data because that point may be on the edge of a pixel that could be unrepresentative of the actual location where the Pileated Woodpecker is occurring. Furthermore, since Pileated Woodpeckers home ranges span an extensive area (Renken and Wiggers 1989, Mellen *et al.* 1992, Bull and Holthausen 1993, Bonar 2001), they may be selecting for areas that contain more suitable habitat (i.e., bigger trees) at a larger than a local scale. We found comparable predictive accuracies and relationships between 565-meter and 1000-meter scale models, suggesting these buffers are within the same domain of scale for Pileated Woodpeckers. This is consistent with Savignac *et al.* (2000), who used a 1000-meter scale to build their models. However, small scale buffers (i.e., 150 meter) may be more valuable for understanding drumming near nests or foraging trees, so we caution against using a single buffer size in future studies. However, we emphasize that researchers should aim to match the relevant scales associated with wildlife to the available land cover data resolutions to ensure that the resolution is not coarser than the scale.

### *Summary and Management Implications*

Very few studies have attempted to assess Pileated Woodpecker habitat use at a regional extent, especially in the western boreal forest. As a species of conservation concern due to their role as ecosystem engineers and associations with declining old-growth forest types (Bull and Holthausen 1993, McClelland and McClelland 1999, Bonnar 2000, 2001, Aubry and Raley 2002, Hartwig *et al.* 2004, Krementz *et al.* 2012), it is crucial to determine how Pileated Woodpeckers



use habitat to inform their management. This is especially important in our study area, as industrial activities of forestry and the energy sector's interests overlap with old-growth species specialists, such as the Pileated Woodpecker. Currently, we have a weak baseline for understanding this species. Our results emphasize the importance of biomass as an indicator of Pileated Woodpecker habitat use. We believe that biomass is a proxy for tree stem thickness, which is a limiting factor for Pileated Woodpecker nesting, foraging and roosting habitats (Bull *et al.* 1992, Renken and Wiggers 1993, Flemming *et al.* 1999, McClelland and McClelland 1999, Savignac 2000, Bonar 2001, Hartwig *et al.* 2004, Bull *et al.* 2007, Raley and Aubry 2010, Krementz *et al.* 2012). Additionally, our results suggest a negative relationship between Pileated Woodpecker occupancy and intensity of use with canopy closure. Canopy closure indicates denser forests, typically occurring at earlier seral stages in forest development (Duncanson *et al.* 2015). This suggests that Pileated Woodpeckers rely on mature and old forests with complex gap structural dynamics caused by the death and decay of trees (Conner *et al.* 1976, McClelland and McClelland 1999, Jackson and Jackson 2004, Nappi *et al.* 2015, Tremblay *et al.* 2015, Dufour-Pelletier *et al.* 2020, Martin *et al.* 2021). However, despite the logic of these predictor variables, they were only weakly predictive, suggesting more information is needed to fully understand and map the habitat use of the Pileated Woodpecker.

## 4. Chapter 4. Conclusions

### *Summary of key findings*

Little research has been conducted on Pileated Woodpecker behaviour and habitat use at the northern edge of their range in the western Canadian boreal forest. Throughout this thesis, I attempted to assess how to best sample and model habitat relationships for this species in Alberta, Canada.

Previous attempts at habitat modeling in this area (conducted by ABMI) used data from temporal periods in which detection probability is suboptimal (Alberta Biodiversity Monitoring Institute and Boreal Avian Modeling Project 2023). This potentially increases false negative rates, which impact the accuracy of habitat selection models. In addition, these models are based primarily on single-visit data. Our findings in Chapter 2 suggested that surveys for Pileated Woodpeckers in Alberta should be conducted earlier than traditional bird surveys like the BBS. Early to mid-April periods are optimal. Our analysis indicated that the peak timing may change due to the observed temperature on a given day but is also heavily influenced by static interannual variables such as day length. Additionally, we demonstrated that Pileated Woodpeckers' highest period of detectability during any given day is in the morning hours around sunrise. These results are consistent with BBS protocol and other passerine survey techniques (Staicer *et al.* 1996, Da Silva and Kempenaers 2017, Ziolkowski *et al.* 2023).

In Chapter 3, we assessed how variation in how habitat use models are created impacts predictive accuracy. Our habitat use associations were consistent with previous studies demonstrating positive relationships for old-growth forests undergoing stand gap dynamics. We showed that the response variable, land cover measurement techniques (datasets), and land cover extraction scale influenced model prediction accuracy. Occupancy models were slightly more accurate in predicting Pileated Woodpecker habitat use than intensity of use models. Only the land cover data measured using the methods described by Beaudoin *et al.* (2017) produced meaningful model results, suggesting that the measurement and resolution of land cover data greatly impact model performance. Finally, larger-scale buffers produced more meaningful models, implying that

Pileated Woodpeckers likely react to environmental attributes more represented at a regional or landscape scale.

We were surprised that our models did not include the percentage of deciduous forest variables. Previous work has demonstrated that Pileated Woodpeckers are strongly associated with old-growth forests with high deciduous tree compositions (Bull and Holthausen 1993, Renken and Wiggers 1993, Hartwig *et al.* 2004, Martin *et al.* 2004, Kremenz *et al.* 2012, Hu and Tong 2022). While the land cover data we used may not represent the true forest composition, it may be possible that other regional or compositional factors may influence the importance of deciduous trees for Pileated Woodpecker habitat use.

### *Conservation implications*

The Pileated Woodpecker is a species of special concern for conservation due to its vital role as a keystone species and strong associations with increasingly rare old-growth forest types (Bonar 2000, 2001, Aubry and Raley 2002, Aitken and Martin 2007, Trzcinski *et al.* 2022). The correlation between drumming behaviour (and presumably breeding state) and dynamic environmental conditions (mainly temperature) suggests that the Pileated Woodpecker may be less at risk of phenological shifts due to climate change. Mismatches in breeding phenology and food availability have been demonstrated for many birds. It is important to note that this non-migratory bird may change their breeding timing in response to local weather and environmental conditions which may lead to more successful breeding and survival (Stenseth *et al.* 2002, Powell and Logan 2005, Dunn *et al.* 2011, Visser *et al.* 2012, Lany *et al.* 2016). However, better continuous monitoring is needed to understand and track changes in Pileated Woodpecker populations and potential phenological mismatches that may be caused due to climate change.

Challenges imposed by climate change are not the only threat Pileated Woodpeckers face. As old-growth forests become increasingly scarce across North America, having accurate population estimations of old-growth specialist species, such as the Pileated Woodpecker, is essential to maintaining populations. Chapter 3 confirmed the Pileated Woodpecker's old-growth forest associations observed in other local studies (Bull *et al.* 1992, Renken and Wiggers 1993,

Flemming *et al.* 1999, McClelland and McClelland 1999, Savignac 2000, Hartwig *et al.* 2004, Bull *et al.* 2007, Raley and Aubry 2010, Krementz *et al.* 2012, Hu and Tong 2022). These habitat associations are at odds with the growing demands of the forestry sector in Alberta, which harvests large-diameter trees preferentially. Balancing the demands for wood products with the need to maintain a stable population of Pileated Woodpeckers in Alberta is an increasingly complex conservation challenge.

### *Recommendations for future research*

Throughout this thesis, I highlighted considerations for future biologists who aim to sample and model relationships and distributions of the Pileated Woodpecker in Alberta. The Government of Canada recently imposed legislation protecting Pileated Woodpecker nest sites, so the incentives to survey and study this species are high (Government of Canada 2022).

As survey methods are imperfect at detecting Pileated Woodpeckers, we recommend that optimizing survey timing may increase the accuracy of use data, and we demonstrated techniques that may help eliminate or reduce detection error. Important questions remain regarding how to optimize the detection and observation of other behaviours/vocalization to improve monitoring. In Chapter 2, we did not detect many calls across our recordings. Future research can build on our data and results to determine optimal periods in which calls may be observed, the environmental triggers of calling, and whether they can help us inform different scales of habitat selection (i.e., nest locations).

Our results from Chapter 2 outline recommendations that future research should consider when surveying Pileated Woodpeckers. We recommend that surveys should be conducted during the observed peak detection periods. However, with existing large datasets that do not sample during peak detection periods for Pileated Woodpeckers, it is important to note that high confidence in Pileated Woodpecker occupancy at a site can still be achieved through repeated surveys. The number of repeated surveys required to have high confidence in Pileated Woodpecker occupancy will increase as the surveys become less temporally optimized (i.e., at least 10 surveys required during peak detection periods versus at least 30 during standard BBS protocol timing).

In Chapter 3, we demonstrated that the response variable intensity of use can create species-habitat models with comparable predictive accuracy to occupancy models for Pileated Woodpeckers. However, neither of these approaches was particularly predictive. Different methods to conduct passive acoustic monitoring surveys using ARUs may reveal new insights. Research examining optimized sampling effort and coverage, varied grids or arrays of ARUs, and targeted sampling at nesting and foraging trees should be conducted to improve our understanding of intensity of use as a response metric and perhaps bolster the predictive capabilities of these models. In doing so, we may be able to use passive acoustic monitoring to determine areas of highest importance and preference for Pileated Woodpeckers within their home ranges.

It is possible that passive acoustic monitoring may ultimately not be an effective method for measuring the habitat use of highly mobile animals such as Pileated Woodpeckers. Additional targeted studies using woodpeckers tagged with GPS transmitters may be needed to obtain detailed habitat use and selection data at multiple scales and orders of selection. However, the logistic challenges of conducting this work at a regional extent, the high cost, and the invasive nature and impacts on Pileated Woodpeckers suggest the need to investigate various passive acoustic monitoring approaches.

Finally, I emphasized the importance of accurate land cover data. Smaller-scale regional land cover datasets such as the Alberta Vegetation Inventory (AVI) and LiDAR need to be evaluated as they may give a more accurate representation of the localized environment. AVI also contains additional land cover variables not represented in the datasets examined in Chapter 3. The trade-off between creating many local models using high-resolution data versus models made at larger extents using lower-resolution data is a crucial challenge for wildlife management. Many high-resolution vegetation cover products (i.e., AVI and LiDAR) are not publicly available, which creates numerous challenges for developing effective models for conservation and is necessary for governments and industry to continually improve.

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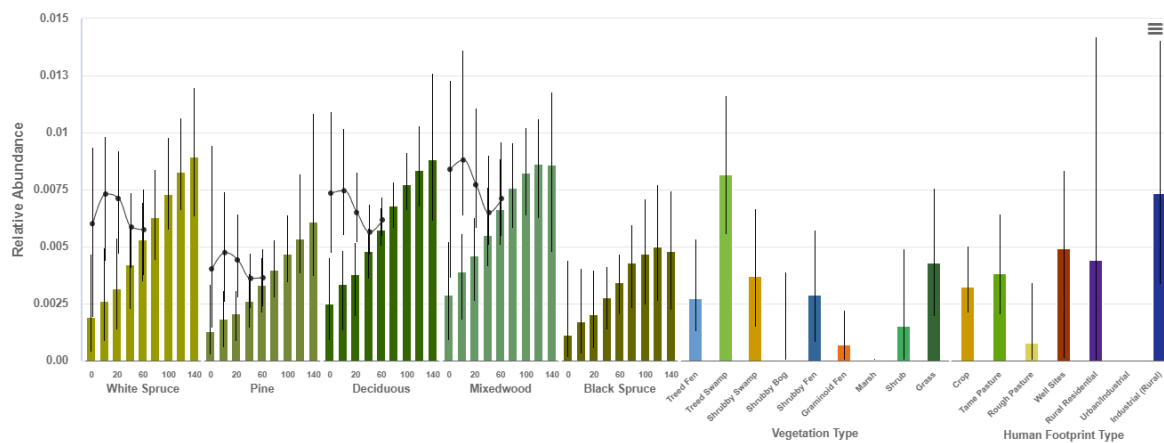
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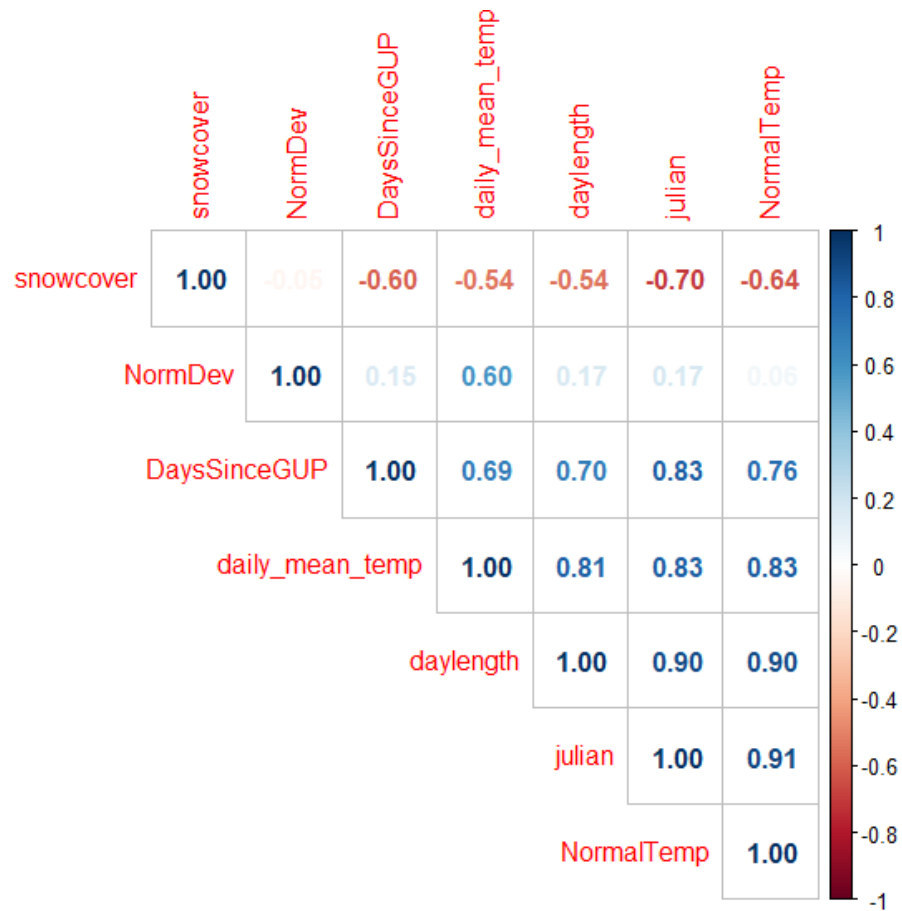
## 6. Appendices

Annotated code for Chapter 2: Temporal variation in Pileated Woodpecker behaviour: ecological explanations and management implications can be found online in the open repository: [https://github.com/austinczeller/Temporal\\_PIWO](https://github.com/austinczeller/Temporal_PIWO).

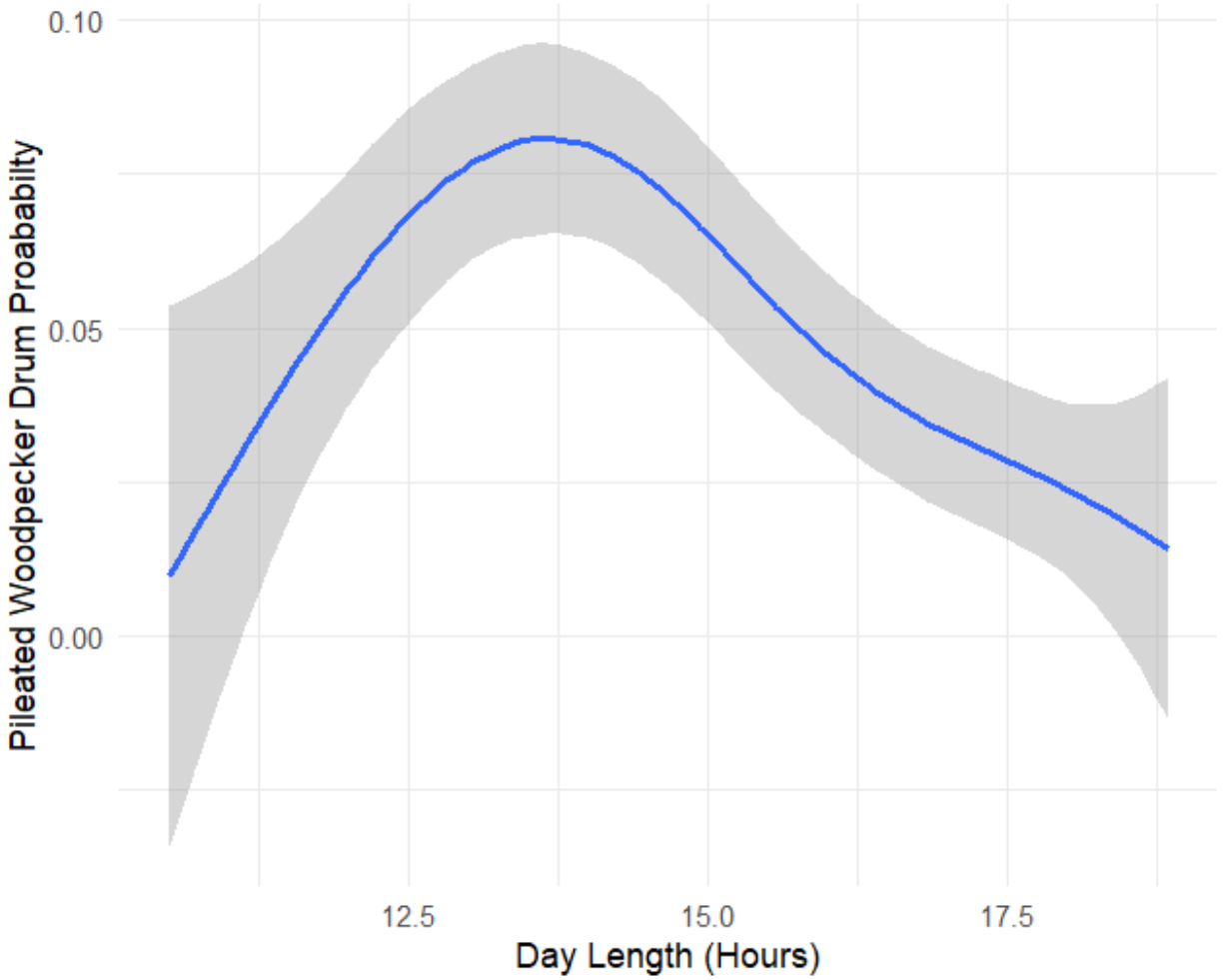
Annotated code for Chapter 3: Pileated Woodpecker habitat use in the boreal forest of Alberta: The relative importance of response variables, land cover, and scale can be found online in the open repository: [https://github.com/austinczeller/PIWO\\_Model\\_Comparison](https://github.com/austinczeller/PIWO_Model_Comparison).



**Figure 6.1** Current species habitat associations in forested regions of Alberta for the Pileated Woodpecker derived by ABMI (Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2023). Bars show the predicted relative abundance of Pileated Woodpecker as a function of habitat type. 90% confidence intervals are depicted by vertical lines. Additional information on these model results can be found through ABMI’s “Biodiversity Browser”: <https://beta.abmi.ca/species/pileated-woodpecker>.



**Figure 6.2** Correlation matrix for variables examined in Chapter 2, objective 2: environmental factors influencing Pileated Woodpecker drumming. “NormDev” is the deviation from the expected normal temperature and “DaysSinceGUP” is the days since green up.



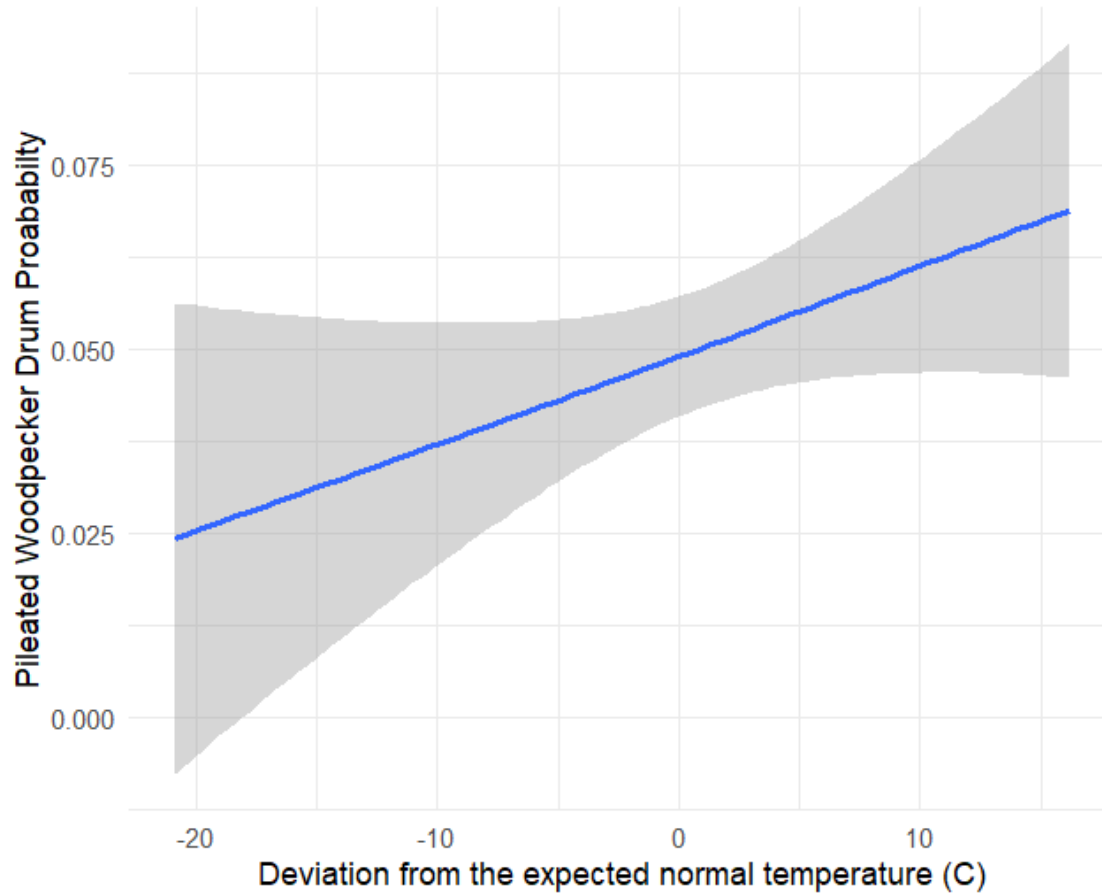
**Figure 6.3** Relationship of day length (hours) and Pileated Woodpecker drumming as estimated by the smoothing term generated via GAMM (Chapter 2). Dotted lines represent the bounds of the 95% confidence intervals.

**Table 6.1** Ridge regression model results for the multivariate models containing interannual static and flexible terms. Quadratic terms were used in these models because they demonstrated nonlinearity within the GAMs.

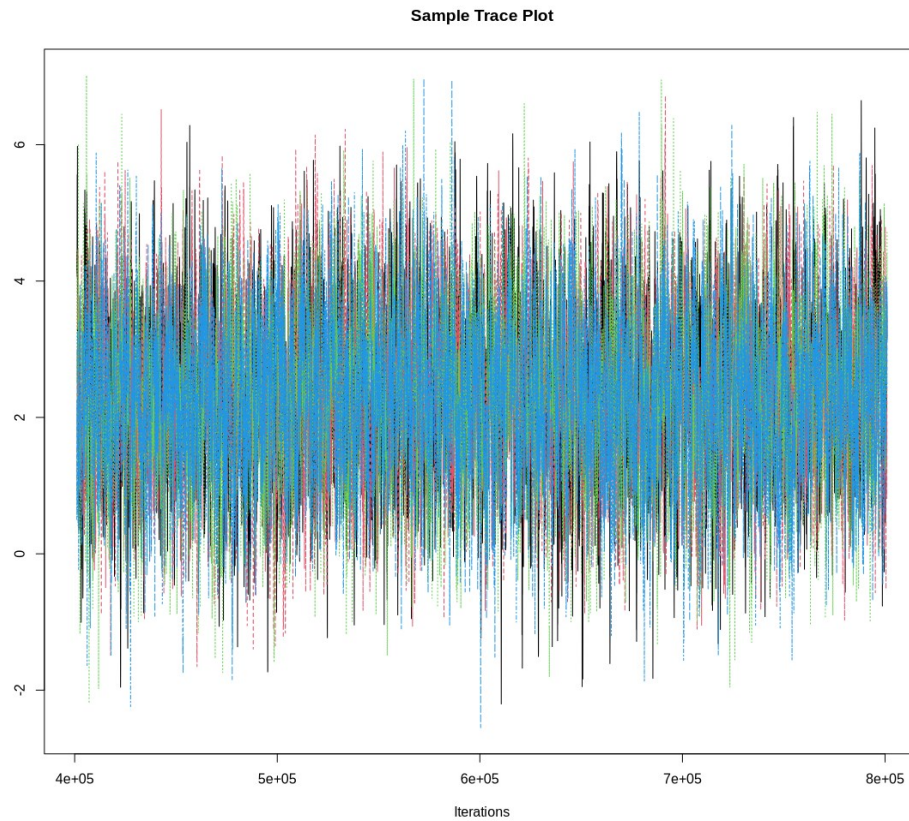
<b>Model</b>	<b>Variable</b>	<b>Beta coefficient</b>
<i>Julian date + mean temperature</i>	Julian date	-2.648e-04
	Julian date <sup>2</sup>	-7.637e-07
	Mean temperature	1.015e-03
	Mean temperature <sup>2</sup>	-1.195e-04
<i>Day length+ mean temperature</i>	Day length	-1.566e-03
	Day length <sup>2</sup>	-1.114e-04
	Mean temperature	5.460e-04
	Mean temperature <sup>2</sup>	1.374e-04

**Table 6.2** Model results for multivariable models with/without interactions between variables explored in Chapter 2, objective 3. Interaction term represents the interaction between precipitation and deviation from the expected mean temperature.

<b>Model</b>	<b>Variable</b>	<b>Beta coefficient</b>	<b>P-value</b>	<b>AIC</b>
<i>Precipitation + deviation from the expected mean temperature</i>	Precipitation	-0.009	0.755	1128.929
	Deviation from the expected mean temperature	0.038	0.022	
<i>Precipitation X deviation from the expected mean temperature</i>	Precipitation	-0.033	0.376	1128.026
	Deviation from the expected mean temperature	0.043	0.009	
	Interaction Term	-0.013	0.075	

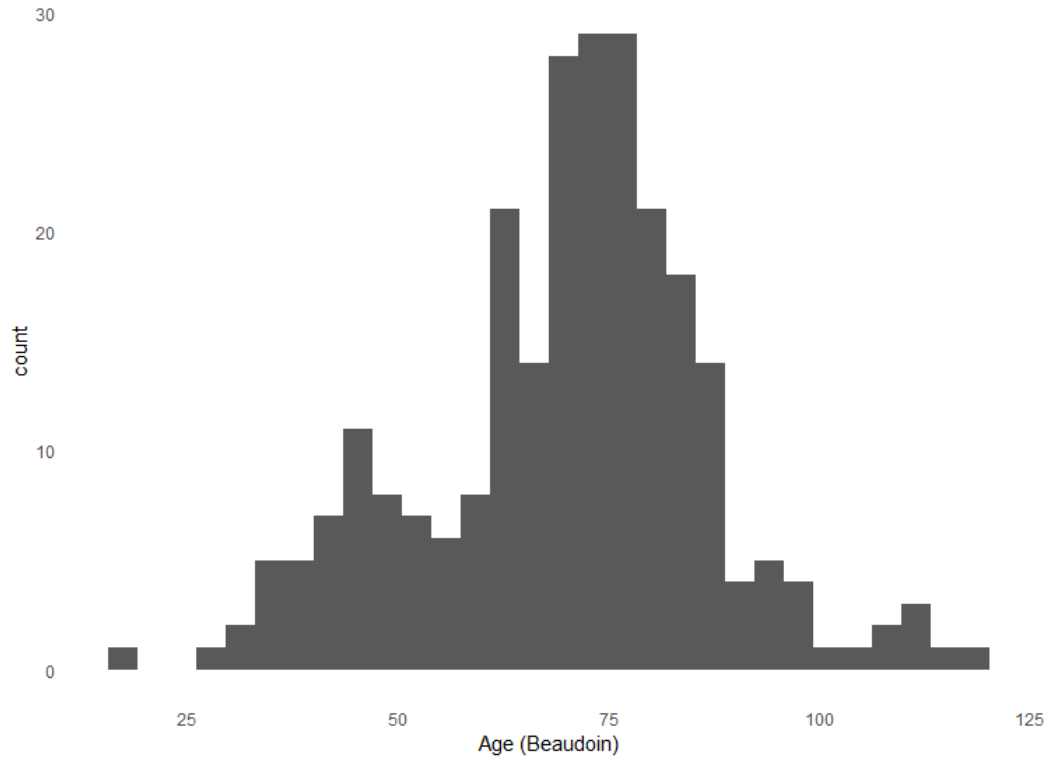


**Figure 6.4** The relationship between the deviation from the expected normal temperature (Celsius) and the probability of detecting a Pileated Woodpecker drum. Shaded area represents the 95% confidence interval.

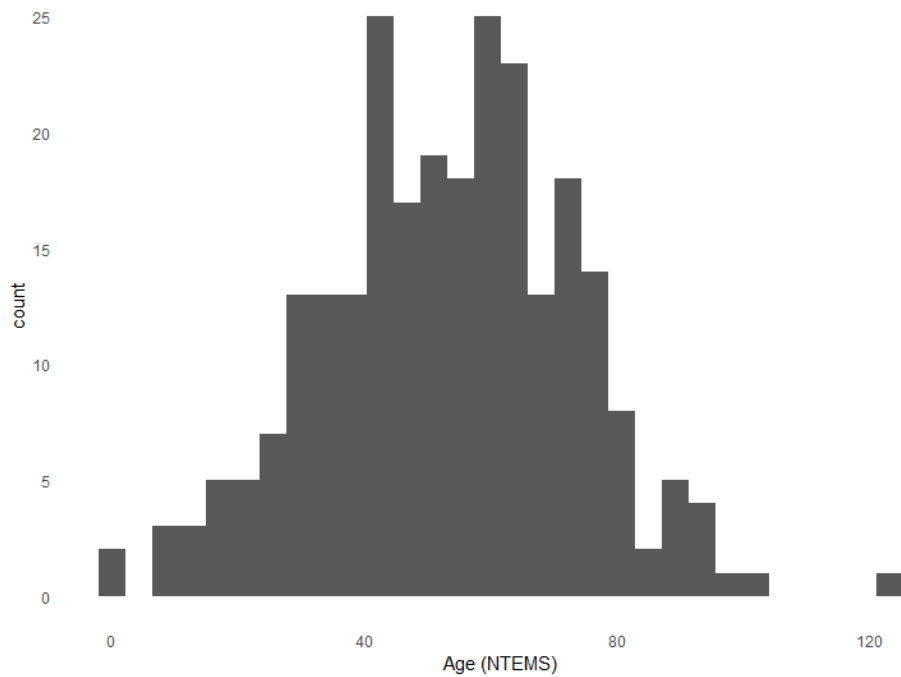


**Figure 6.5** Sample trace plot. The abscissae represent the iterations run through JAGS after burn-in, starting at 400,000. The ordinates represent the values taken by the sample variable at each iteration, and the colours of the different trace lines represent the four independent Markov Chains. This plot displays significant overlap, and the traces span most of the same ordinates' values, indicating exploration of the same approximate probability space.

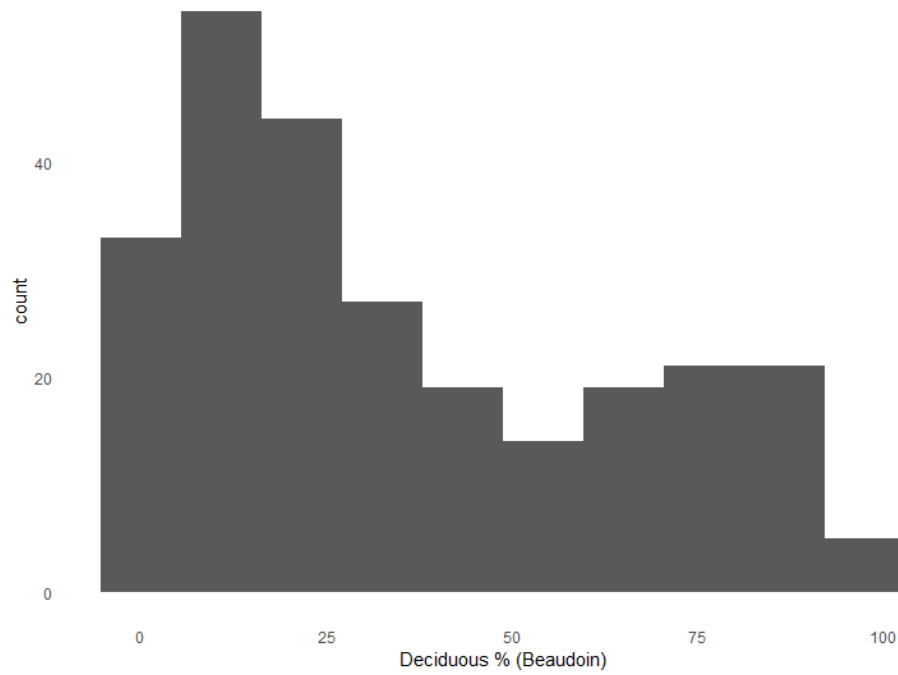




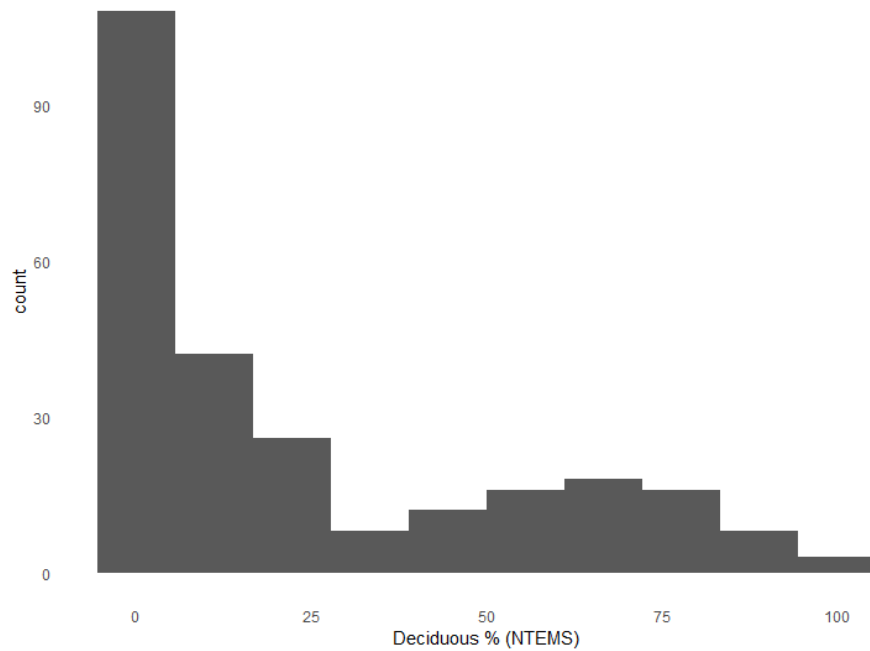
**Figure 6.6** Histogram showing the distribution of age values extracted from Beaudoin *et al.* (2017) at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.



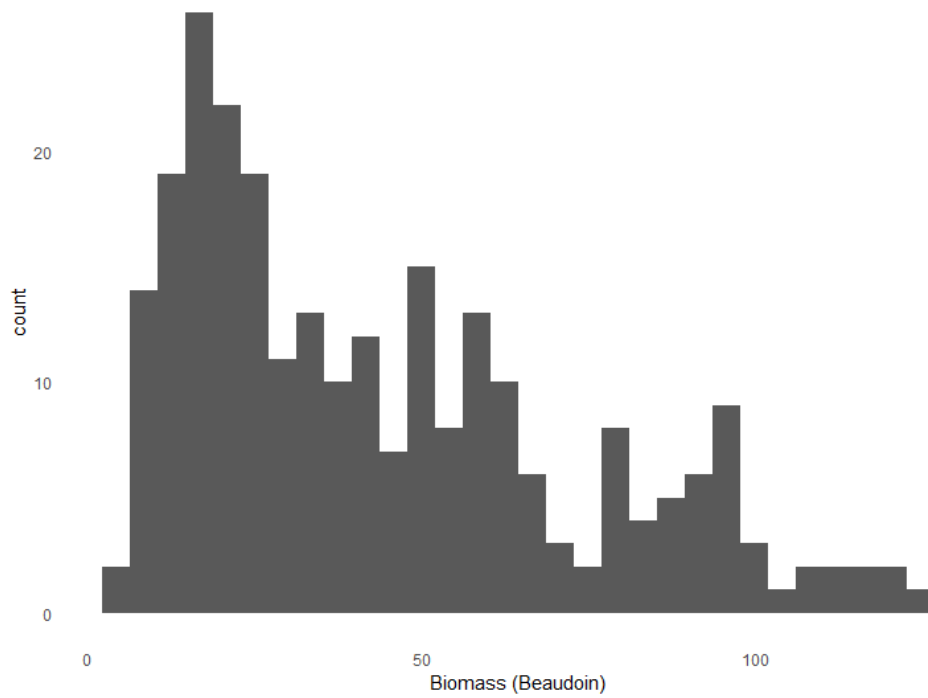
**Figure 6.7** Histogram showing the distribution of age values extracted from NTEMS at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.



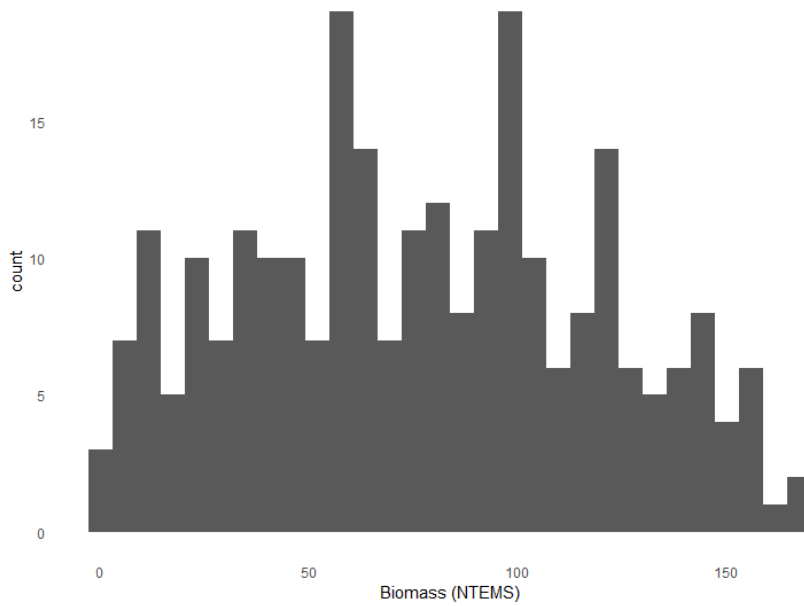
**Figure 6.8** Histogram showing the distribution of deciduous percentage values extracted from Beaudoin *et al.* (2017) at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.



**Figure 6.9** Histogram showing the distribution of deciduous percentage values extracted from NTEMS at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.



**Figure 6.10** Histogram showing the distribution of biomass values extracted from Beaudoin *et al.* (2017) at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.



**Figure 6.11** Histogram showing the distribution of biomass values extracted from NTEMS at 565-meter buffer scale (used as a representative) for locations used in Chapter 3.