INFLUENCE OF FOREST DISTURBANCES ON SUMMER FORAGING ACTIVITY OF BOREAL BATS AT THREE SPATIAL SCALES

By

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Abstract

Bat species worldwide have declined for several reasons, including natural and anthropogenic forest disturbances. In Gros Morne National Park (GMNP), Newfoundland, browsing by hyperabundant moose after insect disturbances has caused conversion of mature forests to open meadows (“moose meadow”, MM). I studied the influences of MM formation in GMNP on bat activity at fine (habitat), intermediate, and broad scales; the first investigation of such impacts by hyperabundant ungulate populations on bat activity. I hypothesized that bat activity would decrease in disturbed areas due to lower insect prey and incompatibility with foraging behaviour. I acoustically monitored bat activity and collected insects in disturbed, regenerating, and mature stand types throughout GMNP at 36 and 63 sites in 2017 and 2018, respectively. I used generalized linear mixed models (GLMMs) to determine significant predictors of bat activity. At the habitat scale, insect prey biomass varied among stand types, but bat activity did not; instead, fine-scale vegetation measurements were the most significant predictors of bat activity. At both the intermediate and broad scales, MM formation was positively associated with bat activity among species-specific responses to other variables. I concluded that MMs positively impacted activity of both species by increasing habitat heterogeneity at the broader landscape scale.

Keywords: acoustic monitoring; disturbances; habitat; landscape; bat foraging activity; insect activity; hyperabundant moose; Gros Morne National Park; Newfoundland, Canada; GLMM

General Summary

Newfoundland is home to two endangered bat species that actively forage and roost in forests during summer. In Gros Morne National Park (GMNP), moose in high densities eat understory vegetation in areas disturbed by insect outbreaks, thus altering natural regeneration and creating open meadows where forests used to stand (“moose meadows”, MM). I set up acoustic detectors and collected insects to develop statistical models of bat activity as a function of habitat and landscape variables at multiple spatial scales to determine how bats are using their environment. At the smallest scale, I collected fewer insects in moose meadows than in other habitat types, but bat activity did not differ among habitats. At the broader scales, bat activity increased with the amount of MM landscape. I conclude that disturbed landscapes are beneficial to bats as these disturbances result in habitat heterogeneity and provide bats with different resources for roosting and foraging.

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List of Abbreviations and Symbols

AIC: Akaike information criterion

AICc: Second order Akaike information criterion corrected for small sample size

ANOVA: Analysis of variance

COSEWIC: Committee on the Status of Endangered Wildlife in Canada

dB: Decibel

DBH: Diameter at breast height

df: Degrees of freedom

FRI: Forest resource inventory

GIS: Geographic Information System

GLMM: Generalized linear mixed model

GMNP: Gros Morne National Park

g: grams

IUCN: International Union for Conservation of Nature

kHz: Kilohertz

km: Kilometers

LABO: *Lasiurus borealis* (Eastern red bat)

LACI: *Lasiurus cinereus* (Hoary bat)

logLik: Log-likelihood

m: Meters

MCF: Mature coniferous forest

MM: Moose meadow

MMF: Mature mixedwood forest

mg: Milligrams

ms: Milliseconds

MUN: Memorial University of Newfoundland

MYLE: *Myotis leibii* (Eastern small-footed myotis)

MYLU: *Myotis lucifugus* (Little brown myotis)

MYSE: *Myotis septentrionalis* (Northern myotis)

NB: New Brunswick

NL: Newfoundland and Labrador

NS: Nova Scotia

PC: Parks Canada

Pd: *Pseudogymnoascus destructans*

QC: Quebec

r: Pearson correlation coefficient

REGEN: Regenerating forest

ROWr: Right-of-way road

ROWt: Right-of-way transmission line

s: Seconds

SNR: Sound to noise ratio

TNNP: Terra Nova National Park

USD: United States dollar ($)

w_i : Akaike weight

WNS: White-nose syndrome

Δ_i : Difference between

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Chapter 1: Introduction and Overview

1.1 Introduction

In recent years, widespread species declines across numerous taxonomic groups have been common globally (Johnson et al. 2017), which may indicate the start of the planet's sixth mass extinction (Barnosky et al. 2011). Bats are no exception to broadly-based trends of species declines, with many factors contributing to their decline, such as anthropogenic alterations to the environment, genetic variation, global climate change, pollution, habitat degradation, invasive species, pathogens, etc. (Voigt and Kingston 2016). While some species can tolerate rapid changes in their environment, others are less resilient.

Bats are often unable to adapt to rapid changes in their environment because they have low birth rates, often have specific habitat requirements, and have high metabolic rates that require high food intake (Safi and Kerth 2004, Voigt and Kingston 2016). Sixteen percent of the 1,304 bat species identified globally are considered at some risk for extinction: categorized as vulnerable, endangered, or critically endangered (IUCN 2020). Bats are important both economically and ecologically (Harvey et al. 2011, Altringham 2011) and scientists have been working to identify threats to different bat species, monitor populations, and conserve habitats or landscape elements important to maintaining bat biodiversity and stabilizing bat populations (Kunz and Racey 1998, Altringham 2011). Top ranked threats worldwide to bat species include biological resource extraction, agriculture, hunting, human intrusion and disturbances, urbanization, energy production (i.e. mining and wind turbines), climate change, and diseases (O'Shea et al. 2016, Frick et al. 2019, IUCN 2020).

In North America, 6 of the 48 bat species recognized are endangered, primarily due to human disturbances, energy production (i.e., wind turbines), urbanization, and white-nose syndrome (Altringham 2011, Frick et al. 2019, IUCN 2020). Nearly half (22 of 48) of North America's bats species are found in the boreal forest, including three species that migrate to warmer latitudes for the winter. At the most northerly extent of the boreal forest, only a few species have been recorded (three species in northwestern Canada [Yukon; Slough et al. 2014) and two species in northeastern Canada (Labrador; Burns et al. 2015)].

Disturbances – both anthropogenic and natural – are common in the boreal biome and may have both direct and indirect impacts on bat populations. However, responses of boreal bats to disturbances have received relatively little study compared to bats in temperate regions (Kalcounis et al. 1999, Jung et al. 2014, Jung 2020). Several studies have suggested positive impacts of silviculture on boreal bat activity by creating gaps and edge habitat (Hogberg et al. 2002, Patriquin and Barclay 2003, Deans et al. 2004). Also, Thomas and Jung (2019) observed increased bat activity with urban development in the Yukon as anthropogenic features in the rural villages provided suitable roosting habitat. Boreal bat populations and their responses to natural disturbances have received even less attention. Jung (2020) compared bat activity between unburned and burned areas, suggesting that severe wildfires may have a negative impact on bat activity. Several studies have investigated impacts of beetle outbreaks on bat populations and found little to no correlation (Randall et al. 2011, Lawson et al. 2019). The responses of boreal bats to natural disturbances is an important knowledge gap, as boreal forest disturbances are likely to increase in the future as global climates shifts (Seidl et al. 2017, Boulanger et al. 2018).

Island ecosystems are often distinctive compared to their mainland counterparts, containing altered competition among species, modified climate, limited resources, and unique disturbances (Whittaker and Fernandez-Palacios 2007). Due to the limited resources and isolation of island ecosystems, anthropogenic disturbances or invasive species can significantly threaten native island species (Jones et al. 2009b). On the Island of Newfoundland, Canada (hereafter referred to as "Newfoundland"), harvesting, wildfire, windthrow and insect outbreaks are the primary disturbances affecting forests. Across the island, insect outbreaks have affected a large proportion of forests, with eastern spruce budworm (*Choristoneura fumiferana*) and hemlock looper (*Lambdina fiscellaria*) as leading defoliators (Arsenault et al. 2016). While these areas would typically undergo natural regeneration following the disturbance, the introduction of moose (*Alces alces*) has altered regeneration patterns in areas with hyperabundant populations (McLaren et al. 2004). National parks, for example, prohibited moose hunting until the 2010s, allowing populations to reach densities higher than anywhere in North America (McLaren et al. 2009). Consequently, in previously disturbed stands, hyperabundant moose browsing has inhibited natural regeneration, resulting in the conversion of mature forests to open meadows, aptly named "moose meadows" (Gosse et al. 2011). Hyperabundant ungulate populations are common in North America and Europe and frequently modify the environment to the detriment of other species (McLaren et al. 2009, Côté et al. 2004, Tremblay et al. 2007, Teichman et al. 2013). For example, Rae et al. (2014) found guild-specific effects of moose meadow presence on forest songbird populations in Newfoundland. To my knowledge, the impacts of forest alteration by hyperabundant ungulates on local bat populations – in Newfoundland or elsewhere - has received no attention.

I used acoustic monitoring methods to investigate the effects of forest disturbance by a hyperabundant ungulate (moose) on local bat populations in Gros Morne National Park (GMNP) in Newfoundland, Canada. I took a multi-scale approach, investigating summer bat activity at fine, intermediate, and broad scales across forest stand types of different successional stages.

1.2 Literature Review

1.2.1 Ecosystem roles of bats

Bats occur worldwide and occupy a variety of niches providing various ecosystem services (Muscarella and Fleming 2007, Kelm et al. 2008, Kunz et al. 2011, Trejo-Salazar et al. 2016). The majority of bats in North America are insectivores, consuming thousands of insects per night, and acting as pest controls. Arthropod destruction of crops, forests, and/or gardens is a problem worldwide and pesticides are expensive and potentially harmful to the environment (Kunz et al. 2011). Bats may eat more than 50% of their body mass in a single night (Kurta et al. 1989, Harvey et al. 2011); consequently, consumption of insects may have substantial economic and ecological implications. Boyles et al. (2011) estimated that North American bats have an economic value of more than $3.7 billion USD/year through their roles in agricultural pest control; similarly, Wanger et al. (2014) found bats contributed $1.2 million USD to food security by protecting local rice crops from a planthopper pest. There has also been some research on the role of pest suppression of disease-carrying mosquitoes. Wray et al. (2018.) observed a high incidence of smaller insectivorous bats consuming a variety of mosquito species and Reiskind and Wund (2009) observed bat predation reducing the egg-laying behaviours of mosquitoes in artificial habitats; however, more research is needed to directly connect mosquito suppression with bat predation (Kunz et al. 2011). In addition to their importance to humans, bats are vital ecologically for the top-down control of herbivorous arthropods, contributing to forest ecosystems (Williams-Guillén et al. 2008, Kalka et al. 2008, Böhm et al. 2011). Bats may be useful as bioindicators of forest health, thereby contributing to our understanding of human impacts on the environment (Jones et al. 2009a, Clare et al. 2014, Russo and Jones 2015, Park 2015, Syaripuddin et al. 2015).

1.2.2 Threats to North American bat populations

In North America, several bat species are currently undergoing decline primarily due to human intrusions into and disturbance of important habitats; this is occurring through energy production and mining, as well as habitat loss associated with residential development (IUCN 2020). Since 2000, bat mortality in North America has been most strongly associated with white-nose syndrome (WNS) and collisions with wind turbines (O’Shea et al. 2016).

The spread of WNS is a recent and dramatic example of the impacts of human intrusions. The epizootic disease, white-nose syndrome, followed the introduction of the fungal pathogen (*Pseudogymnoascus destructans,* hereafter *Pd*) into North American cave systems, likely by humans entering those cave systems. Detected in 2006, WNS has caused mass mortality in multiple North American bat species (n=13) across multiple winters over multiple years (O'Shea et al. 2016). During hibernation, *Pd* causes infections, damages skin membranes, disrupts torpor, and depletes energy reserves, which in combination often results in mortality (Blehert et al. 2009, Frick et al. 2010, Reeder and Moore 2013). Both humans and bats spread *Pd* (Ballman et al. 2017) and once introduced into a hibernaculum, there can be up to 99% mortality (Frick et al. 2010). In just 5 years after the first detection, over 6.7 million bats across North America died due to WNS (Reeder and Moore 2013). Frick et al. (2015) described a ten-fold decrease in bat abundance in hibernacula and local extinctions in some species, making WNS one of the most dangerous threats to North American bats. Currently, WNS is found in 33 states in the United States and 7 Canadian provinces, including Newfoundland and Labrador, where it was first detected in 2016 (Gov NL, 2018).

Energy production, specifically the growing use of wind turbines, also poses a significant threat to bats. Over 30% of bat mortality events reported in North America were caused by collision with wind turbines (O'Shea et al. 2016). Bats may collide with turbines or experience internal hemorrhaging due to barotrauma when near active turbines (Baerwald et al. 2008, Baerwald and Barclay 2011, Arnett and Baerwald 2013). Fatalities may happen randomly, coincidentally during migration, or because bats are actually attracted to wind turbines (Cryan and Barclay 2009). Regardless of the cause, bat mortality at wind energy facilities is heavily biased towards three species, all of which are known to engage in long-distance migratory behaviours (*Lasiurus cinereus* [hoary bat], *Lasiurus borealis* [red bat], and *Lasionycteris noctivagans* [silver-haired bat]). Frick et al. (2017) suggested that hoary bat populations may decline by more than 50% in the next 50 years as a result of mortality at wind energy facilities. Mortality at wind energy facilities is not restricted to the three species listed above; it affects 25% of North American bat species, including several smaller endangered species (e.g., *Myotis lucifugus* [little brown myotis], *Myotis septentrionalis* [northern myotis], and *Perimyotis subflavus* [tri-colored bats]) (Arnett et al. 2008, Zimmerling and Francis 2016). The combined effects of WNS and expanding wind energy sector on these endangered species is particularly problematic (Arnett and Baerwald 2013). Additionally, the indirect impacts of habitat loss following the development of wind energy facilities may impact some bat species (Barré et al. 2018).

Habitat loss is a threat to species around the world, including bats, though the effects are often species- and region-specific. Approximately 56% of bats in North America depend on forests for roosting and summer foraging (Brigham 2007). However, forests are also often habitats that are disturbed by human-related activities, such as forest management and silviculture (Hayes and Loeb 2007, Law et al. 2015) or urban development (Jung and Threlfall 2015). The loss of standing dead trees (snags) and foraging habitats found in forests can be detrimental to bat species, depending on their habitat needs (Law et al. 2015).

1.2.3 Life history of North American bats

The majority (80%) of bat species in Canada are cave bats that make local movements annually to overwinter and hibernate in caves, mines, or abandoned structures (Harvey et al. 2011). During autumn (late August), bats swarm and mate before entering winter roosts for hibernation (Fenton 1969, Fenton 1983, Harvey et al. 2011). In temperate species, females store sperm for the entirety of winter for delayed implantation. Following emergence from hibernation in spring, females ovulate and fertilization ensues (Altringham 2011). This monoestry cycle is a response to shorter summers in higher latitudes that allows females to become pregnant as soon as warmer temperatures occur in spring (Altringham 2011). Females only give birth to one or two pups per year and this low birth rate may contribute to species' inability to recover after major changes to their environment (Voigt and Kingston 2016).

In summer, bats must find locations to roost and forage; both behaviours are essential for survival and successful reproduction (Pierson 1998, Barclay and Kurta 2007). During summer, males and females normally segregate, with males and nonreproductive females roosting individually or in small groups; while females form maternity colonies that may include hundreds or thousands of individuals. The formation of large maternity colonies offsets the thermoregulatory costs of rearing young (Broders and Forbes 2004, Barclay and Kurta 2007, Altringham 2011). Bats may roost in cavities, under the bark of snags, in caves or mines, in rock crevices, or in anthropogenic features, depending on species (Vonhof and Barclay 1996, Hayes 2003, Brigham 2007). Bats that roost in trees often choose taller snags with larger diameters that are located in more open canopies (Kalcounis-Rueppell et al. 2005). Bats may also select roosts near foraging grounds or water (Barclay and Kurta 2007) or, because they frequently switch roots, locations that are near other potential roost sites (Vonhof and Barclay 1996, Arnett and Hayes 2009).

The habitats used for foraging vary considerably among bat species. The majority of North American bats can forage within forests or along forest edges (Fenton 1990, Lacki et al. 2007, Altringham 2011) and productive foraging areas may include riparian habitats (Walsh and Harris 1996, Fukui et al. 2006), complex and mature forests (Crampton and Barclay 1998, Kalcounis et al. 1999, Charbonnier et al. 2016), and contiguous forest (Pierson and Racey 1998, De La Cruz and Ward 2016). Forests provide ample opportunity for bats to hunt as insect diversity and abundance often increases with increasing complexity of vegetation (Ober and Hayes 2008).

1.2.4 Biology of Newfoundland bats

There are two permanent resident bat species on Newfoundland, the little brown myotis and the northern myotis; additionally, hoary bats (*Lasiurus cinereus*) are infrequent vagrants (Washinger et al. 2020). Both *Myotis* species usually depend on forest habitats during summer. In North America, northern myotis have decreasing populations and are listed as near threatened (IUCN 2020); in Canada, they have been listed as endangered since 2013 (COSEWIC 2013). This designation is a consequence of logging, pesticide use, human disturbances during hibernation, and white-nose syndrome (Alves et al. 2014, IUCN 2020). Alves et al. (2014) predicted that relative population reduction of this species could be more than 30% annually due to WNS and consequently this species may be at serious risk of extinction (Langwig et al. 2012, Frick et al. 2015, Langwig et al. 2017). Little brown myotis are also listed as endangered, primarily due to the spread of white-nose syndrome and as a result of mortality at wind turbines (Frick et al. 2010, Zimmerling and Francis 2016, IUCN 2020). Alves et al. (2014) predicted a 16.9% reduction annually in their expected relative population in North America, though there are also more pessimistic (22.9%) and optimistic (6.9%) scenarios. While populations have gone regionally extinct, recent literature has indicated the ability of some little brown myotis to persist after WNS for unknown reasons, which may indicate a capacity for the population to recover given a sufficient amount of time (Langwig et al. 2017).

Northern myotis were historically common in forests of Eastern USA and Canada, extending as far south as Florida. During summer, northern myotis females form relatively small maternity colonies, often underneath exfoliating bark, in crevices, or in cavities of a variety of live trees and snags. Though they are often found in larger trees at or below the canopy (Menzel et al. 2002, Lacki et al. 2009), Park and Broders (2012) found that female northern myotis in Newfoundland roost in trees smaller and shorter than those used by mainland populations.

Northern myotis are clutter-specialists, meaning that they can forage effectively in physically complicated environments (e.g., areas with a lot of dense foliage). Members of this species primarily glean insects off the surfaces of leaves, although they are also able to hawk airborne prey (Ratcliffe and Dawson 2003). They are often found in old-growth, unharvested, closed-canopy, structurally complex forests that allow for ample prey availability and roosting trees required for summer habitat (Caceres and Barclay 2000, Lacki et al. 2009). Northern myotis are generalist predators and consume insects of many orders, depending on season and availability. Several studies show northern myotis feeding on mostly beetles, flies, and moths, a dietary composition that does not differ much from other *Myotis* species (Lee and McCracken 2004, Whitaker 2004). A high proportion of moths in their diet may be due to their specific eco-morphology. Northern myotis emit low intensity, high-frequency echolocation calls that moths cannot hear (Faure et al. 1993). Northern myotis may also prey on spiders (Whitaker 2004) and orthopterans (Lee and McCracken 2004) more than other *Myotis* species.

Little brown myotis are widely distributed across the United States and Canada and are one of the most common bats in Canada, although their populations have declined precipitously following the spread of white-nose syndrome. In summer, little brown myotis use buildings and trees to form maternity colonies and rear their young (Fenton and Barclay 1980, Olson and Barclay 2013). Little brown myotis are fairly flexible in their roosting behaviour and exploit anthropogenic structures more easily than other species (Bergeson et al. 2015). Males and nonreproductive females are more solitary, with males roosting predominantly in rocks and trees (Johnson et al. 2019); meanwhile, female bats are consistently found roosting in anthropogenic structures (Pierson 1998, Bergeson et al. 2015, Johnson et al. 2019) or trees with a large diameter at breast height (DBH), often to accommodate colony size (Olson and Barclay 2013) and provide suitable temperature for preserving energy during torpor and rearing young (Barclay and Kurta 2007).

Little brown myotis are most often observed foraging in aquatic habitats (Anthony and Kunz 1977, Fenton and Barclay 1980, Loeb et al. 2014, Nelson and Gillam 2017, Jung 2020), but have also been observed gleaning insects from vegetation, particularly at higher latitudes (Ratcliffe and Dawson 2003, Shively et al. 2018). They are usually considered generalists (Feldhamer et al. 2009) with a wider dietary niche than the sympatric northern myotis (Broders et al. 2014). Little brown myotis consume insects ranging from 3-10 mm in length, including members of the orders Araneae, Diptera, Coleoptera, Lepidoptera, Trichoptera, Ephemeroptera, Neuroptera, Hemiptera, and Hymenoptera (Anthony and Kunz 1977, Clare et al. 2011). They forage heavily on aquatic-emerging insects, predominantly mayflies, though they have a broad dietary breadth and can also forage in terrestrial habitats (Lee and McCracken 2004, Clare et al. 2011, Broders et al. 2014).

1.2.5 Types of bat surveys

Surveying bat populations is difficult because bats are nocturnal and elusive, making observation and capture of most species challenging. Survey techniques include capturing individuals using harp traps or mist nets, subsequent tracking of captured bats to roost sites using radio telemetry, counting bats emerging from roosts, detection using thermal imaging, and monitoring of free-flying bats using acoustic surveys (Tuttle 1974, Kunz and Kurta 1988, Lacki et al. 2007, Harvey et al. 2011). Each method has its own benefits and drawbacks. Physically capturing bats allows the researcher to collect biological data from bats, including sex, reproductive status, age class, tissue damage following WNS infection, parasite load, tissue samples, and a confident species identification (Kuenzi and Morrison 1998, O'Farrell and Gannon 1999). However, many microchiropterans are very difficult to capture and capture techniques are invasive and introduce the possibility of disease transmission among bats and between bats and humans. For many studies, acoustic recording methods offer a non-invasive and effective way to survey local bat communities.

Around 80% of bats use echolocation when flying in the dark (Walters et al. 2013). Echolocation calls emitted by bats have characteristic structures that often can be identified to species, although identifications can be difficult, as intra-individual and intra-specific call variation is considerable (Simmons et al. 1975, Fenton and Bell 1981, Grinnell et al. 2015). During studies that use acoustic monitoring, bat detectors with specialized microphones are deployed and used to capture the species-specific echolocation calls of local bats. Detectors can be deployed remotely for days, weeks, or months. Recordings of echolocation calls are then displayed using specific software and can often be identified to species or phonic group (Schnitzler and Kalko 2001). There are several software programs that have been developed to automatically identify recordings of echolocation calls to species, but there is much debate on their reliability (Lemen et al. 2015, Russo and Voigt 2016, Rydell et al. 2017). Many researchers choose to manually identify all, or a subset, of their recordings for comparison with automated results (Heim et al. 2015, Kubista and Bruckner 2017) or use multiple software packages to conduct automated identifications (Lemen et al. 2015, Grider et al. 2016, Rydell et al. 2017). Acoustic monitoring can be used to obtain presence/absence data and a relative measure of bat activity in an area (Hayes 1997). Some high-flying and otherwise elusive bats are more detectable acoustically than through capture methods (O'Farrell and Gannon 1999, Sherwin et al. 2000, Jung et al. 2014, Silva and Bernard 2017). There are several significant drawbacks to acoustic monitoring. For example, it can be difficult or impossible to differentiate among some species based on recordings of their echolocation calls due to interspecific similarities between characteristic echolocation calls, which can further be exacerbated by intraspecific variation (Russo et al. 2018). Further, some species produce very low-intensity calls that are often difficult to record (Obrist 1995, Kalko 2004, Broders et al. 2004, Russo and Voigt 2016, Silva and Bernard 2017, Fraser et al 2020).

1.3 Thesis Objectives

The objective of my thesis was to investigate the impacts of forest disturbances on summer bat activity in Gros Morne National Park (GMNP), Newfoundland, with a specific focus on habitat alterations resulting from hyperabundant moose populations. Because bats are highly mobile and require multiple habitats for roosting and foraging, I examined bat activity at three scales: fine-scale (habitat), intermediate (500m), and broad landscape scale (2km). The majority of studies of bat activity are completed at the fine scale, which may not accurately capture all aspects of bat resource requirements (Miller et al. 2003, Duchamp et al. 2007). Fine-scale studies are essential to determine vegetative structure in the immediate surroundings and how it relates to prey abundance. Larger landscape-level analyses can take into account the substantial home ranges of many bat species, and are better suited to determining the role that landscape-level heterogeneity may play in influencing bat activity. Approaches that incorporate multiple scales are most appropriate to inform forest management decisions (Akasaka et al. 2012, Kalda et al. 2015, Gallo et al. 2017).

Chapter 2 includes a fine-scale analysis of bat activity and prey (insect) abundance and species richness in forest stands at different stages of succession: disturbed (moose meadows), regenerating, mature coniferous forest, and mature mixedwood forests. My objective in this chapter was to identify the most important vegetation, environmental, and prey-related predictors of bat activity.

Chapter 3 includes intermediate (500 m buffer) and broad (2,000 m buffer) scale investigations of the influences of forest disturbances on bat activity during summer. I selected the 500 m buffer as an intermediate scale that would ensure uniqueness among sites (no overlap) while reflecting mean linear nightly travel distances observed in *Myotis* species (Grindal 1998, Broders et al. 2006); meanwhile, the larger buffer was selected to include the maximum range of nightly distances traveled by local *Myotis* species in Newfoundland (Park and Broders 2012) and New Brunswick (Broders et al. 2006).

1.4 Co-authorship Statement

This thesis is the result of a collaboration between researchers at Memorial University of Newfoundland (Grenfell Campus) and Parks Canada (Gros Morne National Park). The idea to investigate the impacts of forest disturbance on bat activity in Gros Morne

National Park was conceived by Drs. Darroch Whitaker and Tom Knight. I developed the proposal under the supervision of Dr. Erin Fraser (MUN) and Dr. Tom Knight (PC). The project was funded by Parks Canada and grants held by Dr. Fraser. I planned and conducted all data collection in both the field and laboratory, with the help of two field technicians under my supervision – Vanessa Manuel and Ian Walker – and staff from Parks Canada, who provided necessary maps, insights, and equipment. I conducted data analysis and subsequent interpretation for both manuscripts and wrote the drafts of both manuscripts. Dr. Erin Fraser provided guidance during the data analysis and, along with Dr. Tom Knight, extensively reviewed and edited the chapters. I received advice and support on the project during several meetings with the members of my advisory committee (Dr. Ian Warkentin and Dr. Andre Arsenault).

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Chapter 2: Impacts of habitat conversion by hyperabundant moose on boreal bat activity

2.1 Abstract

Large herbivores can drastically alter local vegetation structure, subsequently affecting biotic communities. Forest dwelling bats are susceptible to a variety of disturbances in their environment. In Gros Morne National Park (GMNP), Newfoundland, intense browsing by hyperabundant moose has suppressed forest regeneration, inducing the conversion of previously disturbed mature forest stands into open meadows, deemed “moose meadows.” This shift in vegetation structure has affected habitat use by other fauna (e.g. songbirds) and has the potential to affect insectivorous bats that use forests for foraging and roosting. I hypothesized that moose meadows would be less suitable habitat for both bats and insect prey than would be regenerating or mature forests. I predicted that reduced vegetation in moose meadow habitat would result in lower insect biomass and consequently, lower levels of bat acoustic activity compared to the other habitat types. I acoustically monitored bats and collected nocturnal insects during summer 2017 and 2018 from four stand types ranging from moose meadows to mature forests. A two-way repeated measures analysis of variance (ANOVA) was used to measure insect activity. Bat activity was modelled using generalized linear mixed models with three model sets, each incorporating a different set of explanatory variables – vegetation, environmental, and insect – and compared them using second-order Akaike information criterion (AICc). Insect activity differed among stand types (ANOVA, $F_{df = 3} = 5.555$, $p<0.01$), with the lowest mean biomass in moose meadows. Contrary to my prediction, generalized linear mixed models did not identify stand type as an important predictor of bat activity in either year. The vegetation model had the best fit (AICc = 1130.6) and suggested that average snag abundance, percent deciduous dominance, and bat species interactions with vegetation height classes were the most influential predictors of bat activity. While *a priori* habitat designations did not predict variation in bat activity, vegetation structure was important and may still indicate a potential effect of forest conversion by moose on summertime bat activity at the fine scale.

Keywords: bat acoustic monitoring; moose meadows; insect biomass; Gros Morne National Park; Newfoundland, Canada; *Myotis*; generalized linear mixed models

2.2 Introduction

Large herbivores, such as ungulates, have the potential to dramatically affect the structure and species composition of biotic communities, especially when their populations reach high densities (Côté et al. 2004, Tremblay et al. 2007, McLaren et al.

2009). In areas where predator populations are reduced or absent, the lack of top-down control facilitates unimpeded population growth in wild ungulates, which can lead to over-browsing and trampling of vegetation. These hyperabundant populations can have cascading effects on a variety of ecological processes, predominantly through changes to vegetation composition (McLaren et al. 2004, Hidding et al. 2013, Charron and Hermanutz 2015). Such changes may cause shifts in local vertebrate and invertebrate communities (Stewart 2001, Côté et al. 2004, Langor et al. 2014). Teichman et al. (2013) found a decrease in yellow warbler (*Dendroica petechia*) and Canadian tiger swallowtail (*Papilio canadensis*) populations after browsing by hyperabundant moose (*Alces alces*) caused a decline in shrub cover that the warblers use for nests and chokecherry (*Prunus virginiana*) density that swallowtails use as larval host plants.

In North America, many bat species are insectivores that use forest ecosystems for roosting, foraging, and commuting. In general, bats forage in areas of old-growth mature forests, edge habitats, riparian systems, and/or use areas with sufficient linear features with minimal obstacles that interfere with echolocation (“flyways”) for commuting (Lacki et al. 2007). While these are general trends, habitat use is species-specific and varies regionally, spatially, and temporally (Lacki et al. 2007) and may be affected by environmental factors, such as disturbances. Disturbances have been documented to be both positively and negatively associated with bat activity, depending on the type of disturbance and the foraging style of the species. For example, open-habitat foragers may exploit disturbed areas if there are ample prey sources, meanwhile, edge- and closed-habitat foragers use a broader range of habitats (Müller et al. 2012) and may be positively (Jantzen and Fenton 2013) or negatively (Morris et al. 2010) associated with edge habitat created by disturbances. In general, bat activity has been positively associated with silviculture (Hogberg et al. 2002, Menzel et al. 2002, Patriquin and Barclay 2003, Dodd et al. 2012), negatively associated with agriculture (Frey-Ehrenbold et al. 2013, Heim et al. 2015), and there have been mixed effects associated with prescribed fires (Armitage and Ober 2012, Silvis et al. 2016), tornadoes (Wolff et al. 2009), urbanization (Johnson et al. 2008, Dixon 2012, Coleman and Barclay 2013), and insect outbreaks (Randall et al. 2011). While there have been documented positive effects of small-scale disturbances on bat activity (Grindal and Brigham 1998), I am unaware of any investigations of the impacts of forest conversion by hyperabundant ungulates on summer bat activity or prey availability.

Moose were successfully introduced to the Island of Newfoundland (hereafter referred to as "Newfoundland") in 1904, and populations have since expanded rapidly in the absence of significant natural predators, competitors, or disease (McLaren et al. 2009, Gosse et al. 2011). In regulated areas, such as Gros Morne National Park (GMNP) and Terra Nova National Park (TNNP), a historical lack of hunting has allowed populations to reach hyperabundant densities (Gosse et al. 2011, Zhu et al. 2010) with resultant landscape-level impacts. In response, moose hunting was introduced by Parks Canada officially in 2011 to reduce moose population size. Since the 1970s, GMNP has suffered extensive, small-scale disturbances from hemlock looper and spruce budworm (Gosse et al. 2011). These insects defoliate conifers and stimulate regeneration cycles. However, moose exploit areas of new growth and preferentially consume early successional species, such as balsam fir (*Abies balsamea*) and palatable hardwoods (specifically, white birch [*Betula papyrifera*]), thus disrupting natural regeneration cycles (Thompson et al. 1992, Langor et al. 2014). As a result, mature forests modified by insect outbreaks may not regenerate naturally and thus could ultimately be converted from closed canopy, balsam fir-dominated forests to open-canopy meadows dominated by spruce species (McLaren et al. 2004), aptly named "moose meadows." Previous work from Rae et al. (2014) found that the probability of occurrence of early successional bird species was positively impacted by moose-altered habitats in GMNP, while both forest interior specialists and generalist bird species were negatively impacted by the creation of moose meadows.

Two bat species are known residents in Newfoundland: little brown myotis (*Myotis lucifugus)* and northern myotis (*M. septentrionalis*). There are also infrequent records of vagrant hoary bats (*Lasiurus cinereus,* Washinger et al. 2020). Both *Myotis* species are listed as endangered in Canada following catastrophic population declines resulting from the introduction and spread of white-nose syndrome (COSEWIC 2013). Little brown myotis and northern myotis are morphologically similar and often co-occur (Lee and McCracken 2004) but may differ in habitat use and diet. Both *Myotis* species use aerial-hawking and gleaning hunting strategies (Ratcliffe and Dawson 2003), but little brown myotis are better adapted for aerial hawking and use a variety of habitats, particularly edge habitats and over open water sources (Saunders and Barclay 1992, Fenton and Bogdanowicz 2002, Broders et al. 2003, Broders et al. 2006, Nelson and Gillam 2017). Water sources seem to be an essential habitat to little brown myotis, and some individuals have been observed traveling over 1 km from a roost site to a water body (Broders et al. 2006). Meanwhile, northern myotis are primarily gleaners that forage within intact forested areas and are often considered clutter-specialists (Fenton and Bogdanowicz 2002, Broders et al. 2003, Altringham 2011). The diet of little brown myotis often consists of aquatic insects and small beetles while northern myotis prey primarily on moths, flies, and slightly larger beetles (Lee and McCracken 2004, Clare et al. 2014).

Insects may also experience taxon-specific effects of alterations to their surrounding environment. Typically, insect abundance and diversity increase with an increase in plant species richness and abundance (Haddad et al. 2001, Crist et al. 2006, Ober and Hayes 2008, Taki et al. 2010, Dodd et al. 2012), edge habitats (Crist et al. 2006, Christie et al. 2010), and canopy cover (Lassau and Hochuli 2007). Therefore, the formation of moose meadows may have an impact on the insect communities, which may subsequently have a bottom-up effect on local bats.

I measured bat activity and nocturnal insect abundance and diversity in four stand types corresponding with various stages of forest succession in GMNP. I hypothesized that forest conversion resulting from extensive browsing by hyperabundant moose impacts bat and insect communities during the summer months and tested the following predictions: (1) that insect abundance and diversity would be lowest in moose meadows, where the lack of trees and other vegetation necessary for many insect orders is largely absent, resulting in (2) a corresponding decrease in bat activity over moose meadow stands, varying by species. (3) I predicted that northern myotis, a species known as a forest-interior specialist, would be more negatively impacted by the presence of moose meadows than would little brown myotis, who are typically more generalist in their habitat selection and may be able to exploit edge habitat created by moose meadows.

2.3 Methodology

2.3.1 Site description

Newfoundland is a large (108,860 km^2) island in the boreal biome and GMNP (1,805 km^2) is located on its west coast. Bat acoustic monitoring and insect collection were conducted in the Western Newfoundland Forest Ecoregion (Damman 1983) of GMNP and some associated enclaves, an area that spans 416 km^2 of the southern portion of GMNP (Figure 2.1). There were also two sites located outside the park (1.9 and 10.6 km away) to compensate for the lack of regenerating plots within GMNP. The Western Newfoundland Forest Ecoregion is characterized by balsam fir-dominated forests with a fern understory and a significant proportion of paper birch and white spruce (*Picea glauca*), as well as black spruce (*P. mariana*) and alder (*Alnus spp.*) thickets on wet sites and lesser amounts of yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), trembling aspen (*Populus tremuloides*), and white pine (*Pinus strobus*) on productive sites (Damman 1983). On average, the Western Newfoundland Forest Ecoregion receives 180 days of precipitation throughout the year (Damman 1983) with precipitation occurring once every two days in the summer (Government of Canada 2019). During the summer, average temperatures range from 16-25°C during the day (Government of Canada 2019). Throughout my study period (June – August), temperatures at night (sunset - sunrise) ranged from 5-22°C (mean: 13.88°C) and I had a total of three rain nights in 2017 and nine nights in 2018.

2.3.2 Site Selection

I sampled 36 sites in each of 2017 and 2018: nine of each forest stand type, as identified by the Parks Canada Forest Resource Inventory (FRI) database: mature conifer forests (MCF), mature mixed forests (MMF), regenerating forests (REGEN), and moose meadows. In 2018, I resampled sites in reverse chronological order compared to 2017. The FRI classified MCF stands as being >60 years and dominated (<50% of basal area) by coniferous species, primarily balsam fir, black spruce, and white spruce; MMF as stands >60 years and dominated by three species, including both coniferous and deciduous species (“softwood-Hardwood” or “Hardwood-softwood” in the FRI); REGEN forest stands as having experienced a disturbance in the past 20 years with progression through normal early succession; and moose meadows (“NSR” in the FRI), which had also undergone recent disturbances, but, in contrast, were unable to regenerate normally in the presence of hyperabundant moose populations, and were defined by open, meadow-like areas.

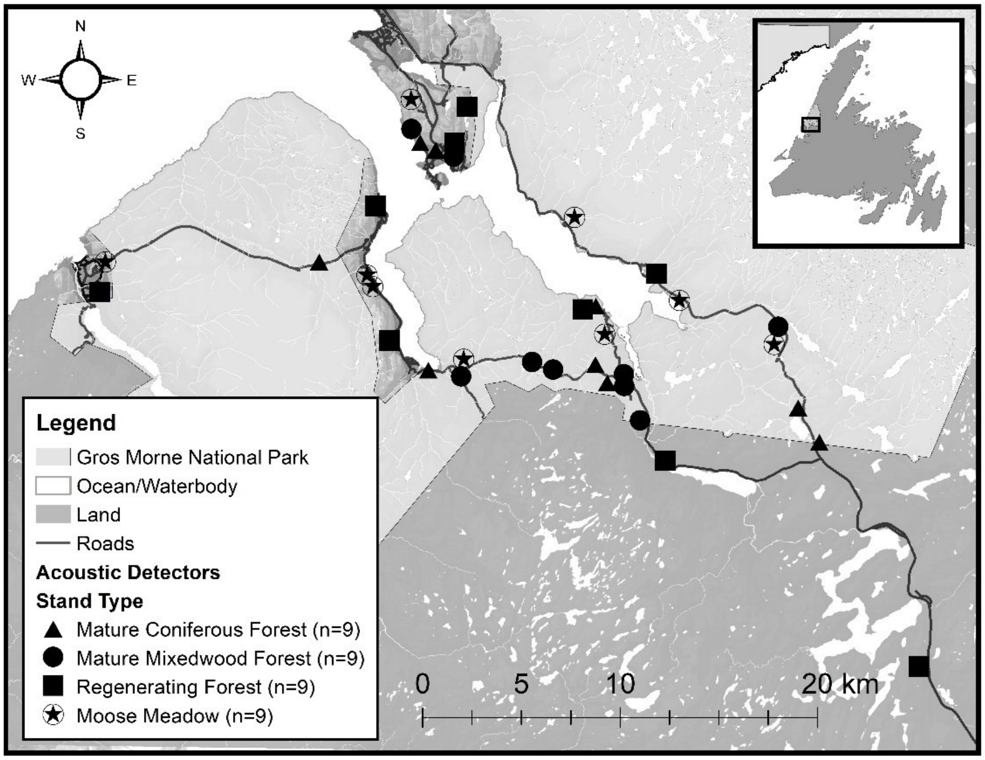

Figure 2.1. Sites sampled throughout Gros Morne National Park, NL and associated enclaves during the summer monitoring periods in each 2017 and 2018.

I selected sites from a set of points randomly generated using ArcGIS 10.2 with the following parameters: located in one of the four forest stand types of interest; situated within stands >3 hectares; <2 km from a road (for access); >500 m from the nearest adjacent point; and >50 m from a water source, hiking path, or road (Figure 2.1). From the 491 points randomly generated, I chose study sites that were accessible by foot and based on forest stand type (making an effort to sample all stand types as evenly as possible). I also selected sites with dimensions suitable to deploy a bat detector and an insect light trap 100 m apart from each other (to avoid insects congregating near bat detectors and potentially attracting bats) and each 50m from the stand edge (to minimize edge effects).

Due to the nature of the landscape in GMNP, stands were patchy and in some cases not able to provide the necessary separation between the bat detector, the insect trap, and the stand edge. Consequently, I slightly adjusted the parameters of the study to increase the number of available study sites. At 10 sites, I set acoustic detectors less than 50 m from the stand edge; at 12 sites, I placed insect traps less than 50 m from the stand edge. However, all but one acoustic detector and one insect trap were at least 40 m from the stand edge. Because I was unable to place all acoustic detectors more than 50 m from a stand edge, distance from edge was taken into consideration during the subsequent statistical analyses. Due to the low number of appropriate regenerating stands within GMNP and the associated enclaves, two REGEN sites were located south of the park; one in Birchy Head and one near Bonne Bay Big Pond (Figure 2.1).

2.3.3 Acoustic Monitoring

I deployed Wildlife Acoustic SM2BAT+ detectors (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com) for a minimum of four nights at each site. Detectors were deployed as close to the predetermined coordinates as possible but were preferentially located in areas with relatively open canopies and minimal acoustic clutter (i.e., objects that interfere with detection). At each detection site, I connected an SMX-U1 external ultrasonic omnidirectional microphone to the detector via a 10 m cable and affixed it to the top of a 6 m metal conduit pole. I drove the pole into the soil and fastened to a tree, preferably one that was shorter than 5 m to avoid obstructing the microphone. I oriented the microphone at a -45° angle (in accordance with Wildlife Acoustics recommendations to maximize weatherproofing) and positioned it in the direction with the least amount of clutter. I programmed settings for SM2BAT+ in accordance with manufacturer guidelines (Appendix A) and set the detector to record during the period from thirty minutes prior to sunset until thirty minutes after sunrise. I placed Onset HOBO pendant temperature/light data loggers (Part # UA-002-08, Onset Computer Corporation, Bourne, Maine) near each detector to measure and record the temperature at thirty-minute intervals for the length of the deployment. To monitor precipitation, I used a rain gauge at an off-site location (near the Bonne Bay Marine Station, 49.51744 N, 57.876472 W) and compared with online weather data. If there was more than thirty minutes of continuous rain on a given night, I omitted that night from the sampling period and the detectors remained deployed for an additional night. There was a total of three rain nights affecting nine sites in 2017 and nine rain nights affecting 15 sites in 2018 that were omitted from the analysis. While I recorded at each site for a minimum of four survey nights, if detectors were deployed longer, recordings were used in subsequent data analysis with an offset variable to account for different lengths of deployment. In 2017, 19 sites had more than four survey nights (nine sites recorded for five nights, four for six nights, six for seven nights) and there were 10 sites in 2018 that with recordings for five nights. For sites that were missing temperature data due to equipment malfunction, I obtained nightly averages using Environment and Climate Change Canada (2019) historical data for the closest weather station located in Rocky Harbour.

2.3.4 Insect Sampling

To measure insect abundance and diversity, I deployed insect light traps at each site in both 2017 and 2018 (Dodd et al. 2008, Dodd et al. 2012, Ketzler et al. 2017). I placed insect traps at least 100 m away from the acoustic detectors to prevent potentially inflating measures of bat activity in the event that bats were attracted to higher-than-normal concentrations of insects around the insect traps (Froidevaux et al. 2018). I constructed traps using five-gallon buckets with large plastic vanes and lit using a battery-operated outdoor string of 67 LED lights (Appendix B). The battery-operated lights (Product #052-8027-6, NOMA, Illinois, USA) worked on a 6-h on, 18-h off timer and were set to turn on at sunset the night before deployment. While a pilot study showed some of the timers were slightly offset, the light traps still ran between sunset and sunrise for the duration of each sampling period. I suspended a water-activated insecticidal strip (Hercon Environmental Vaportape II) in each bucket, hung insect traps from tree branches ~2 m above ground, and collected it after the four-day survey period. I preserved collected insects in 70% ethanol until I were able to identify them in the lab.

I counted and identified insects to taxonomic order (Borror et al. 1989), separated samples by order, and dried first in a fume hood overnight and then in a drying oven for four days at 60°C (Threlfall et al. 2012). To obtain dry biomass, I weighed samples (to the nearest 0.1 mg) of each order: Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, and Trichoptera. In subsequent analyses, Hemiptera and Hymentopera biomass were not considered as they are not part of the five main prey groups documented for the *Myotis* species that inhabit GMNP (Clare et al. 2014). I separated arachnids and non-flying insects (i.e., Collembola) and omitted them from further analysis due to the ineffectiveness of light traps on these non-targeted species (Scanlon and Petit 2008). I calculated the mean dry biomass by night and used this mean value in subsequent analyses as a measure of nocturnal insect biomass per site.

2.3.5 Vegetation Measurements

I characterized fine-scale habitat at each study site in 2017 using three parameters: canopy cover, vegetation cover, and dominant species presence. At each site, I conducted two strip transects; in most cases, one transect was located at the acoustic detector and one at the insect trap. Transects were 20 m long and 2 m wide, similar to vegetation sampling completed in the Park (Government of Canada 2017), beginning at the acoustic detector/insect trap and oriented north. When the acoustic detector and insect trap were located at the same coordinates, I took the second vegetation transect 25 m east, still oriented north.

For each transect, I counted the number of woody tree stems present and categorized them by diameter at breast height (DBH), height class, and tree type (deciduous, coniferous, or snag). Following O'Keefe et al. (2014), I characterized height into three classes: understory (<1.4 m tall; <4 cm DBH), midstory (>1.4 m tall; 4-10 cm DBH), and canopy (tallest trees >10 cm DBH). During each transect, I used a spherical densiometer to measure percent canopy cover every 4 m, for a total of six readings per transect; I used average percent canopy cover in subsequent analyses. At each site, I recorded the dominant tree species in the immediate surrounding habitat along with any other observations deemed relevant.

2.3.6 Acoustic Recordings Analysis

I analyzed each sound file using two automated identification programs: Sonobat 4.2.1 (Arcata, CA, USA; www.sonobat.com) and Kaleidoscope Pro 4.3.2 (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com). Initially, I filtered each file by using the noise scrubbers of both programs to eliminate recordings of non-bat sounds. I then used each program to identify recordings to species or, in the case of atypical or low-quality recordings, classified them as an unidentified bat. Differentiating between the echolocation calls of little brown myotis and northern myotis can be difficult or impossible (Obrist 1995, Barclay 1999, Broders et al. 2004, Russo and Voigt 2016). To increase the likelihood of correctly identifying calls of these species, I only accepted species-level identifications that corresponded between the two programs. In a preliminary examination of 2017 recordings, I used the recommended settings for both programs (Appendix C), which resulted in a low species-identification agreement between the two packages (15% of the dataset). Therefore, I re-analyzed the recordings using less restrictive parameters (Kaleidoscope: sensitivity setting was changed to "-1 More Sensitive [Liberal]"; Sonobat: the number of minimum pulses was changed to ≥ 2 [Farrow and Broders 2011, Randall et al. 2011, Heim et al. 2015, Silvis et al. 2016] with a probability of > 0.98). This analysis resulted in an increased rate of species-identification agreement (34% of the dataset), hereafter referred to as "accepted identifications", and was used in the 2018 analysis of sound files (Appendix D).

Additionally, I manually examined each of the accepted identifications (DPW) to corroborate the species identification. Due to the high number of calls classified as noise, I further manually examined the remaining files (under supervision of Dr. Erin E. Fraser) to confirm which of the remaining recordings were of unidentified bat calls. If echolocation passes were detected, I made a species-level identification or labeled the recording as unidentified. All recordings determined to be from a bat were used in further analyses.

2.3.7 Statistical Analyses

I conducted all statistical analyses using R v.3.6.1 (R Core Team 2019). To determine if mean insect biomass (insect biomass night^{-1}) per site differed among forest stand types or years, I ran two-way repeated measures analysis of variance (ANOVA) on log-transformed insect biomass. I log-transformed insect biomass to fix failed assumptions of normality (Shapiro-Wilk; $w = 0.59108$, $p < 0.001$).

First, I compared bat activity, defined as the number of bat passes per site, among forest stand types and between years. Subsequently, I modeled bat activity as a function of three different model sets of fixed predictor variables: vegetation-related variables, environmental variables, and variables related to the local insect community (Table 2.1). For all analyses, I used negative binomial generalized linear mixed models (GLMMs, function *glmer.nb* in "lme4" package [Bates et al. 2015]) with log-link functions. The negative binomial distribution was used to address overdispersion in the data and the log-link function ensured positive fitted predictions in the count data. Because each site was resampled in both 2017 and 2018, I included site as a random factor to avoid pseudo-replication and violations of assumed independence in all models. I also added an offset variable to account for the difference in the number of nights surveyed. Before running models, I examined variables using Pearson's correlation matrix to test for collinearity and ensure independence. The only covariates with a correlation $|r| > 0.5$ (Dormann et al.

2013) were mean canopy stem density (which I removed) and average canopy cover (r = 0.717).

I centered and scaled all fixed predictors to avoid issues with convergence and make main effects more interpretable (Schielzeth 2010). I incorporated bat species identifications, including unidentified bat recordings, into models as a fixed categorical predictor to account for species-level responses between the two resident species. Variable interactions with bat species and year were the only interactions considered due to small sample size.

I used information criterion-based model selection to achieve the best model for each of the three model sets. I sequentially removed variables based on likelihood ratio tests via the *drop1* command in R (R Core Team 2019) until the minimal Akaike information criterion (AIC) value was achieved (Zuur et al. 2009). To ensure no patterns appeared in the residuals, I visually inspected all simulated residuals using the DHARMa package in R (Hartig 2019). I used second-order Akaike information criterion (AICc) corrected for small sample size for model comparison (*model.sel* function in "MuMIn" package, Barton 2019) among model sets and the null model, which only included the random term.

Table 2.1. Predictor variables used in each of three model sets to explore variation in bat activity among sites in the Western Newfoundland Ecoregion of Gros Morne National Park, Newfoundland, Canada. Mean vegetation variables were calculated from two 20 x 2m line transects at each site.

Predictor Variables	**Type**	**Description**
Vegetation		
Mean Number of Snags	Continuous	Mean number of snags (dead trees) >1.4m tall per 20x2m transect
Mean Number of Understory Stems	Continuous	Mean number of understory stems (<1.4m tall; <4cm DBH) per 20x2m transect
Mean Number of Midstory Stems	Continuous	Mean number of midstory stems (>1.4m tall; 4-10cm DBH) per 20x2m transect
Canopy Cover (%)	Continuous	Mean percentage canopy cover
Deciduous Dominance (%)	Continuous	Number of total deciduous stems divided by the total number of stems per site
Stand Type	Categorical	Pre-established forest stand types: Mature Conifer Forest; Mature Mixed Forest; Moose Meadow; Regenerating
Year	Categorical	Survey year: 2017 & 2018
Environmental		
Julian Date	Continuous	Mean Julian date from all nights that bat detectors ran
Mean Temperature	Continuous	Mean temperature logged from each survey night (sunset to sunrise) per site
Distance to Edge	Continuous	Distance from the bat detector to nearest stand edge
Elevation	Continuous	Elevation (m) of the bat detector
Moon Luminosity	Continuous	Average percent luminosity of the moon on nights the bat detector was deployed
Distance to Water	Continuous	Distance from the bat detector to the nearest water source
Nearest Water Feature	Categorical	Closest water source: Lake, Stream, or River
Year	Categorical	Survey year: 2017 & 2018
Insect		
Mean Insect Biomass	Continuous	Mean nocturnal insect biomass per night per site collected from light traps
Number of Orders	Continuous	Total number of orders collected from light trap
Shannon Weaver Diversity Index	Continuous	Calculated Shannon Weaver index from samples collected in the light trap (vegan package in R, Oksanen et al. 2019)
Year	Categorical	Survey year: 2017 & 2018
Accepted Identifications		
Species	Categorical	Species identification: *Myotis lucifugus*, *Myotis septentrionalis*, or unidentified

2.4 Results

2.4.1 Effects of Stand Type on Insect Biomass

Light traps collected 6,717 nocturnal flying insects of 10 different orders with total biomass of 4.60 g in 2017, and 15,750 insects of 12 different orders with total biomass of 10.64 g in 2018 (Appendix E-Appendix H). There was a significant difference (two-way ANOVA, $F_{(1,61)} = 5.89$, $p = 0.018$) in mean insect biomass night^{-1} site^{-1} between 2017 (mean ± SE: 3.01 ± 0.62 mg) and 2018 (7.05 ± 1.75 mg) and among stand types ($F_{(3,61)} = 5.48$, $p = 0.002$), but no interaction effect ($F_{(3,61)} = 0.35$, $p > 0.05$). Mean insect biomass night^{-1} site^{-1} in moose meadows (1.38 ± 0.28 mg) was significantly lower than in both mature stands, MCF (9.21 ± 3.08 mg, Tukey post-hoc test, $p < 0.01$) and MMF (6.29 ± 1.59 mg, $p < 0.01$). Mean insect biomass night^{-1} site^{-1} in regenerating stands (3.52 ± 1.44 mg) did not differ significantly from moose meadows or mature stands ($p > 0.05$, Figure 2.2).

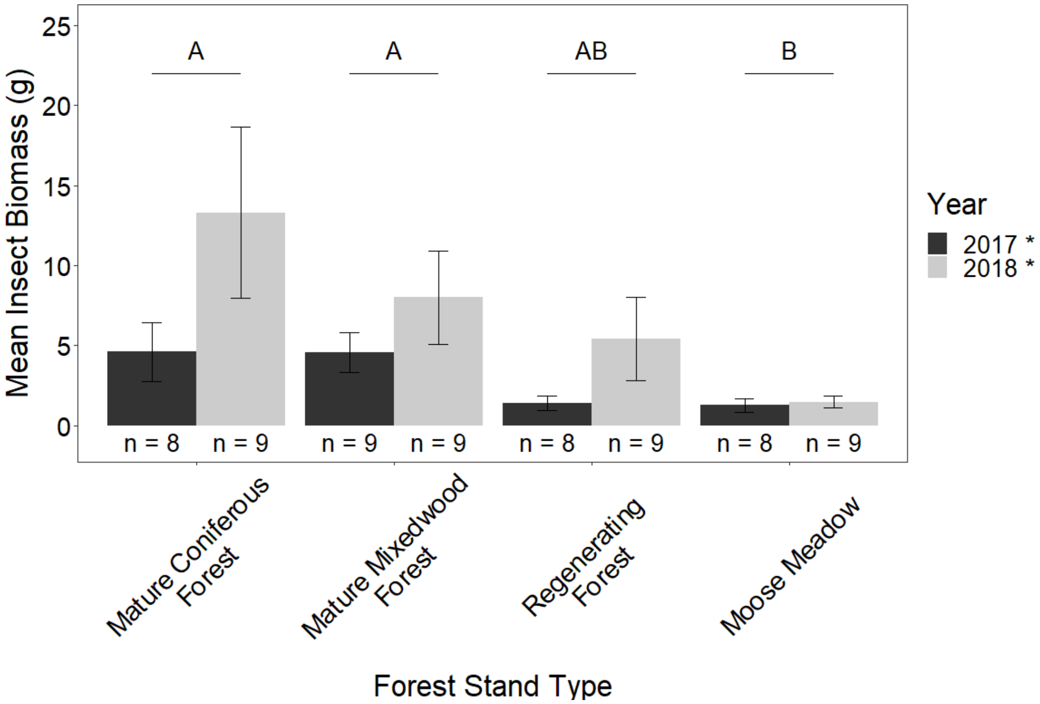

Figure 2.2. Mean insect biomass (g) per night (±SE) in each forest stand type collected during the summers (June – August) of 2017 and 2018. Means that are significantly different among stand types are denoted with letters and between years with an "*" (Tukey post-hoc test, $p<0.05$).

2.4.2 Effects of Stand Type on Bat Activity

Bat detectors recorded 1,900 files in 2017, of which 1,614 were determined to be bat passes; 2,496 files were recorded in 2018 with only 692 bat passes. Across both 2017 and 2018, I was unable to identify the majority (67.0% and 69.2%, respectively) of detections to species. In 2017, I attributed 23.7% of activity to little brown myotis bats; versus only 15.6% of activity in 2018 (Figure 2.3). A detection made on 01 Aug 2017 from a moose meadow site was manually confirmed to be from a hoary bat (*Lasiurus cinereus*) but was omitted from further analyses due to lack of multiple detections. When comparing bat activity among forest stand types, there was a significant interaction effect between forest stand type and year for moose meadows ($z_{df=3} = -2.44$, $p < 0.05$), with 970 detections in 2017 and 85 detections in 2018 (Figure 2.3). There were four moose meadow sites in 2017 that had >100 bat recordings per site, while the highest number of recordings in moose meadow sites in 2018 was 19. A post-hoc analysis was completed to compare bat activity among stand types in 2017 and 2018, separately. Contrary to my hypothesis, there was no significant effect of stand type on bat activity in 2017 (Likelihood Ratio Test; $X^2_{(3, N = 99)} = 2.14$, $p > 0.05$) or 2018 ($X^2_{(3, N = 108)} = 1.44$, $p > 0.05$).

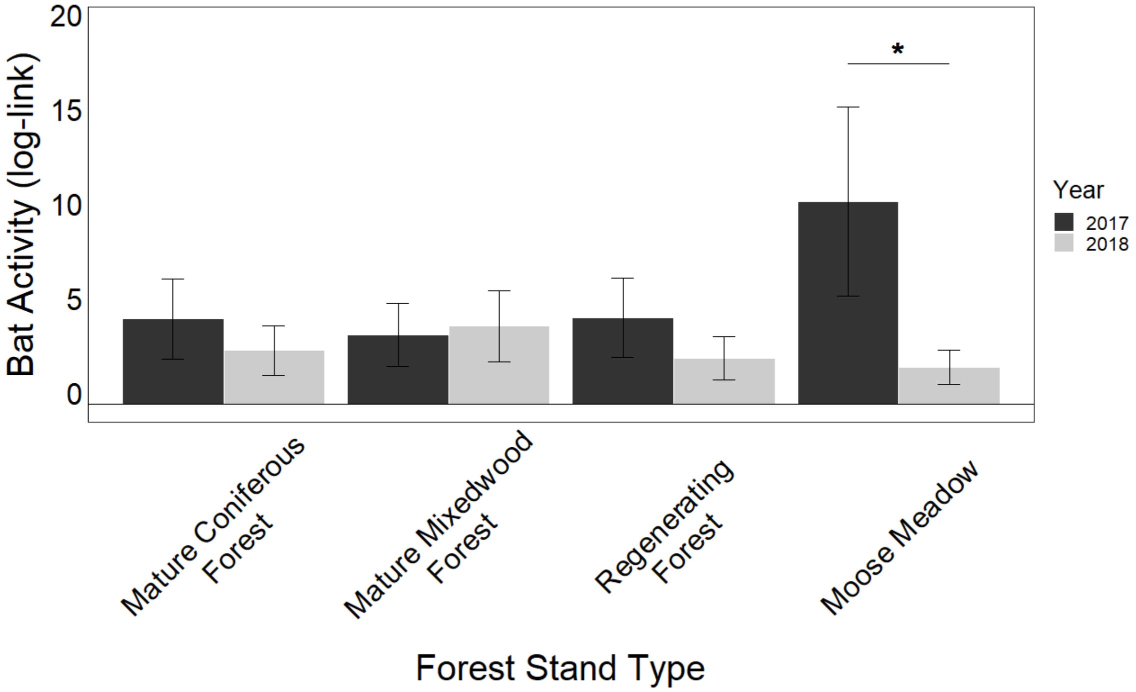

Figure 2.3. Predictor effect plot for bat activity per night (log-link) and the interaction between forest stand type and year with standard error bars. Significant interaction effect ($p < 0.05$) is marked using "*".

2.4.3 Modelling Bat Activity

The best GLMM based on AICc containing vegetation-related variables identified average snag density, percent deciduous dominance, year, and interactions between bat species and stem density at each vegetative height class as influencing bat activity (Table 2.2). Bat activity increased with average snag density ($z_{df=1}$=3.53, p <0.001; Figure 2.4A) and percent deciduous dominance ($z_{df=1}$=4.33, p <0.001; Figure 2.4B) but decreased from 2017 to 2018 ($z_{df=1}$= -3.07, p <0.01). Snags were observed more frequently at transects in mature sites, with snags present at nine transects in MCF sites (n=18) and nine transects in MMF sites (n=18); conversely, snags were observed at two transects in REGEN sites (n=18) and five transects in moose meadow sites (n=18).

Significant interactions terms between species and vegetative height classes revealed that little brown myotis activity was more positively associated with understory stem density than that of northern myotis; little brown myotis activity was positively associated with midstory stem density while northern myotis was negatively associated; little brown myotis activity was negatively associated with canopy cover while northern myotis were positively associated (Figure 2.4C-E). Significant interactions between understory and midstory stem densities and unidentified bat recordings consistently showed trends in between the two species; interactions between canopy cover and unidentified recordings had a positive trend, similar to that of northern myotis.

Table 2.2. Summary of the three best generalized linear mixed models (GLMMs) model sets explaining bat activity (# bat recordings per site) based on vegetation, environmental, and insect variables. Estimated regression parameters, standard errors, *z*-values, and *p*-values of negative binomial GLMMs explaining bat activity in Gros Morne National Park, Newfoundland. The best models were compared using AICc and Akaike's weight (*w*). Interactions are indicated by "x". Significant effects are marked in bold.

Predictor Variable	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
Best Vegetation Model				
$\sigma_{Site} =$ 0.7216				
logLik = -540.3				
AICc = 1132.7				
w = 0.995				
(Intercept)	-0.3725	0.2231	-1.67	0.095
Avg Snag Density	0.7291	0.2066	3.528	**<0.001**
Avg Understory Density	1.0243	0.2222	4.61	**<0.001**
Species: *Myotis septentrionalis*	-0.3534	0.2155	-1.64	0.101
Species: Unidentified	1.4896	0.1927	7.731	**<0.001**
Avg Midstory Density	0.4758	0.2042	2.33	**0.020**
Avg Canopy Cover (%)	-0.3075	0.232	-1.325	0.185
Deciduous Dominance (%)	0.9556	0.2205	4.333	**<0.001**
Year: 2018	-0.5284	0.1722	-3.069	**0.002**
Avg Understory Density x *Myotis septentrionalis*	-0.6051	0.1979	-3.057	**0.002**
Avg Understory Density x Unidentified	-0.497	0.1913	-2.598	**0.009**
Avg Midstory Density x *Myotis septentrionalis*	-1.2213	0.2681	-4.556	**<0.001**
Avg Midstory Density x Unidentified	-0.3967	0.1785	-2.223	**0.026**
Avg Canopy Cover (%) x *Myotis septentrionalis*	0.4817	0.2369	2.033	**0.042**
Avg Canopy Cover (%) x Unidentified	0.5149	0.2099	2.453	**0.014**
Best Environment Model				
$\sigma_{Site} =$ 1.105				
logLik = -557.8				
AICc = 1143.4				
weight = 0.005				
(Intercept)	-0.06633	0.91438	-0.073	0.942
Avg Julian Date	0.44198	0.09648	4.581	**<0.001**
Elevation	-0.41209	0.21267	-1.938	0.053

Water Feature: River	-0.58887	0.94653	-0.622	0.534
Water Feature: Stream	1.38296	1.2809	1.08	0.280
Species: *Myotis septentionalis*	-2.14507	1.00601	-2.132	**0.033**
Species: Unidentified	0.05803	0.75804	0.077	0.939
River x *Myotis septentionalis*	2.03192	1.03121	1.97	**0.049**
Stream x *Myotis septentionalis*	-1.64231	1.35232	-1.214	0.225
River x Unidentified	1.44761	0.78636	1.841	0.066
Stream x Unidentified	0.41814	1.02567	0.408	0.684
Best Insect Model				
σ_{Site} = 1.225				
logLik = -566.1				
AICc = 1148.9				
weight = 0.000				
(Intercept)	0.035	0.255	0.136	0.892
Number of Insect Orders	0.659	0.157	4.193	**<0.001**
Year: 2018	-0.786	0.182	-4.324	**<0.001**
Species: *Myotis septentionalis*	-0.409	0.222	-1.843	0.065
Species: Unidentified	1.260	0.200	6.292	**<0.001**
Number of Insect Orders x Year: 2018	-0.395	0.241	-1.642	0.101

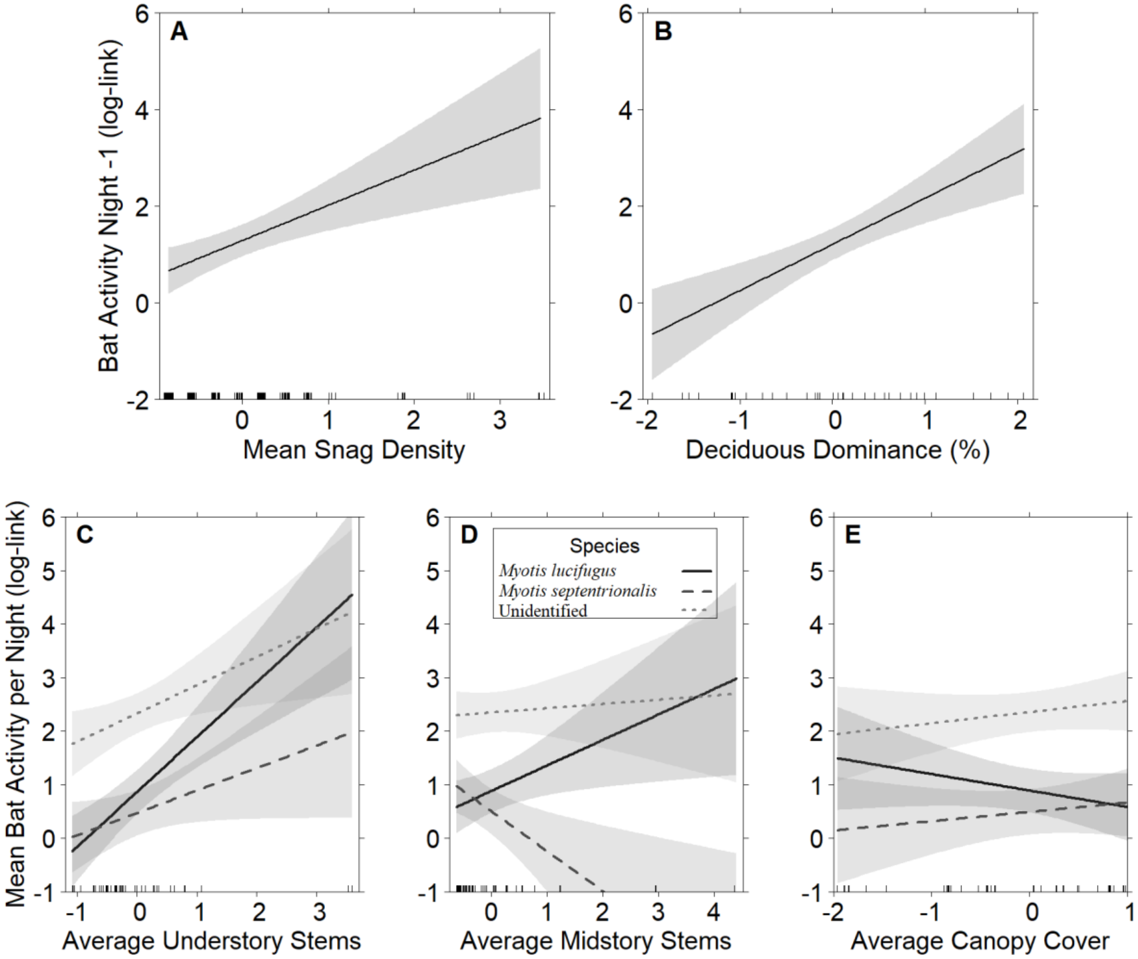

Figure 2.4. Fit of vegetation predictor variables plotted against bat activity per night (log-link) of the best generalized linear mixed model. Interactions between species and vegetation height class are denoted by different line types. Shaded area indicates 95% pointwise confidence intervals.

Within the environmental model set, the best model identified date, elevation, and the interaction between species and the nearest water feature as influencing bat activity (Table 2.2). Contrary to what I expected, temperature was dropped from the best model. Bat activity decreased with an increase in elevation ($z_{df=1} = -1.94$, $p = 0.053$; Figure 2.5A) and increased with date ($z_{df=1} = 4.41$, $p < 0.001$; Figure 2.5B). There was a significant interaction between bat species and nearest water feature type (Figure 2.5C). Little brown myotis activity was consistently higher than northern myotis activity, but was highest when the nearest water feature was a stream or lake while northern myotis activity was highest when the closest water feature was a river. Unidentified bat activity was highest near streams followed by rivers, then lakes.

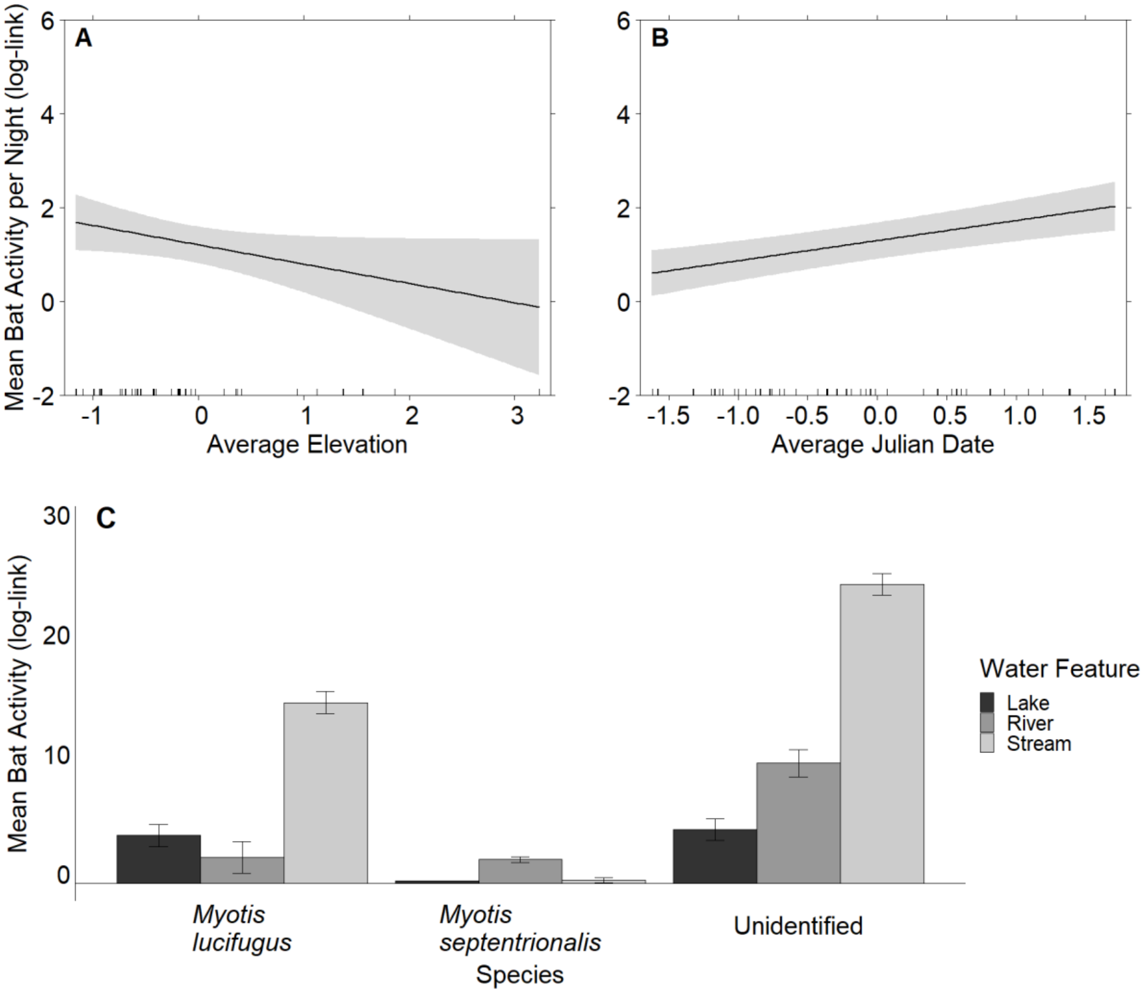

Figure 2.5. Fit of linear environmental predictor variables plotted against bat activity per night (log-link) of the best environmental generalized linear mixed model. Shaded area indicates 95% pointwise confidence intervals; similarly, standard error bars are given for means.

Within the best insect model, bat activity was influenced by bat species and the interaction between number of insect orders and year (Table 2.2). Contrary to my hypothesis, insect biomass was dropped from models, even when considering an interaction with year. There was an insignificant interaction between year and insect diversity retained in the best model ($z_{df=1} = -1.64$, $p > 0.05$; Figure 2.6A); but overall bat activity increased with insect diversity in both years (number of orders; $z_{df=1} = 4.19$, $p < 0.001$). There was significantly more unidentified bat activity than species-level identifications ($z_{df=2} = 6.22$, $p < 0.001$; Figure 2.6B). Most bat activity was classified as unidentified (22.28 ± 42.87) followed by little brown myotis activity (7.01 ± 27.37) and northern myotis activity (3.37 ± 7.35).

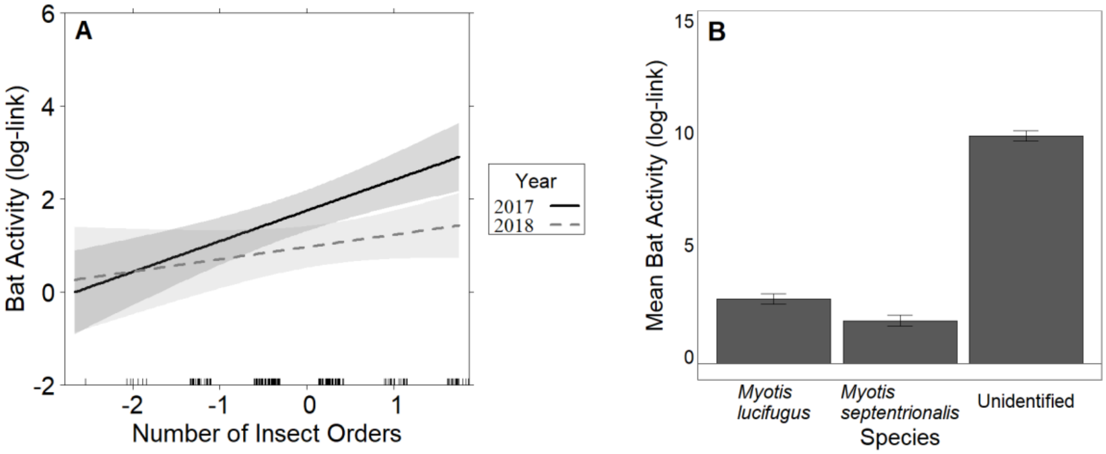

Figure 2.6. Predictor effect plots from the best insect model set for bat activity per night (log-link) and (A) the interaction between year and number of insect orders (scaled and centered) and (B) difference in means of bat species. Shaded area indicates 95% pointwise confidence intervals; similarly, standard error bars are given for means.

When comparing the three best models from each model set (Table 2.2), the best vegetation model set had the lowest AICc and an Akaike weight of .995, followed by the environmental model set (w_i = 0.005) and insect model set (w_i = 0.000). The empirical support for the final vegetation model is >100 times higher than the next best model set, making it the best model to predict bat activity in GMNP, given the dataset (Burnham et al. 2011).

2.5 Discussion

As hypothesized, insect biomass was significantly lower in moose meadows than in mature stands. There was no effect of pre-assigned categorical stand type designation on bat activity. Instead, fine-scale vegetation structure was the most important predictor of bat activity in GMNP, with particular influence associated with snag density, availability of deciduous-dominated habitats, and vegetative height classes. This suggests that pre-established forest stand type was not as informative as fine-scale vegetation measurements in understanding local-scale variation in activity. Other environmental factors, such as elevation, date, available water, and insect diversity played a secondary role.

Structurally complex environments are essential to the life cycles of many arthropod species (Ober and Hayes 2008, Müller et al. 2012, Threlfall et al. 2012, Treitler et al. 2016) that use vegetation for shelter, food, and mating habitats (Müller et al. 2012). In moose meadow stands, moose trample on and browse understory vegetation (Thompson et al. 1992), reducing structural diversity and eliminating features that may be critical for the life history of many local arthropods, and likely contributing to the lower insect biomass that I detected in this habitat.

I observed a disconnect between insect biomass and local bat activity, similar to that reported in other studies (Threlfall et al. 2012, Cox et al. 2016, Pereira et al. 2016, Moore and Best 2018). Total sampled insect biomass may not accurately reflect the availability of insects that bats preferentially prey upon (Pereira et al. 2016, Rainho et al. 2010). For example, an increase in insect biomass may be attributed to larger insects that resident *Myotis* spp. are not morphologically capable of eating (i.e., >10mm, Lee and McCracken 2004, Anthony and Kunz 1977). Additionally, due to limitations with sample size, I was unable to consider interactions with other covariates that may have had an impact on insect abundance (i.e., moon luminosity, temperature, vegetation density).

There is no clear explanation for the decrease in bat activity between study years one and two, as there were no interactions among year and any of the environmental or insect variables, except insect diversity, in this study. It is possible that Newfoundland bat populations are beginning to experience the impacts of white-nose syndrome (WNS), the deadly fungal disease that was first confirmed on Newfoundland in 2016. However, more long-term research is needed to confirm this.

The importance of fine-scale vegetation structure on bat activity has been well documented (Adams et al. 2009, Morris et al. 2010, Dodd et al. 2012, Cox et al. 2016, Threlfall et al. 2017, Moore and Best 2018) and it is possible that the categorical stand designations did not capture the various elements of greatest importance to local bat populations. Firstly, stand structure at sites from the same categorical stand type can vary considerably. For example, some mature stands may have more complex mid- and understory vegetation than others, which can affect species differently. Additionally, some important habitat features, like snag presence and density, did not vary predictably among forest stand types. Snags were one of the most significant predictors for bat activity in GMNP, and yet were found in every stand type. Therefore, I believe that fine-scale vegetation measurements gave better insights into individual features (e.g., snags) than major stand classifications, and that the structural heterogeneity of individual stands better predict bat activity (Jung et al. 2012) than major stand classifications.

Snags have frequently been identified as important features to bat populations (Baker and Lacki 2006, Kalcounis-Rüppell et al. 2005, Arnett and Hayes 2009, Fabianek et al. 2015). They are important for the ecology of both of my study species as summer habitats for roosting, socializing, rearing young, and protection from environmental elements and predators (Barclay and Kurta 2007, Arnett and Hayes 2009, Fabianek et al. 2015). Increased snag density allows greater availability of suitable roosts and ease of roost switching (Arnett and Hayes 2009). Grindal (1998) observed that bats in Newfoundland did not appear to select individual tree roosts based on percentage exfoliating bark or DBH, but instead chose roosting areas that contained a high number of snags with abundant cavities and moved between roosts almost daily. Similarly, Owen et al. (2002), observed northern myotis roosting in areas with an abundance of snags. This study supports these observations that *Myotis* species tend to select roost habitats with a higher abundance of snags.

In the present study, I found snags in every stand type, though at a higher frequency in mature stands. This is unlike other studies that report lower snag density in open habitats (Baker and Lacki 2006, Smith et al. 2009, Moroni and Harris 2010). This is unsurprising, as moose meadows typically occur following insect outbreaks, a type of disturbance that does not usually result in complete tree loss and generates a large number of snags (Moroni 2006). Residual live trees remaining after an insect outbreak can eventually become snags (Moroni and Harris 2010) that may be relevant to local bats. However, these snags typically fall within 30-40 years after a disturbance in Newfoundland (Moroni 2006, Moroni and Harris 2010), due to increased susceptibility to windfall and domestic harvesting (Garber et al. 2005, Smith et al. 2009). Moose meadow formation occurred in GMNP after spruce budworm outbreaks during the 1972-1992 and hemlock looper outbreaks during 1960s-2010s, with the most area disturbed by hemlock looper in the 1980s (McLaren et al. 2009, Arsenault et al. 2016). I expect the conversion of forests to moose meadows to decrease potential roosting habitats as all snags will fall as the 30-40 year snag longevity expires without potential for natural regeneration to create more. This is opposed to mature stands where snags regularly form due to senescence (Thompson et al. 2003, Moroni 2006) or insect defoliators. This is already evident as snags were observed at fewer transects in moose meadow sites than mature sites.

Numerous studies have identified the importance of deciduous dominance for temperate insectivorous bats, as hardwood and mixed forests provide roosts and suitable foraging grounds for bats (Walsh and Harris 1996, Kalcounis et al. 1999, Broders et al. 2006, Akasaka et al. 2010, Bergeson et al. 2013). Deciduous-dominated forests may have higher insect abundance and diversity (Grindal et al. 1999, Johnson and Lacki 2013), potentially offering more productive foraging habitat. Additionally, these habitats offer less vegetative clutter and a more open understory (Broders et al. 2006), protection from wind (Russ and Montgomery 2002), and access to riparian zones (Akasaka et al. 2010), all of which are associated with flying corridors that support commuting activity of bats.

Given the apparent importance of deciduous trees to bats in GMNP, the effects of hyperabundant moose populations may extend beyond the initial formation of moose meadows. Thompson et al. (1992) found that moose significantly reduced balsam fir and sometimes eliminated species of deciduous plants through selective browsing outside of exclosures, resulting in regeneration with fewer deciduous plants. Altered regeneration patterns that do not lead to moose meadow formation, but that also do not include normal deciduous growth, may have a direct impact on bat activity as the stands grow older.

Vegetation structural complexity was particularly important in differentiating the habitat associations of the two resident study species. Similar to Jung et al. (2012), activity of both *Myotis* species was positively associated with understory (ground cover) stem density, which may be related to insect availability, as increased ground cover often contributes to higher insect abundance and diversity (Rainho et al. 2010, Threlfall et al. 2017), although my findings about the association between bat activity and local insect diversity and abundance were mixed. Some of the species-specific findings are contrary to previous evidence. Northern myotis are frequently considered clutter-specialists and are well adapted to foraging in structurally complex habitats (Brooks and Ford 2005, Broders et al. 2006). This life-history characteristic is not supported by the negative association between midstory stem density and activity of this species that I found, particularly as it contrasts with the positive association for little brown myotis. It is possible that the majority of these calls were recorded as bats were flying above the midstory in areas with little or no canopy cover (i.e., regenerating stands). In this case, it would be expected that northern myotis activity would be negatively associated with these areas as they have been known to avoid canopy gaps (Patriquin and Barclay 2003, Morris et al. 2010).

This is further supported by the relationship found between both species and percentage canopy cover. As expected, northern myotis activity increased with increasing canopy cover whereas little brown myotis decreased (Brooks and Ford 2005, Ford et al. 2005, Johnson et al. 2010, Segers and Broders 2014). These findings may indicate the presence of niche partitioning between the two species, as northern myotis primarily forage in closed-canopy habitats and little brown myotis may avoid such areas. It may also suggest that northern myotis would be more susceptible to habitat loss via the loss of canopy cover than the little brown myotis (Arlettaz 1999, Segers and Broders 2014).

While the best model from the vegetation model set had the strongest support for predicting bat activity, many of the factors identified in the other top models can contribute to an understanding bat activity in the boreal forest environment. Similar to Morris et al. (2010), the effect of insect variables was weak in comparison to vegetation measurements, indicating that both insects and environmental variables may play a secondary role in influencing bat activity.

Aquatic habitats are typically very important for bats and distance to water is often an important predictor of bat activity (Bergeson et al. 2013, Fern et al. 2018). The absence of this association in the present study may be due to the abundance of water in

Newfoundland. Approximately 10% of GMNP is covered by over 15,000 freshwater lakes and ponds, which is likely an underrepresentation as it does not include small order streams and bogs. Additionally, the wet climate in GMNP includes over 180 days/year of precipitation (Damman 1983); consequently, surface water is likely not a limiting resource. Little brown myotis show particular affinity for aquatic habitats (Fenton and Bell 1979, Saunders and Barclay 1992, Broders et al. 2006, Bergeson et al. 2013) and prefer standing water, such as lakes, to fast-moving, rippled water (von Frenckell and Barclay 1986, Gehrt and Chelsvig 2003). This preference may be related to insect availability (Broders et al. 2003) or difficulty foraging due to noise associated with moving water (Grindal and Brigham 1999, Schaub et al. 2008). My study supported this as I detected a positive association between little brown myotis in GMNP and the slower-moving bodies of water, lakes and streams.

Bat activity was significantly positively associated with number of insect orders in both years, which may indicate these species are preferentially foraging in areas with higher insect diversity. Both *Myotis* species have adapted to forage in a variety of habitats, which may indicate that they are not limited by prey abundance like open-habitat foragers tend to be (Morris et al. 2010, Müller et al. 2012). Müller et al. (2012) demonstrate that open-habitat bat guilds were limited by prey abundance because they were morphologically unable to forage in dense forests; meanwhile, *Myotis* spp. are able to forage in a variety of habitats, so may preferentially forage in areas with higher insect diversity of the optimal size and maximum nutritional value (Grindal and Brigham 1999, Pereira et al. 2016). Therefore, areas with higher insect diversity may have a higher likelihood of providing prey ideal for consumption by local bat species.

2.6 Conclusion

My study highlights the importance of vegetation structure for both bat and insect communities in a Canadian boreal forest environment. I observed clear effects of the changing landscape caused by hyperabundant moose populations on insect biomass, but did not find a significant effect of categorical stand type on local bat activity. While bat activity was lower in 2018 compared to 2017, there was not a significant difference in bat activity among stand type in either year. I believe that the pre-assigned forest stand type designations did not capture the various elements of greatest importance to local bat populations. Instead, fine-scale vegetation structure was the most significant predictor of bat activity and highlighted the positive associations of bat activity with snag density, percent deciduous dominance, and average understory stem density. Species-specific variation in bat activity among forests with different height class profiles may indicate some niche partitioning. Additionally, there were associations between bat activity and environmental factors – date, elevation, and water features – and insect diversity; however, bat activity was most strongly associated with vegetation structure. These results reveal hyperabundant moose populations may still have an impact on the fine-scale elements of vegetation structure that are relevant to local bat populations.

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Chapter 3: Multi-scale landscape analysis of the effects of disturbances on bat activity in Gros Morne National Park, Newfoundland

3.1 Abstract

Disturbances in the boreal forests of Canada have been known to affect many species at a variety of landscape scales. Because bats travel long distances and can use several habitats in a single night, they may be particularly susceptible to changes in their environment at multiple scales. The present study investigates the effects of natural and anthropogenic disturbances on bat activity in Gros Morne National Park (GMNP), where ~5% of the landscape is classified as disturbed. Using generalized linear mixed models with a negative binomial distribution, I investigated the influence of a suite of landscape variables, with a focus on natural and anthropogenic disturbances, on bat activity at two spatial scales: intermediate (500 m) and broad (2,000 m). At both spatial scales, overall bat activity increased with the amount of naturally disturbed landcover. Anthropogenic disturbances, such as transmission lines and roads, were also important predictors of bat activity. The broad scale analysis had a higher predictive power than did the intermediate level investigation, which highlights the importance of larger landscape-level studies. My study demonstrates the importance of disturbances for local bat species in GMNP and can be used to inform forest management practices.

3.2 Introduction

Boreal forest landscapes frequently experience both natural and anthropogenic disturbances (Boucher and Grondin 2012), with various disturbance types contributing distinctively to the structure of the boreal forest environment (Moloney and Levin 1996). Natural disturbances, such as wildfires, insect outbreaks, and windthrow, are often cyclic (Burton et al. 2003, De Grandpré et al. 2018), and result in a mosaic across the landscape of age and community composition within forest stands (Cyr et al. 2009). Large-scale anthropogenic disturbances have been prevalent in North American boreal forests since the early 1900s (Boucher and Grondin 2012) and include logging, clear cutting for agricultural or residential use, and resource extraction (Angelstam and Kuuluvainen

2004). Humans can also indirectly contribute to landscape alterations by introducing non-native invasive species (e.g., herbivores) that may exacerbate the effects of a disturbance (McLaren et al. 2004, Langor et al. 2014). Additionally, as human-caused climate change progresses, natural disturbances in boreal forests are projected to increase in severity and intensity (Boulanger et al. 2018).

Boreal forests encompass over 14 million km^2 globally and are home to a diversity of birds and mammals, including bats, that must respond to environmental disturbances (Burton et al. 2003, Angelstam and Kuuluvainen 2004). Many North American bat species are sensitive to disturbances, including habitat loss (Miller et al. 2003), forest fragmentation (Ethier and Fahrig 2011), forest management (Hayes and Loeb 2007), insect disturbances (Randall et al. 2011), wildfires (Jung 2020), prescribed fires (Armitage and Ober 2012, Silvis et al. 2016), urban development (Duchamp and Swihart 2008, Coleman and Barclay 2013), and windthrow (Fukui et al. 2011). The effects of these disturbances vary geographically and spatially and may influence bat populations in both positive and negative ways. While most studies focus on stand-level effects of disturbances, it is essential to look at bat activity at broader spatial scales as bats depend on several distinct habitats, each of which may provide distinct resources (Duchamp et al. 2007, Limpert et al. 2007).

Because they fly long distances and use a variety of different landscape elements in a single night (Ethier and Fahrig 2011), insectivorous bats can be especially sensitive to forest disturbances. During the summer months, these bats rely on their environment to provide several major resources – roosts, foraging grounds, water resources, and commuting corridors (Bennett and Hale 2018) – with suitability for each varying temporally, spatially, and by species. In general, roosting habitats require abundant snags with exfoliating bark or cavities for bats to use as roosts and multiple representatives to facilitate roost switching (Fabianek et al. 2015). Foraging habitats need to provide sufficient insect prey, depending on the foraging style of the bat species (Lacki et al. 2007). Because of the unique features required for each resource type and their spatial segregation in many environments, bats may travel substantial distances from foraging grounds to their roosts and may use different roosts on subsequent nights (Barclay and Kurta 2007), and so may also be dependent on commuting corridors that facilitate movement among locations (Henry et al. 2002, Rainho and Palmeirim 2011). Commuting corridors are especially important in windy locations as they often provide shelter from wind (Verboom and Spoelstra 1999).

On the Island of Newfoundland (hereafter referred to as "Newfoundland"), there are two resident bat species: little brown myotis (*Myotis lucifugus*) and northern myotis (*M. septentrionalis*). These two species are similar morphologically but often have differing habitat requirements. Northern myotis are forest-interior specialists that glean their prey from leaves underneath the forest canopy (Caceres and Barclay 2000, Fenton and Bodanowicz 2002). Northern myotis tend to primarily roost in trees, in cavities and under exfoliating bark (Foster and Kurta 1999). Little brown myotis forage mostly in riparian environments (Fenton and Barclay 1980, von Frenckell and Barclay 1987, Lacki et al. 2007), although they use a variety of different foraging habitats. They are opportunistic foragers with a broad diet (Lee and McCracken 2004) and have also been observed foraging in edge habitats and within forests (Fenton and Barclay 1980, Aldridge 1986, Adams 1997, Broders et al. 2006, Bergeson et al. 2013, Nelson and Gillam 2017). Little brown myotis are also flexible in their roost habitats and use both man-made structures and crevices, cavities, and under exfoliating bark of trees (Broders et al. 2006, Barclay and Kurta 2007).

Gros Morne National Park (GMNP, "the Park") was established in 1973 and is located on the western coast of Newfoundland. Nearly 25% of GMNP is covered by balsam-fir dominated boreal forest ecosystems, which are frequently subjected to natural disturbances – insect outbreaks, windthrow, fire, and flooding – in addition to human-related disturbances. Insect outbreaks affect the highest proportion of landcover in the Park, responsible for defoliating over 70 km^2 of forests (Gosse et al. 2011). Typically, these disturbed stands would undergo natural succession, but this process has been altered by non-native moose. Hunting was prohibited in the Park from the establishment until 2011, allowing moose populations to reach densities higher than anywhere else in North America (McLaren et al. 2009). Consequently, moose have altered regeneration of previously-disturbed forests by browsing on saplings, reducing understory stem density, and creating open meadows (termed "moose meadows"; Gosse et al. 2011). Rae et al. (2014) have observed positive associations of moose meadows on early successional bird species and negative associations with forest-interior specialists and generalists. Currently, there has been no research on the impacts of moose meadow formation on bat activity.

My objective was to investigate the impacts of forest disturbances on bat activity in the Park during the period of summer residency in the context of two spatial scales: intermediate (500 m buffer) and broad (2,000 m buffer). Multiple spatial scales were used to inform forest management more accurately as bats may respond to both intermediate and broad scale landscape features (Gorresen et al. 2005). I hypothesized that disturbances at both the intermediate and broad scales, including disturbed landcover and the presence of anthropogenic linear elements (e.g., roads, trails) would influence local bat activity (Grindal and Brigham 1998), depending on species. I predicted that little brown myotis activity would be positively associated with disturbed landcover due to the increased availability of edge habitat; conversely, I predicted the forest-interior specialist northern myotis would be more active in areas with lower proportions of disturbed landcover and more mature forest. I further predicted that linear elements facilitating bat commuting, such as hiking trails, secondary roads, and transmission lines, would have a positive influence on the activity of both species at both scales.

3.3 Methodology

3.3.1 Site description

Gros Morne National Park is the largest national park on the island of Newfoundland (1,805 km^2) spanning three ecoregions – Western Newfoundland Forest, Northern Peninsula Forest, and Long Range Barrens Ecoregions – that contain a wide variety of different landscapes and vegetation types depending on altitude, lithology and climate (Damman 1983). Topography is rugged and elevations in the Park range from 0 – 813 m and include three ecosystems: forest, arctic-alpine, and freshwater. Acoustic monitoring of bats was completed only in the Western Newfoundland Forest ecoregion, which is known for its favourable climate for plant growth and diversity (Damman 1983). Forest stands in this ecoregion are predominantly composed of balsam fir (*Abies balsamea*), which is the most dominant tree type, black spruce (*Picea mariana*), white birch (*Betula papyrifera*), thickets of mountain maple in nutrient-rich sites (*Acer spicatum*), and a diverse understory composed of ferns, alluvial alder swamps, and other hardwood species. Wildfires are rare in this ecoregion (Damman 1983); instead, insect outbreaks, windthrow and logging are the top forest disturbances.

In GMNP, the Western Newfoundland Forest ecoregion encompasses 497.1 km^2 of the southern extent of the park. The landscape is made up of 45.6% (226.9 km^2) boreal forests, 20.6% (102.2 km^2) barren land, 14.0% (69.8 km^2) scrub cover, 6.9% (34.2 km^2) wetlands, 6.7% (33.1 km^2) disturbed land, 5.5% (27.3 km^2) lakes and rivers, and 0.7% (3.6 km^2) residential lands (see Table 2.1 for descriptions). Major disturbances include insect outbreaks (9.3 km^2), wind (3.7 km^2), transmission lines (2.7 km^2), clear-cut forest (1.3 km^2), agriculture (0.14 km^2), and logging (0.10 km^2). Moose meadows cover 15.9 km^2.

3.3.2 Site selection

I sampled nine sites in each of the four pre-established forest stand types as identified by Parks Canada Forest Resources Inventory (FRI) database – mature conifer forest (MCF), mature mixed forest (MMF), regenerating forests (REGEN), and moose meadows – in both 2017 and 2018 using field details from Chapter 2 (*2.3.2 Site*

Selection). During the 2018 sampling period (June – August), I was able to acoustically survey an additional 27 sites: 7 in MCF, MMF, and moose meadow stands and 6 in REGEN stands. I used the data from the 36 sites sampled in both 2017 and 2018 from Chapter 2 (Figure 2.1) and the additional 27 sites surveyed in 2018, resulting in a total of 63 sites; there were 60 sites within GMNP and associated enclaves, and three sites up to 10 km outside of GMNP (Figure 3.1)

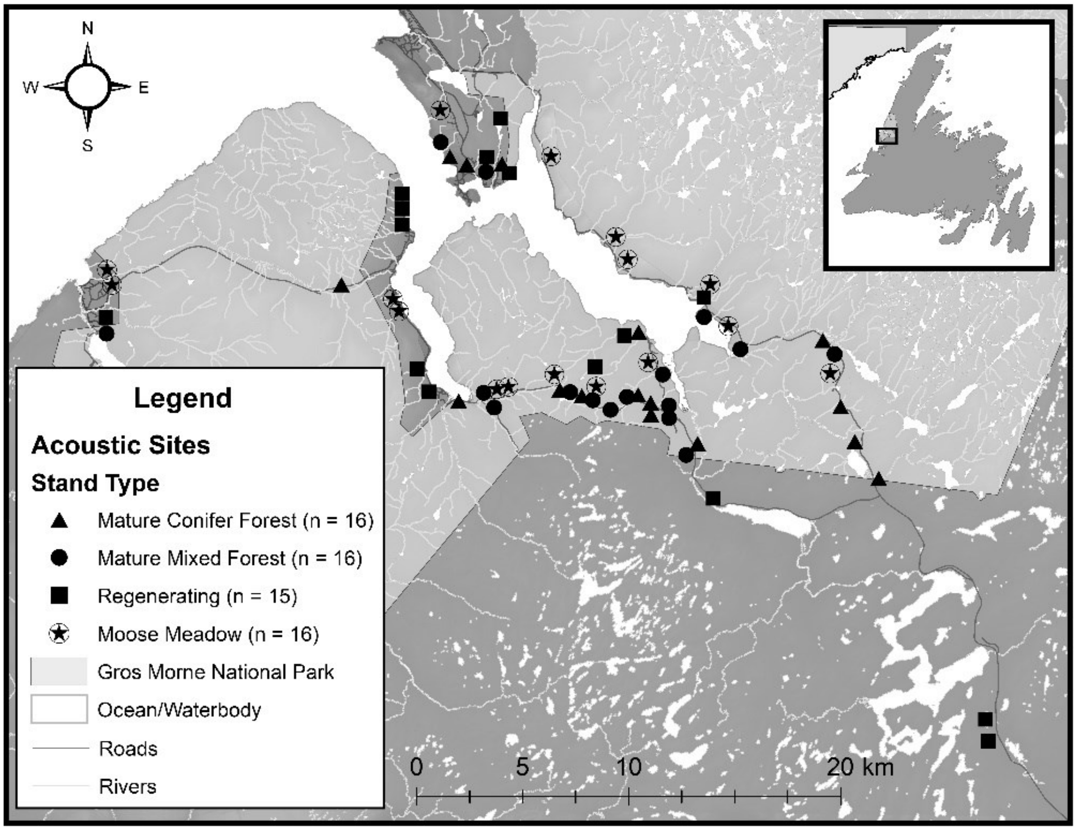

Figure 3.1. Sites sampled throughout Gros Morne National Park, Newfoundland and surrounding areas during the summer monitoring periods (June to August) in 2017 and 2018.

3.3.3 Acoustic Monitoring

Refer to *2.3.3 Acoustic Monitoring* for technical details.

3.3.4 Spatial Analysis

I analyzed bat activity as a function of landscape structure within 500 m and 2,000 m buffers from the recording locations (Figure 3.2). I chose these scales because previous research completed in Newfoundland reported individual bats traveling anywhere between 71 – 2,300 m from the capture site to the roosts (Grindal 1998, Park and Broders 2012) and I wanted to conduct my analyses at both intermediate and broad landscape scales in the context of the home range of local bat populations. I selected the 500 m buffer as an intermediate scale that would ensure uniqueness among sites (no overlap) while reflecting mean linear distances observed in *Myotis* species in NL (Grindal 1998, Park and Broders 2012), Quebec (QC; Henry et al. 2002), and New Brunswick (NB; Broders et al. 2006). The larger buffer was selected to include the maximum range of distances traveled by local *Myotis* species in Newfoundland (Park and Broders 2012) and NB (Broders et al. 2006). Henry et al. (2002) tagged female little brown myotis on an island in QC and recorded flight activity up to 1,000 m. Broders et al. (2006) estimated movement-distances for *Myotis* species in NB: 500 m and 2,000 m for male and female northern myotis, respectively, and 1,000 m for male little brown myotis.

At each survey site, I obtained landscape-level habitat information from ArcMap Geographic Information System (GIS, Esri 2019) geodatabases using Parks Canada (Rocky Harbour, Newfoundland and Labrador, Canada) and Provincial Government (Wildlife Division, Corner Brook, Newfoundland and Labrador, Canada) FRIs. I merged all coordinates from the 63 sites into a shapefile in ArcMap 10.7.1 and drew buffers at two spatial scales: 500 m and 2,000 m around each site (e.g. Figure 3.2). I ensured that there was no overlap between geodatabase layers and that each buffer was standardized with 100% land coverage.

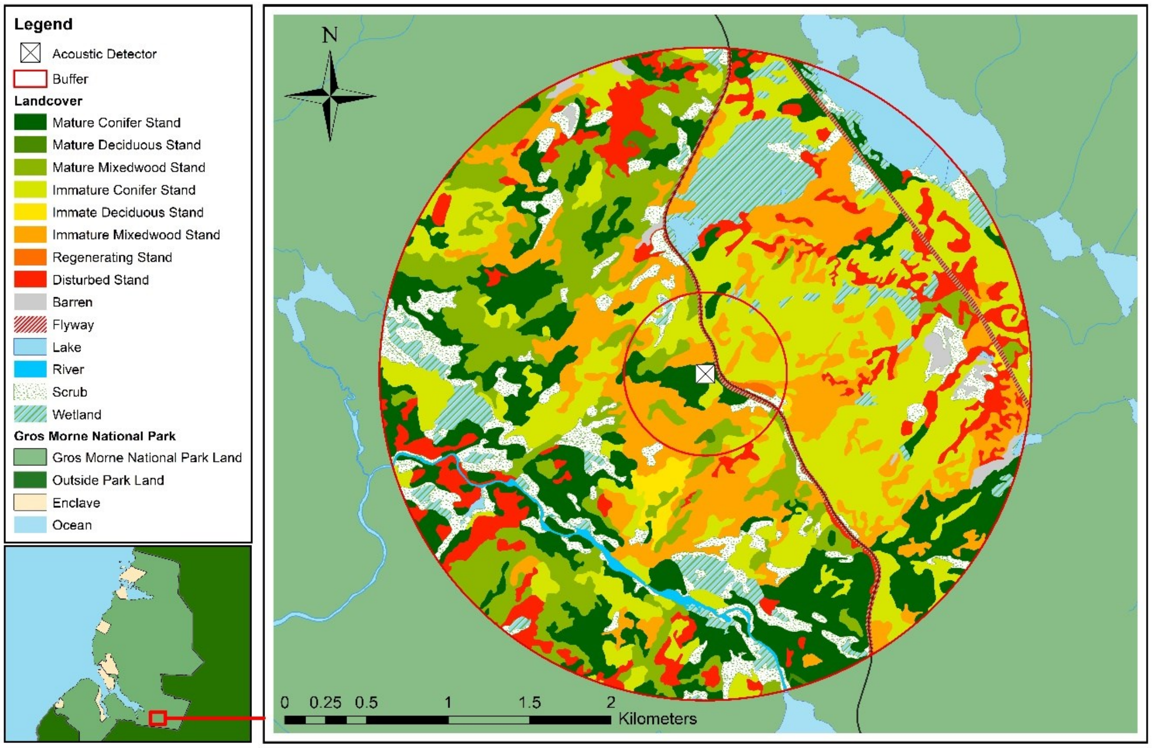

Figure 3.2. An example of different landcover classes encompassing both a 500 m and a 2000 m buffer around a bat acoustic monitoring site in Gros Morne National Park, Newfoundland, Canada.

The FRI classifies the landscape using a variety of different cover types, resulting in 16 non-forest classifications (i.e., agriculture, bog, clear-cut, etc.), 7 different age classes, and 51 different species compositions (Appendix I). From these codes, I consolidated the classifications based on biological relevance into 8 non-forest categories and 8 forest categories (Table 3.1). My prior research (Chapter 2) highlighted the importance of fine-scale vegetation structure on bat activity, so I focused predominantly on forest age class and species composition when defining variables to describe the habitat at a landscape scale. As I was also interested in moose meadows, I focused on disturbed landscapes and consolidated the disturbance categories denoted in the FRI: logged, fire, insect, wind, flooding, and not sufficiently restocked (moose meadows). Although moose meadows are not technically a disturbance, I incorporated them within the disturbance category as they shared many characteristics with the other disturbed habitats within the disturbance category: they had previously undergone a disturbance, had <25% crown cover, a distinct edge habitat, and were not capable of producing forest crop (as defined in the FRI). In addition to landcover data, I also measured the length of linear features within the two buffers using the same methodology (Table 3.1).

Table 3.1. Landcover and linear variables used to model bat activity (bat recordings per site) in Gros Morne National Park, Newfoundland and surrounding area. The mean and standard deviation of the area or linear amount occurring within the buffers around each site are reported for both scales: 500 m and 2,000 m. Average proportion of landcover is given in parentheses. Variables were derived from GMNP Forest Resource Inventory.

Landcover Variables	Description	500 m Buffer	2,000 m Buffer
		Mean landcover ± SD (m^2)	**Mean landcover ± SD (m^2)**
Non-Forest		**195,681 ± 148,631 (24.9%)**	**4,670,199 ± 2,882,121 (37.2%)**
Agriculture	Land cleared for agriculture purposes.	758 ± 3,962 (0.1%)	9,515 ± 21,499 (0.1%)
Ocean	Ocean and coastal landcover	44,695 ± 94,176 (5.7%)	1,858,578 ± 2,182,967 (14.8%)
Freshwater	Rivers and lakes	13,144 ± 30,130 (1.7%)	326,533 ± 410,038 (2.6%)
Wetland	Wetlands, fens, bogs	18,317 ± 29,415 (2.3%)	382,698 ± 381,129 (3.0%)
Scrub	Deciduous and coniferous scrub cover	72,958 ± 83,645 (9.3%)	1,134,530 ± 961,068 (9.0%)
ROWr	Right-of-way roads	11,455 ± 9,742 (1.5%)	91,542 ± 36,302 (0.7%)
ROWt	Right-of-way transmission lines that form stand boundaries	4,924 ± 8,512 (0.6%)	39,777 ± 41,293 (0.3%)
Barren	Rocky barren, sandy, soil barren (<10% tree cover)	10,764 ± 20,683 (1.4%)	613,007 ± 1,052,283 (4.9%)
Residential	Land cleared for residential or commercial development	18,560 ± 44,885 (2.4%)	211,473 ± 279,994 (1.7%)
Other	Non-classified land	108 ± 845 (0.0%)	2,548 ± 4,371 (0.0%)
Forest		**589,510 ± 148,631 (75.1%)**	**7,904,999 [1,055,607 - 11,415,638]**
Disturbed	Age class: 0 years; recently disturbed land that is no longer capable of producing forest crops and has <25% canopy cover; includes moose meadows	72,649 ± 63,858 (9.3%)	812,104 ± 446,386 (6.5%)
Regenerating	Age class: 1-20 years	31,684 ± 57,025 (4.0%)	322,537 ± 586,111 (2.6%)
Immature	Age class: 21-60 years		
Coniferous	Dominated by softwood species	145,322 ± 102,404 (18.5%)	1,920,346 ± 985,117 (15.3%)
Deciduous	Dominated by hardwood species	2,648 ± 12,419 (0.3%)	59,726 ± 153,551 (0.5%)

Mixedwood	Dominated by a mixture of hard- and softwood species	85,504 ± 94,497 (10.9%)	1,063,710 ± 684,607 (8.5%)
Mature	61-121+ year old stands		
Coniferous	Dominated by softwood species	132,107 ± 128,145 (16.8%)	1,977,981 ± 1,620,202 (15.7%)
Deciduous	Dominated by hardwood species	3,252 ± 8,934 (0.4%)	55,502 ± 48,549 (0.4%)
Mixedwood	Dominated by a mixture of hard- and softwood species	116,344 ± 120,135 (14.8%)	1,683,577 ± 1,254,198 (13.4%)
		Mean Length (m) [range]	**Mean Length (m) [range]**
Linear Features		**20,849 ± 4,083**	**274,134 ± 52,762**
Roads	Major paved roads	645 ± 640 (3.0%)	5,430 ± 2,754 (2.1%)
Flyways	Resource roads, utility lines, hiking trails, cut lines	1,107 ± 1,167 (5.0%)	10,583 ± 4,606 (4.0%)
Stream	Continuous watercourse that forms a stand boundary	397 ± 542 (1.9%)	12,849 ± 11,149 (4.4%)
Intermittent Streams	Discontinuous watercourses	555 ± 547 (2.7%)	4,370 ± 3,488 (1.6%)
Water Edge	Edges of rivers and lakes	894 ± 1,654 (3.8%)	8,792 ± 4,119 (3.2%)
Stand Edge	Edge of forest stands	16,983 ± 3,124 (82.1%)	228,653 ± 47,883 (83.2%)
Coastline	Ocean coastlines	268 ± 499 (1.6%)	3,457 ± 3,615 (1.5%)

3.3.5 Statistical Analysis

I conducted all statistical analyses using R v.3.6.1 (R Core Team 2019). I modeled bat activity, defined as the number of bat recordings per site, in the context of the two spatial scales (500 m and 2,000 m) using several different model sets. Due to the number of landcover variables (Table 3.1), a global model with all variables would have resulted in over parameterized models. Therefore, I separated landcover variables into different model sets: non-forest, 3 forest-related model sets, and linear features. My previous research (Chapter 2) showed the importance of forest vegetation variables at fine spatial scales on bat activity, so I ran and compared a total of three mutually exclusive forest models sets, with the intention of selecting and using the best one for subsequent analyses. These three model sets included: forest age and stand type (i.e., immature coniferous, mature mixedwood, etc.), forest stand type (coniferous, deciduous, and mixedwood) and forest age class (mature, immature, regenerating, disturbed).

Before running models, I performed correlation tests at each spatial scale and removed any variables that exceeded $r \geq |0.6|$ from further analysis (Dormann et al. 2013). To decide which correlated variable to retain, I ran univariate models and chose the variable that resulted in the lowest Akaike Information Criterion value corrected for small sample size (AICc) and highest rank (McConville et al. 2014). Consequently, at the 500 m scale, I removed oceans, water edges, right-of-way roads, flyways, residential land, immature forests, and coastlines; at the 2,000 m scale, I removed oceans, right-of-way roads, water edges, coastlines, barren, residential, immature mixedwood forests, mature coniferous forests, and flyways (Appendix J). After correlated variables were removed, I ran negative binomial generalized linear mixed models (GLMMs) with log-link function using the *glmer.nb* function in “lme4” package (Bates et al. 2015). A negative binomial distribution was used to address overdispersion in the data and the log-link function ensured positive fitted predictions in the count data. Site was the random variable and an offset variable was used to account for the number of survey nights completed.

I used backward stepwise selection (*drop1* command in R [R Core Team 2019]) on each model set – non-forest variables, linear elements, forest age and stand, forest stand type, and forest age – to sequentially remove variables until the most parsimonious model with the minimum Akaike Information Criterion (AIC) value was achieved (Zuur et al. 2009). Because I examined forest at several mutually exclusive classifications, the best model of each forest-related model set was compared using *model.sel* function (package: "MuMIN", Barton 2019) and the classification with the lowest AIC and highest Akaike weight (Wagenmakers and Farrell 2004) was used in subsequent analyses. I created a global model with all significant factors from each model set – the best forest-related, non-forest, and linear features – and completed backward stepwise selection until the minimum AIC was attained at each spatial scale. To compare the global model of each spatial scale, I compared AICc values and tri-gamma estimates of the conditional R^2_{GLMM} using *r.squared.GLMM* (package: "MuMIN", Barton 2019) (Nakagawa et al. 2017). For all constructed models, residuals were inspected using the "DHARMa" package (Hartig 2019) to ensure that there were no patterns. I visualized all predictor effects for GLMMs using the "effects" package (Fox 2003, Fox and Weisberg 2018, 2019).

3.4 Results

3.4.1 Bat Activity

I recorded bat activity at 36 sites between June 26 and August 11, 2017 and at 63 sites between June 20 and August 10, 2018. Bat recorders detected 1,852 bat passes (54.4 ± 88.6 bats per site) in 2017 and 1,892 (30.0 ± 55.4 bats per site) in 2018. While the majority of calls in both years (65.3% and 68.9%, respectively) could not be identified to species, for those calls which I was able to distinguish *Myotis lucifugus* was the most frequently detected species in 2017 and *Myotis septentrionalis* was the most frequently detected species in 2018 (Table 3.2).

Table 3.2. Total number of species identifications made during the summer sampling period (June to August) of 2017 and 2018.

Year	***Lasiurus cinereus***	***Myotis lucifugus***	***Myotis septentrionalis***	**Unidentified**
2017	1	393	249	1,209
2018	0	223	365	1,304
Grand Total	**1**	**616**	**614**	**2,513**

3.4.2 Landcover

Among the 500 m buffers, immature coniferous forests made up the largest mean percentage of landcover (18.51%), followed by mature coniferous forests (16.82%) and mature mixedwood forests (14.82%). Disturbances made up 9.35% of the landcover in the 500 m buffer, on average, and were predominantly composed of moose meadows (55.1%). Among the 2,000 m buffers, mature coniferous forests made up the largest mean percentage of landcover (15.74%), followed by immature coniferous stands (15.28%) and oceans (14.79%). Disturbances made up 6.5% of the landcover in the 500 m buffer, on average, and were predominantly composed of moose meadows (52.2%). Stand edges, water edges, and flyways made up the top linear elements in both buffers.

3.4.3 Importance of Landscape Elements

At the 500 m scale, the best forest age model set had the lowest AICc value (1729.38) and the highest weight compared to the other two forest-related model sets (Table 3.3). The forest age model set ($w_i = 0.715$) performed 4 times better than the best forest age and stand type model set (AICc = 1732.11, $w_i = 0.183$) and 7 times better than the forest stand type model set (AICc = 1733.3, $w_i = 0.102$) and was therefore used in subsequent analyses.

Table 3.3. Comparison of the best generalized linear mixed models (GLMMs) of three mutually exclusive forest model sets and their degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion corrected for small sample size (AICc), difference in AICc from top model (Δ_i), Akaike weight (w_i) for each landscape scale (500 m and 2,000 m). Best models were derived by constructing global models of each model set and dropping parameters based on AIC until the lowest AIC is achieved.

Best Model Set	**df**	**logLik**	**AICc**	**Δ_i**	**w_i**
500 m Buffer					
Forest Age	10	-854.31	1729.4	0	0.715
Forest Age & Stand Type	10	-855.67	1732.1	2.73	0.183
Forest Stand Type	11	-859.45	1733.3	3.9	0.102
2,000 m Buffer					
Forest Age & Stand Type	10	-845.75	1712.3	0	0.985
Forest Age	16	-843.39	1720.7	8.45	0.014
Forest Stand Type	10	-852.53	1725.8	13.56	0.001

Within the best forest age model set, there was a positive association with bat activity and disturbed stands ($z_{df=1}$=2.19, $p < 0.05$), a negative association with year ($z_{df=1}$=-3.57, $p < 0.001$), and a species interaction with mature forests. The best non-forest model (AICc = 1733.0) demonstrated a positive association of bat activity with transmission lines ($z_{df=1}$= 1.73, $p = 0.084$), a negative association with barren ($z_{df=1}$= -1.861, $p = 0.0627$) and year ($z_{df=1}$= -3.34, $p < 0.01$), and a species interaction with scrub cover. The linear features model had the lowest AICc (AICc = 1736.76, $w_i = 0.02$) and dropped all terms except for year ($z_{df=1}$= -3.58, $p < 0.01$) and species interactions with flyways and intermittent streams. The forest age model set was the strongest model (w_i = 0.84), followed by the non-forest model (w_i = 0.14) and linear features model (w_i = 0.02).

The global model for the 500 m scale had the lowest AICc (1725.4, w_i = 0.82) when compared to the aforementioned model sets and is the best model at the 500 m scale, given the dataset. With this model, bat activity was positively associated with disturbed landcover and transmission lines and negatively associated with year (Table 3.4). There were also species interactions with mature forests and intermittent streams. Little brown myotis activity was negatively associated with mature forest landcover and intermittent streams; conversely, northern myotis activity increased with mature forests and with intermittent streams (Figure 3.3, Table 3.4).

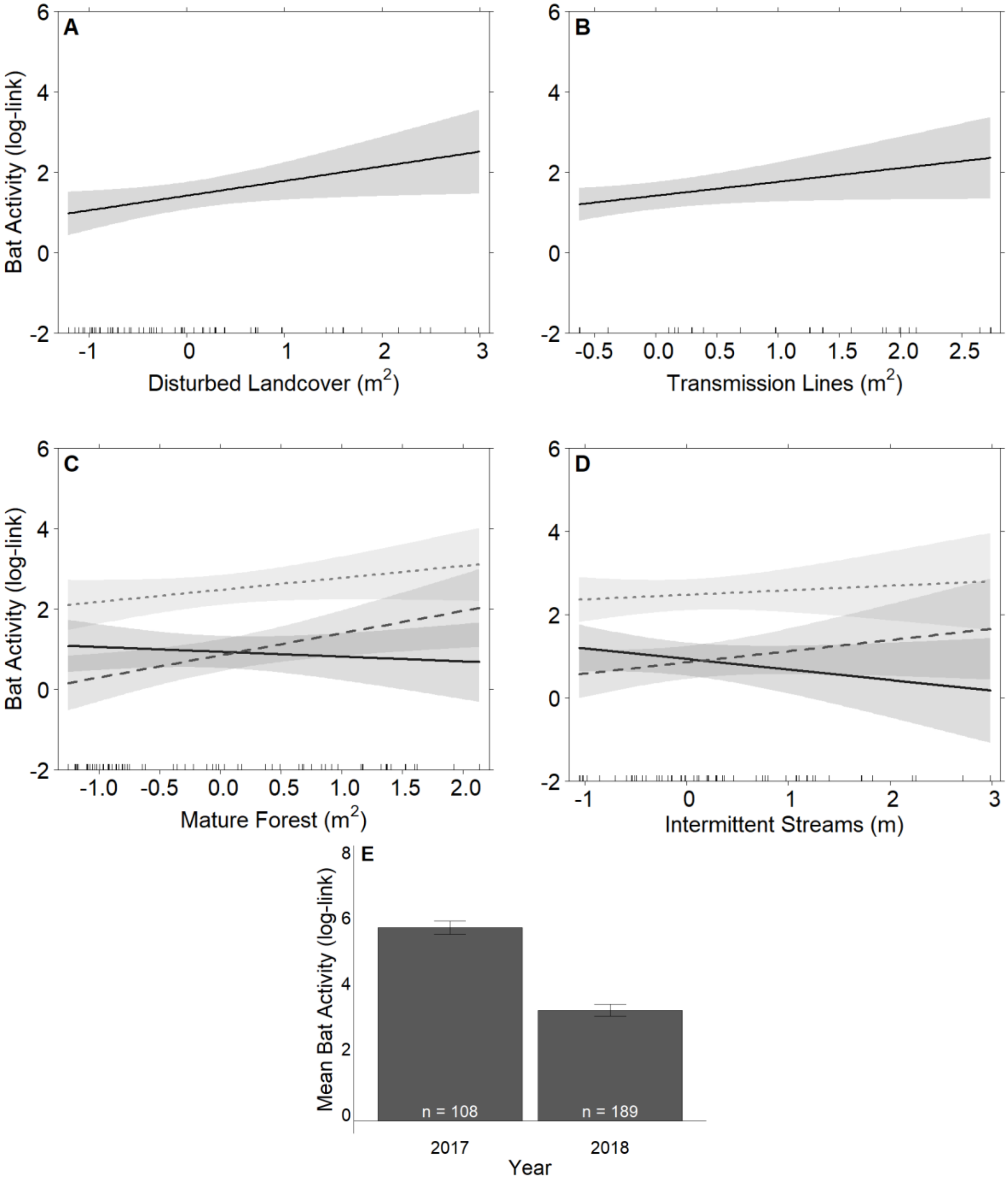

Figure 3.3. Fit of predictor variables (scaled and centered) plotted against bat activity per night (log-link) of the best global model at the 500 m scale. Interactions between species and predictors are denoted by different line types: *Myotis lucifugus* (solid line), *Myotis septentrionalis* (dashed line), and unidentified (dotted line). Shaded area indicates 95% pointwise confidence intervals; similarly, standard error bars are given for means.

At the 2,000 m scale, the forest age and stand type model set had the lowest AICc value (1712.3) and the highest weight (w_i = 0.985) compared to the other two forest-related model sets (Table 3.3). The forest age and stand type model set performed 70 times better than the best forest age model set (AICc = 1720.7, w_i = 0.014). The forest stand type model set had the lowest AICc and weight (AICc = 1725.8, w_i = 0.001). Forest age and stand type was the best forest-related model set, given the data, and was therefore used in subsequent analyses.

The linear features model set had the lowest AICc value (1700.5) and the highest weight (w_i = 0.997) of any other model set. In this model set, year had a negative impact on bat activity ($z_{df=1}$= -3.38, $p < 0.01$) and there were species interactions with roads and streams. The forest age and stand type model set had the next highest AICc (1712.3) and included a positive association between bat activity and disturbed stands ($z_{df=1}$= 2.85, $p < 0.01$), a negative association with year ($z_{df=1}$= -3.60, $p < 0.001$), and species interaction with mature mixedwood forests. In the non-forest model set (AICc = 1716.0), bat activity was negatively associated with residential land ($z_{df=1}$= -2.43, $p < 0.05$) and included species interactions with scrub cover and wetlands.

The global model for the 2,000 m scale had the lowest AICc (1693.5) and highest weight (w_i = 0.97) of all other model sets. Given the dataset and aforementioned candidate model sets, this was the best model for the 2,000 m scale. With this model, bat activity was positively associated with disturbed landcover, negatively associated with year, and had species interactions with streams, shrub cover, and roads (Table 3.4). Little brown myotis activity was negatively associated with streams, positively associated with scrub cover, and weakly associated with roads; conversely, northern myotis activity was positively associated with streams and negatively associated with scrub cover and roads (Table 3.4, Figure 3.4). When comparing the global models at both scales, the 2,000 m had the lowest AIC and explained a greater amount of variance ($R^2_{GLMM(c)} = 0.70$) than the 500 m scale ($R^2_{GLMM(c)} = 0.63$).

Table 3.4. Summary of best negative binomial generalized linear mixed models (GLMMs) describing influences on bat activity (number of bat recordings per site) in Gros Morne National Park, Newfoundland at the 500 m and 2,000 m scales. Akaike's Information Criterion corrected for small sample size (AICc), degrees of freedom (df), and deviance are given for the global model at each scale as well as estimated regression parameters, standard errors, *z*-values, and *p*-values of the predictor variables. Species interactions are indicated with an "x." Significant variables ($p < 0.05$) are indicated in bold.

	Predictor Variable	**Estimate**	**Std. Error**	***z*-value**	***p*-value**
500 m	*Global Model*				
AICc = 1725.4	$\sigma_{Site} = 1.525 \pm 1.2$				
df = 14	(Intercept)	-0.208	0.226	-0.920	0.358
Deviance = 1695.9	Disturbed	0.365	0.170	2.147	**0.032**
$R^2_{GLMM(c)} = 0.633$	Mature Forest	-0.120	0.212	-0.562	0.574
	Myotis septentrionalis	-0.083	0.176	-0.472	0.637
	Unidentified bat	1.543	0.161	9.587	**< 0.001**
	Transmission line	0.343	0.178	1.927	0.054
	Intermittent Stream	-0.253	0.201	-1.262	0.207
	Year: 2018	-0.558	0.159	-3.515	**< 0.001**
	Mature Forest x *Myotis septentrionalis*	0.671	0.182	3.681	**< 0.001**
	Mature Forest x Unidentified bat	0.418	0.163	2.561	**0.010**
	Intermittent Streams x *Myotis septentrionalis*	0.523	0.174	3.004	**0.003**
	Intermittent Streams x Unidentified bat	0.362	0.165	2.190	**0.029**
2,000 m	*Global Model*				
AICc = 1693.6	$\sigma_{Site} = 1.344 \pm 1.159$				
df = 16	(Intercept)	-0.303	0.212	-1.428	0.153
Deviance = 1659.6	Disturbed landcover	0.474	0.166	2.851	**0.004**
$R^2_{GLMM(c)} = 0.699$	Scrub cover	0.284	0.192	1.477	0.140
	Myotis septentrionalis	-0.234	0.169	-1.384	0.166
	Unidentified bat	1.570	0.148	10.617	**< 0.001**
	Roads	-0.088	0.212	-0.415	0.678
	Streams	-0.342	0.192	-1.779	0.075
	Year: 2018	-0.522	0.149	-3.497	**< 0.001**
	Scrub cover x *Myotis septentrionalis*	-0.527	0.189	-2.790	**0.005**
	Scrub cover x Unidentified bat	-0.232	0.145	-1.606	0.108
	Roads x *Myotis septentrionalis*	-0.633	0.218	-2.902	**0.004**
	Roads x Unidentified bat	-0.350	0.164	-2.135	**0.033**
	Streams x *Myotis septentrionalis*	0.788	0.158	4.983	**< 0.001**
	Streams x Unidentified bat	0.410	0.145	2.822	**0.005**

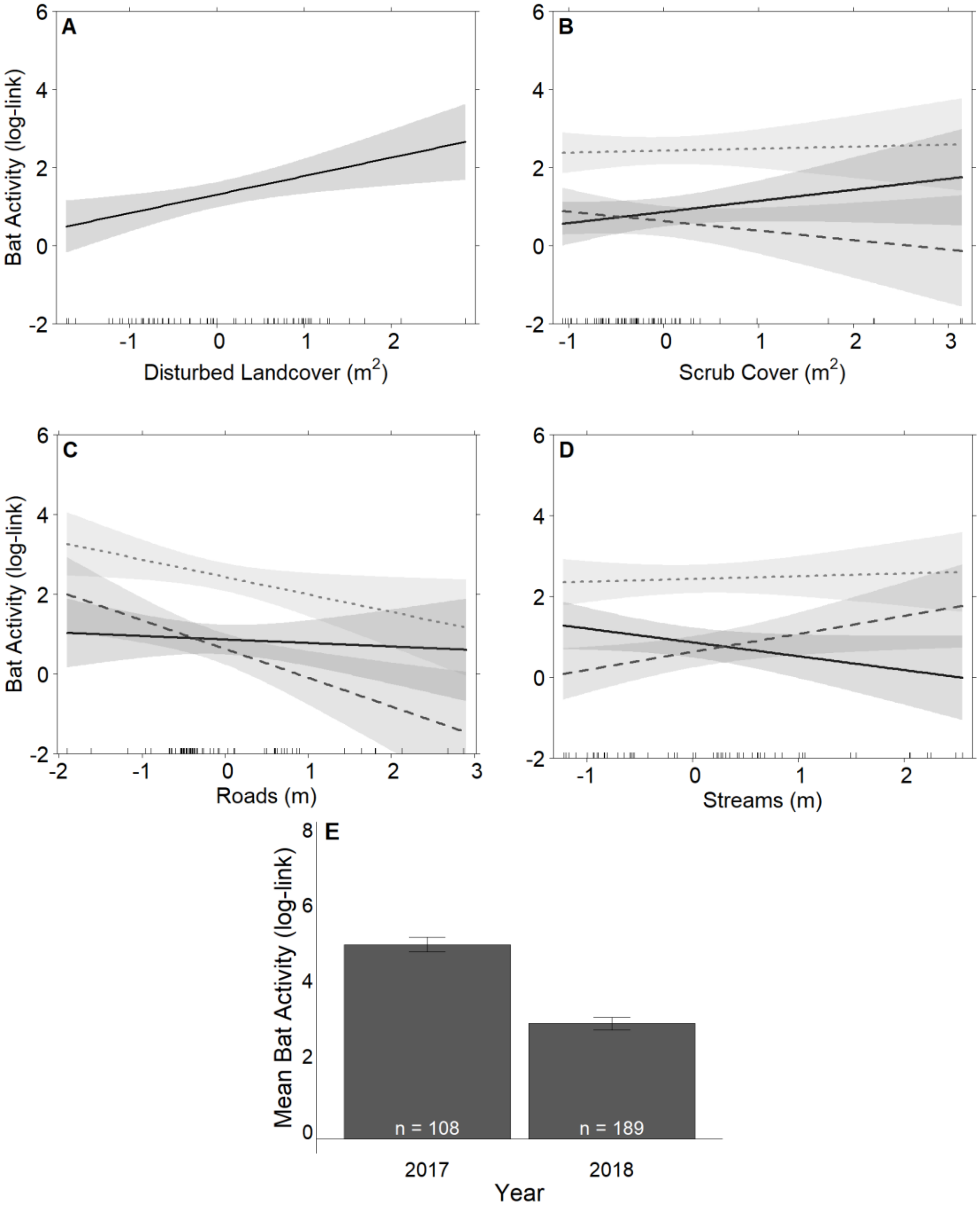

Figure 3.4. Fit of predictor variables (scaled and centered) plotted against bat activity (number of bat recordings per site) (log-link) of the best global model at the 2,000 m scale. Interactions between species and predictors are denoted by different line types: *Myotis lucifugus* (solid line), *Myotis septentrionalis* (dashed line), and unidentified (dotted line). Shaded area indicates 95% pointwise confidence intervals; similarly, standard error bars are given for means.

3.5 Discussion

I detected influences of landscape disturbance – both natural and anthropogenic – on bat activity in GMNP at intermediate and broad scales. Bat activity was positively associated with disturbed forests, the only variable retained in the best models at both spatial scales. Contrary to my predictions, there was no difference in the influence of disturbed forest on the activity levels of the two study species. At the smaller scale, transmission lines were also an important feature for bats detected in the Park, and at the larger scale, roads were a deterrent. Some additional landscape variables unrelated to disturbances emerged as predictors of bat activity: there were similar species-specific influences of intermittent streams and stream availability across scales, and species-specific influences of scrub cover at the larger spatial scale. Additionally, bat activity decreased from 2017 to 2018, as observed in prior results (Chapter 2).

Forest disturbances cause fragmentation, increasing the availability of open- and edge-habitats. Many studies demonstrate the importance of edge habitats as foraging and commuting grounds for bats (Grindal and Brigham 1999, Owen et al. 2004, Pettit and Wilkins 2012, Segers and Broders 2014). These habitats often have increased prey availability and decreased structural clutter, which can be ideal for foraging bats (Brigham et al. 1997, Grindal and Brigham 1999, Deans et al. 2005, Hein et al. 2009, Morris et al. 2010). Little brown myotis have frequently been recorded exploiting edge habitats (Patriquin and Barclay 2003, Segers and Broders 2014, Nelson and Gillam 2017), but northern myotis are considered forest-interior specialists and are often found in mature forests habitats (Owen et al. 2003, Loeb and O'Keefe 2003, Broders and

Forbes 2004, Ford et al. 2005, Broders et al. 2006) as opposed to edge habitats. However, both Jantzen and Fenton (2013) and Pauli et al. (2015) observed increases in northern myotis activity in edge habitats and hypothesized that members of this species show some behavioural plasticity in their foraging strategy. Additionally, Owen et al. (2003) suggested that northern myotis may be exploiting edges where they can glean insects that were swept by the wind and accumulated in nearby trees (Lewis 1970). Further, northern myotis may be predominately exploiting disturbed areas for foraging and commuting when those disturbed areas are surrounded by mature forests (Pauli et al. 2015). In my study area, disturbed stands bordered forests 81.6% of the time (regenerating [2.7%], immature [41.7%], and mature [37.24%]), making it plausible that northern myotis were only exploiting disturbed stands that neighbor forested habitat. This was further supported by the positive association of northern myotis activity and mature forests at the 500 m scale.

The importance of disturbed forest habitat to bats was particularly notable given that disturbed forests represent a relatively small proportion of the available landscape at both spatial scales (~9 and 7% at the 500 and 2,000 m scales, respectively). While both bat species are dependent on forest habitat, GMNP has an abundance of forests and therefore forest cover may not be a limiting factor. Due to the importance at both my landscape-level scales, I argue that disturbed forests are an important feature to bats in GMNP, at least for proportions up to 30% landcover at the 500 m scale and 16% at the 2,000 m scale as observed in this study. Specifically, moose meadows may be a key landscape feature for resident bat populations as they made up the largest proportion

(>50%) of classified disturbances at both scales. In 2011, GMNP lifted hunting restrictions to help control moose populations and improve forest health, subsequently resulting in a decreased moose population. However, the reduction of moose meadows may be disadvantageous to local bat populations. Although I do not know the threshold at which bat activity could become negatively impacted by too much disturbed forests, at the current level of disturbance, bat activity is positively associated with disturbances and moose meadows, which should be considered when making forest management decisions.

The importance of transmission line corridors for local bat communities was not unprecedented: several studies have previously demonstrated that hard linear edges can provide foraging habitat rich in prey (Hein et al. 2009, Morris et al. 2010). Additionally, both *Myotis* species may use these linear features as flight corridors, which allow for easier orientation, minimal clutter interference, and protection from wind and predators (Walsh and Harris 1996, Grindal and Brigham 1999, Verboom and Spoelstra 1999, Thomas and Jung 2019, Jung 2020). Protection from wind may be particularly relevant in Newfoundland, where wind is prevalent most nights. On Newfoundland, mean surface wind speed is 6-8 m/s (21.6 – 28.8 km/h), which increases closer to the coast (Khan and Iqbal 2004). Bat activity is usually higher in conditions with low wind speeds (Arnett et al. 2008, Reynolds 2006) and Wellig et al. (2018) found nearly no bat activity above a wind speed of 5 ms^{-1}. In Newfoundland, linear disturbances such as transmission corridors may provide clutter-free commuting routes for bats that are relatively sheltered from wind. I am unsure as to why this association was only present at the 500 m scale, and as I have no data on the roost locations of the bats detected in this study, it is impossible to determine their nightly commuting distances.

Negative associations between roads and bat activity have also been well-documented (Zurcher et al. 2010, Berthinussen and Altringham 2012, Altrigham and Kerth 2015, Claireau et al. 2019, Medinas et al. 2019). Roads fragment landscapes (Altrigham and Kerth 2015); cause habitat degradation (Berthinussen and Altringham 2012); act as barriers (Fensome and Mathews 2016); and can result in bat mortality following collisions with motor vehicles (Russel et al. 2009). While other disturbances in this study were positively associated with activity, roads may be acting as a barrier rather than an edge habitat, especially for low-flying and clutter adapted *Myotis* species (Kerth and Melber 2009, Fensome and Mathews 2016). The majority (>70%) of road length included in this study was major highway (speed limit 70-80 km/h), with impervious pavement and no streetlights to attract insects, thus providing poor habitat for local bats compared to surrounding landscape. This is especially pertinent because transmission lines in the study area were often situated parallel to roads (but not correlated) and offered the benefits of a vegetated commuting corridor without the risk of vehicle-related mortality. Both bat species were negatively associated with roads, but this effect was stronger for northern myotis than for little brown myotis. One possible explanation for this species-specific response could be the high correlation between roads and residential areas ($|r| = 0.70$). While both species have been shown to avoid residential areas in favor of forested landscapes (Johnson et al. 2008, Fabianek and Gagnon 2011), little brown bats have been observed roosting in anthropogenic features, such as bat boxes, houses, sheds, and garages (Johnson et al. 2008).

Surprisingly, the presence of water features and water edges did not have an impact on little brown bat activity, despite many studies showing the importance of aquatic habitats to this species (Anthony and Kunz 1977, Fenton and Barclay 1980, Loeb et al. 2014, Nelson and Gillam 2017, Jung 2020). This may be due to the ample amounts of water and water features on Newfoundland; there are over 15,000 delineated freshwater lakes and ponds ranging from ~1 m^2 to 23.4 km^2 (Western Brook Pond) within GMNP. Additionally, the Western Newfoundland Forest ecoregion has a wet climate with over 180 days of precipitation (Damman 1983), which would suggest that most rivers, streams, and intermittent streams would contain water for the majority summer. The vast number of water features suggest that little brown myotis were simply not constrained by aquatic foraging grounds.

The only water-related variables associated with bat activity were streams. Stream features had similar species-level associations at both spatial scales. Intermittent streams, which were positively associated with northern myotis activity at the smaller spatial scale, were classified as discontinuous waterways that do not form stand boundaries. Approximately 70% of intermittent streams in my 500 m buffers went through forest stands (35.27% in mature forests) and northern myotis may be exploiting intermittent streams predominately located within intact forests (e.g., Henderson and Broders 2008), where the streams provide habitat for prey (Barclay 1991, Seidman and Zabel 2001) and commuting corridors (Owen et al. 2003). Similarly, northern myotis were positively associated with perennial streams at the larger spatial scale. In similar study areas, such as Labrador (Burns et al. 2015) and Nova Scotia (Segers and Broders 2014), researchers found a positive association between *Myotis* species and streams, specifically northern myotis. One possible explanation is that northern myotis are exploiting streams as linear commuting corridors and using them as a water source. Another possible explanation is the preference of northern myotis for upper elevation hillsides (Jung et al. 2004, Johnson et al. 2008, Harvey et al. 2011, De La Cruz et al. 2018). Streams are indicative of a sloped topography, which may offer roosting habitats for northern myotis (Perry et al. 2008). Because streams were only important at the larger scale, the species-specific association could potentially be explained by the topography rather than the actual waterbody.

At the larger spatial scale, scrub forests were an important predictor of bat activity and differed by species. The majority (91.5%) of scrub cover in the 2,000 m buffers were 0-6.5 m in height, making it likely that little brown myotis are flying above these stands while northern myotis are avoiding these open-canopy habitats. There have been few studies that have examined the use of scrub forests by bats, demonstrating both positive and negative associations (e.g. Nicholls and Racey 2006, Zaele et al. 2012, and Goiti et al. 2011, Roeleke et al. 2018). Downs et al. (2016) observed lesser horseshoe bats (*Rhinolophus hipposideros*) selecting scrub forests for both foraging and commuting in England. Goiti et al. (2011) also found Geoffroy's Bat (*Myotis emarginatus)* foraging opportunistically in scrubland for spiders. Similar to both the lesser horseshoe bat and

Geoffroy's bat, little brown myotis are aerial hawkers (Fenton and Bodanowicz 2002, Harvey et al. 2011) capable of eating prey on the wing. It is possible that the dense heterogeneous vegetation associated with scrub forests provide ideal habitats for insects (Goiti et al. 2011). In general, insect abundance and diversity has been shown to increase with plant diversity and abundance (Haddad et al. 2001, Crist et al. 2006, Taki et al. 2010). Dodd et al. (2012) observed an increase of Lepidopteran occurrence with shrub cover, which could indicate that scrub/shrub may be productive foraging grounds for bats in GMNP; however, more research needs to be done on local scrub forest habitats to determine if prey abundance is attracting little brown myotis or if they are simply using scrub forests as another commuting habitat.

While I expected bat activity to remain relatively constant from year to year (e.g., Agosta et al. 2005), bat activity in GMNP decreased from 2017 to 2018. It is possible that this is simply due to variation in environmental conditions, such as weather or prey availability; however, I did not observe a strong impact of these environmental variables on bat activity at the fine-scale. Another possible explanation for the inter-annual decline in bat activity is that the bat populations in the park have been affected by the presence of white-nose syndrome (WNS), a deadly fungal disease responsible for killing millions of bats in North America. The first records of WNS in bats on Newfoundland were reported in 2016 and it is possible that the local summer populations are beginning to decline. Long-term monitoring of bat populations in GMNP should continue to assess variation going forward.

3.6 Conclusion

Forest dwelling insectivorous bats can be susceptible to local disturbances and I show that forest disturbances in GMNP were significantly positively associated with little brown myotis and northern myotis activity at two landscape-level scales. Further, transmission lines offer a hard linear edge, which may serve as wind-blocking commuting lanes for bats. Conversely, bat activity by both species was negatively associated with major highways, which provide poor habitat and may act as a barrier. Currently, moose meadows compose a substantial proportion of disturbed forest within the park. There are ongoing management efforts within GMNP to restore forest health by reducing hyperabundant moose populations and allowing natural regeneration in forest habitats, thus avoiding the formation of future moose meadows. My findings suggest that the presence of moose meadows within the park may be beneficial for both *Myotis* species during the period of summer residency.

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Chapter 4: Summary and Conclusions

4.1 Overall Summary

In an era of species declines, understanding the habitat requirements of vulnerable species is crucial for effective species management. Generally, species on islands may be particularly susceptible to disturbances; the arrival of the fungus linked to white-nose syndrome will likely increase the pressures on the resident bat populations on insular Newfoundland (hereafter referred to as “Newfoundland”). My study investigated the effects of the conversion of naturally disturbed mature forest stands into open meadows through the browsing of hyperabundant moose in Gros Morne National Park (GMNP), Newfoundland on little brown bats (*Myotis lucifugus*), northern myotis (*M. septentrionalis*) and their insect prey. I investigated this question at three spatial scales: fine (habitat-level), intermediate and broad scales, providing three perspectives on how bats are using their environment in GMNP.

In Chapter 2, I investigated the influence of habitat-level spatial scale variables on bat activity and did not find a response to pre-established stand type, although insect biomass differed significantly among the three stand types. Insect biomass was higher in mature forests than in moose meadows, likely reflecting the importance of plant species richness and abundance in the life cycles of many insects (Ober and Hayes 2008, Taki et al. 2010, Dodd et al. 2012). While pre-established stand type did not significantly affect local bat activity, the habitat-level vegetation measurements taken during the study were the most important predictors of bat activity. Habitats with increased snag density and those that were deciduous dominated had the highest levels of bat activity. Species-level variability corresponded with previously described patterns in the foraging behaviour of the two study species. While the pre-established stand type was not directly associated with bat activity, the importance of some habitat-level vegetation measurements on bat activity may indicate that conversion of forest habitat by moose could have an impact on local bat activity by decreasing deciduous understory, creating open canopies, and creating habitats without snags.

In Chapter 3, the intermediate and broad scale analyses showed a strong, positive influence of disturbed landcover, of which the highest portion was composed of moose meadows, on bat activity at both scales. Additionally, linear disturbances, specifically transmission lines and roads, were important predictors of bat activity at the intermediate and broad scales, respectively. Contrary to my hypotheses, disturbed landscapes (except roads), had significant positive effects on both species, most likely related to the positive effects of habitat heterogeneity (Ethier and Fahrig 2011, Mendes et al. 2017). Diverse land cover offers various resources that likely complement the foraging and roosting requirements of bat populations.

4.2 Discussion/Conclusions

This study demonstrates the importance of investigating multiple scales when identifying important predictors of bat activity. Each scale in the present study provided valuable insights into how bats are using their environment. The fine-scale analysis allowed me to assess how bats and their insect prey were using the immediate surroundings. While I expected insect biomass to decrease in moose meadows due to the lack of vegetation complexity (Rainho et al. 2010, de Oliveira et al. 2015), there did not seem to be a connection between insect prey biomass and bat activity as other researchers have observed (e.g., Kusch et al. 2004, Morris et al. 2010, de Oliveira et al. 2015, Salvarina et al. 2018). The disconnect between bat activity, insect biomass, and stand type may be more appropriately explained using the results of the landscape-scale investigations, which indicated significant, positive associations between disturbed forest stands (>50% of this disturbed landcover was classified as moose meadows) and bat activity at both scales. I suggest that, while one individual moose meadow stand may not serve as an attractant to local bats, a larger scale intact forest with multiple interspersed disturbed stands may offer edge habitat that is important to both bat species in the park.

This is further supported by comparing the intermediate (500 m) and broad (2,000 m) scales. The broad scale analysis explained more variability in the data, thus suggesting bats may be perceiving their environment at the larger landscape scale in GMNP. Park and Broders (2009) reported that Newfoundland bats travel up to 2.4 km from capture site, supporting this conclusion. Additionally, Broders et al. (2006) estimated the movement-distance for female northern myotis to be 2,000 m and male little brown myotis to be 1,000 m in New Brunswick. The *Myotis* species in this study were likely most significantly influenced by variables at the broadest scale because of the importance of habitat heterogeneity in meeting both foraging and roosting requirements of these highly mobile species (Ethier and Fahrig 2011, Fuentes-Montemayor et al. 2013, Kelly et al. 2016). The “habitat heterogeneity hypothesis” assumes that habitats with a complex vegetation composition will provide several different niches, each with unique environmental resources, resulting in increased biodiversity and higher abundance of taxa (Bazzaz 1975, Tews et al. 2004, Mendes et al. 2017). Therefore, the diversity of landcover elements I observed at the broadest scale may be essential to providing various complementing resources (Mendes et al. 2017); for example, how edge habitats are complemented by neighbouring mature forests.

Edge habitat can be important for commuting corridors, protection from wind, increased prey abundance, or higher snag abundance (Walsh and Harris 1996, Grindal and Brigham 1999, Owen et al. 2002, Patriquin and Barclay 2003, Morris et al. 2010, Ethier and Fahrig 2011, Kalda et al. 2015, Pauli et al. 2017). Grindal (1998) tracked *Myotis* spp. in Newfoundland to their roost trees and found that all individuals roosted within mature forests (>80 years old) or disturbed cut-blocks (<20 years old) with >80% of individuals roosting less than 15 m from a forest edge. Because the majority (>80%) of the disturbances in my study neighbored forests, this could further support that bats in GMNP are using mature forests and their edge habitats as important roosting habitats. As Grindal (1998) suggests, it may be easier for bats to locate snags that meet roost tree requirements near edges rather than in the interior of a dense forest, most likely due to reduced clutter (Lauzon 2019).

While edges created by disturbances are significant habitats for both species, it is also essential to emphasize the importance of forests, especially to the clutter-specialist northern myotis. At each spatial scale, there was evidence of bat activity increasing with the complexity of vegetation, with species-specific trends. At the fine scale, I ascertained that vegetation structure influences bat activity while other variables (i.e., insect abundance/diversity and environmental factors) were conceivably secondary drivers (Adams et al. 2009, Morris et al. 2010, Dodd et al. 2012, Müller et al. 2012, Cox et al. 2016, Threlfall et al. 2017, Moore and Best 2018). The intermediate scale further highlighted the importance of mature forest stands and intermediate streams to northern myotis, further supporting their forest-interior foraging style (Caceres and Barclay 2000, Owen et al. 2003, Broders and Forbes 2004, Pauli et al. 2015). At the broad scale, little brown myotis were positively associated with scrub cover, which has a structurally complex vegetation profile.

Another significant outcome of this study was the decrease in bat activity between 2017 and 2018 at all scales. Given the short timescale of the study (two field seasons), it is impossible to confidently attribute this decline to any particular factor. However, it is worth noting that white-nose syndrome (WNS) was first detected in 2016 in the southwestern portion of Newfoundland. Once present in an area, WNS can spread from 200-900 km per year (Lorch et al. 2016). Bats detected in this study were over-summering in GMNP, but I am unsure as to where they over-winter, making it possible that WNS in the southwestern portion of Newfoundland affected local bats before the first cases in GMNP were officially reported in 2018. While my sample size is too restricted to determine population trends, I observed less bat activity in 2018 than 2017, which is certainly justification for continued bat monitoring in the Park in coming years.

In conclusion, my findings can contribute to guiding forest management decisions that are beneficial to local bat populations in GMNP. My fine-scale analysis shows that retention of snags and deciduous habitats can be essential for providing roosting and foraging habitats, respectively, for both bat species in the park. My landscape-level analyses highlighted the importance of forest disturbances – predominantly insect outbreaks, the subsequent formation of moose meadows, and cutting of transmission lines – for both species. The creation of forest patches or hard linear edges can positively affect both species if the surrounding landscape is composed predominantly of forests. However, more research is needed to determine the preferred disturbance threshold for resident bats.

4.3 References

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4.4 Appendices

Appendix A. Settings used for SM2BAT+ detectors using SMX-U1 microphones attached to the left channel.

Function	Setting
Start Recording	Sunset -00:30:00
Stop Recording	Sunrise +00:30:00
Recording Segment Length	30 minutes
Sampling Rate	384,000 Hz
Channels	MONO-L
File Format	.wav
High Pass Filter	fs/24 sampling rate
Low Pass Filter	Off
Trigger Level	12 SNR
Trigger Window	2.0 s
Trigger Maximum Length	20.0 s
Division Ration	16
Gain Switches	12 dB

Appendix B. A lit insect light trap used to collect nocturnal insects in Gros Morne National Park. The light trap was constructed out of a 5-gallon bucket, LED string lights on a battery-operated timer, and an insecticidal strip on the inside.

Appendix C. Recommended settings for the two acoustic software packages used in acoustic analysis: Kaleidoscope Pro 4.3.2 and Sonobat 4.2.1.

Kaleidoscope Signal Parameters		**Sonobat Signal Parameters**	
Frequency	8-150 kHz	Lowest frequency	5 kHz
Duration	2 – 500 ms	Acceptable call quality	0.80
Maximum inter-syllable gap	500 ms	Sqnc decision threshold	0.90
Cluster Analysis	Disabled	Max # of calls to consider per file	16
Classifier / Region	Bats of North America 4.3.0 / NL (LABO, LACI, MYSE, MYLE, MYLU	Classifier / Region	Northnortheastern US / nE[c20170519]
Minimum number of pulses	2	Minimum number of pulses	4
Sensitivity Setting	0 Balanced (Neutral)		

Appendix D. Confusion matrices of the automated species identifications between two acoustic packages - Sonobat 4.2.1 and Kaleidoscope Pro 4.3.2 – using the less restrictive parameters for each program. Matrices are shown for acoustic bat data collected in Gros Morne National Park in (A) 2017 and (B) 2018.

Sonobat

Kaleidoscope

A	*Eptesicus fuscus*	*Lasiurus borealis*	*Lasiurus cinereus*	*Lasionycteris noctivagans*	*Myotis leibii*	*Myotis lucifugus*	*Myotis septentrionalis*	Unidentified	Noise	**Total**
Eptesicus fuscus	**0**									**0**
Lasiurus borealis		**6**				5		7	24	**42**
Lasiurus cinereus			**1**	1				1	13	**16**
Lasionycteris noctivagans				**0**						**0**
Myotis leibii					**0**					**0**
Myotis lucifugus		3				**393**	12	139	170	**717**
Myotis septentrionalis	2				1	48	**251**	154	63	**519**
Unidentified					1	1	7	**28**	33	**70**
Noise					1		65	148	**359**	**573**
Total	**2**	**9**	**1**	**1**	**3**	**447**	**335**	**477**	**662**	**1937**

Sonobat

Kaleidoscope

B	*Eptesicus fuscus*	*Lasiurus borealis*	*Lasiurus cinereus*	*Lasionycteris noctivagans*	*Myotis lucifugus*	*Myotis septentrionalis*	Unidentified	Noise	**Total**
Eptesicus fuscus	**0**								**0**
Lasiurus borealis		**7**			3	2	6	30	**48**
Lasiurus cinereus			**0**	1			4	27	**32**
Lasionycteris noctivagans				**0**					**0**
Myotis lucifugus		10			**219**	21	130	119	**499**
Myotis septentrionalis	1				89	**357**	174	64	**685**
Unidentified						11	**35**	51	**97**
Noise						45	199	**891**	**1135**
Total	**1**	**17**	**0**	**1**	**311**	**436**	**548**	**1182**	**2496**

Appendix E. Frequency of insect order detections using light traps during the summers of 2017 and 2018 in the Western Newfoundland Ecoregion of Gros Morne National Park, Newfoundland, Canada (n=number of sampling bouts).

Insect Order	**2017 (n=33)**	**2018 (n=36)**
Coleoptera	33	36
Diptera	33	36
Ephemeroptera	3	5
Hemiptera	17	18
Hymenoptera	27	33
Isoptera	0	3
Lepidoptera	29	36
Neuroptera	1	3
Plecoptera	10	1
Psocoptera	0	6
Thysanoptera	9	16
Trichoptera	15	18

Appendix F. Total number of nocturnal insects collected in light traps during summers (June – August) of 2017 and 2018 in each forest stand type.

Forest Stand Type	**2017**		**2018**	
Mature Conifer Forest	n=8	1,479	n=9	7,091
Mature Mixed Forest	n=9	1,801	n=9	2,234
Moose Meadows	n=8	2,397	n=9	2,940
Regenerating Forest	n=8	1,040	n=9	3,485
Total	**n = 33**	**6,717**	**n = 36**	**15,750**

Appendix G. Average biomass (g) of each insect order per night per forest stand type: mature conifer forest (MCF), mature mixed forest (MMF), regenerating (REGEN), and moose meadows (MM) – collected during summers (June – August) of 2017 and 2018 deployment of light traps in Gros Morne National Park, Newfoundland.

	2017				**2018**			
Order	MCF (n=8)	MMF (n=9)	REGEN (n=8)	MM (n=8)	MCF (n=9)	MMF (n=9)	REGEN (n=9)	MM (n=9)
Coleoptera	0.939	0.759	0.252	0.182	4.705	3.166	2.485	0.142
Diptera	0.461	0.685	0.339	0.504	1.659	1.124	0.907	0.330
Ephemeroptera	0.005	0.007	0.003	0.005	0.002	0.011	0.001	0.000
Hemiptera	0.031	0.002	0.012	0.036	0.007	0.002	0.002	0.015
Hymenoptera	0.036	0.014	0.017	0.040	0.055	0.005	0.089	0.036
Lepidoptera	3.049	2.971	0.621	0.435	6.359	3.464	1.428	0.806
Trichoptera	0.024	0.043	0.038	0.004	0.242	0.053	0.162	0.033
Other	0.059	0.096	0.117	0.068	0.276	0.183	0.333	0.117
Average Insect Biomass	**4.598**	**4.570**	**1.396**	**1.270**	**0.134**	**0.080**	**0.055**	**0.015**

Appendix H. Average number of insects of each insect order per night per habitat type – mature conifer forest (MCF), mature mixed forest (MMF), moose meadows (MM), and regenerating (REGEN) – collected during 2017 and 2018 deployment of light traps in Gros Morne National Park, Newfoundland.

	2017				2018			
Insect Order	MCF	MMF	REGEN	MM	MCF	MMF	REGEN	MM
Coleoptera	5.4	5.2	6	5.2	6	4.3	5	3
Diptera	28.6	53	19.2	30.9	165.8	64	79.9	40.5
Ephemeroptera	0	0	0.1	0.3	0.1	0.1	0	0
Hemiptera	0.5	0.1	0.5	1.2	0.3	0.1	0.3	0.6
Hymenoptera	0.7	0.5	0.6	7.2	1.5	0.5	0.6	0.5
Isoptera	0	0	0	0	0	0	0	0.1
Lepidoptera	5.1	5.3	2.4	3.3	12.3	8.1	5.6	4.9
Neuroptera	0	0	0	0	0.1	0	0.1	0
Plecoptera	0.1	0.4	0.1	0.2	0.1	0	0	0
Psocoptera	0	0	0	0	0	0	0.2	0.4
Thysanoptera	0.1	0	0.4	0.3	0.3	0.8	0.5	6.6
Trichoptera	0.6	0.4	0.3	0.1	0.4	0.8	1.9	0.3

Appendix I. Gros Morne National Park's Forest Resource Inventory (FRI) classification of landcover and the specified category that was used for this landscape analysis. Refer to Photographic Interpretation Procedures and Technical Specifications (2012) for tree codes and technical details.

Landcover Type	FRI Classification	Specified Category
Non-forest	Agriculture	Disturbed
	Bog	Wetland
	Cleared Land	Disturbed
	Coniferous Scrub	Scrub
	Disturbed	Disturbed
	Deciduous Scrub	Scrub
	Fen	Wetland
	Not Sufficiently Restocked	Disturbed (Moose meadows)
	Rock barren	Barren
	Residential	Residential
	Right-of-way Road	ROWr
	Right-of-way Transmission Line	ROWt
	Soil Barren	Barren
	Sand	Barren
	Treed Bog	Wetland
	Wet Bog	Wetland
Age Class	0 (Disturbed)	Disturbed
	1 (1-20 years)	Regenerating
	2 (21-40 years)	Immature
	3 (41-60 years)	Immature
	4 (61-80 years)	Mature
	5 (81-100 years)	Mature
	6 (101-120 years)	Mature
Species Composition [Working Group]	bF [bF]	Coniferous
	bFbS [bF]	Coniferous
	bFbStL [bS]	Coniferous
	bFbSwB [sH]	Mixedwood
	bFbSwS [bF]	Coniferous
	bFtA [sH]	Mixedwood
	bFtAwB [hS]	Mixedwood
	bFtL [bF]	Coniferous
	bFtLbS [bS]	Coniferous
	bFtLwB [sH]	Mixedwood
	bFwB [sH]	Mixedwood
	bFwB [wB]	Deciduous
	bFwBbS [sH]	Mixedwood
	bFwBtA [hS]	Mixedwood

Species Composition [Working Group]	bFwBtL [sH]	Mixedwood
	bFwBwS [sH]	Mixedwood
	bFwS [bF]	Coniferous
	bFwSbS [bF]	Coniferous
	bFwSwB [sH]	Mixedwood
	bS [bS]	Coniferous
	bSbF [bS]	Coniferous
	bSbFtL [bS]	Coniferous
	bSbFwB [sH]	Mixedwood
	bStL [bS]	Coniferous
	bStLbF [bS]	Coniferous
	bStLtA [sH]	Mixedwood
	tA [tA]	Deciduous
	tAbF [hS]	Mixedwood
	tAbFwB [hS]	Mixedwood
	tAwB [tA]	Deciduous
	tAwBbF [hS]	Mixedwood
	tL [bS]	Coniferous
	tLbF [bS]	Coniferous
	tLbFbS [bS]	Coniferous
	tLbS [bS]	Coniferous
	tLbSbF [bS]	Coniferous
	tLwBbF [sH]	Mixedwood
	wB [wB]	Deciduous
	wBbF [hS]	Mixedwood
	wBbFbS [sH]	Mixedwood
	wBbFtA [hS]	Mixedwood
	wBbFtL [sH]	Mixedwood
	wBbFwS [sH]	Mixedwood
	wBbS [hS]	Mixedwood
	wBbSbF [sH]	Mixedwood
	wBtA [wB]	Deciduous
	wBtAbF [hS]	Mixedwood
	wBtL [hS]	Mixedwood
	wBwS [hS]	Mixedwood
	wSbF [bF]	Coniferous
	wSbFwB [sH]	Mixedwood

Appendix J. Variables with a Pearson's correlation coefficient |≥ 0.55| and the variable removed to avoid collinearity during analyses.

Variables		Pearson's Correlation Coefficient	Variable Removed
500 m Buffer			
Ocean	Stand Edges	0.60	Ocean
Ocean	Coastline	0.90	Ocean
Freshwater	Water Edge	0.56	Water Edge
ROWr	Roads	0.59	ROWr
ROWt	Flyways	0.57	Flyways
Residential	Roads	0.70	Residential
Immature Forest	Mature Forest	0.62	Immature Forest
Stand Edge	Coastline	0.55	Coastline
2,000 Buffer			
Ocean	ROWr	0.59	Ocean
Ocean	Mature Forest	0.64	Ocean
Ocean	Intermittent Streams	0.59	Ocean
Ocean	Water Edge	0.57	Ocean
Ocean	Stand Edges	0.83	Ocean
Ocean	Coastline	0.73	Ocean
Freshwater	ROWr	0.56	ROWr
Freshwater	Water Edge	0.69	Water Edge
Freshwater	Coastline	0.56	Coastline
Scrub	Barren	0.62	Barren
Residential	Roads	0.71	Residential
Residential	Coastline	0.69	Coastline
Immature Coniferous Forest	Immature Mixedwood Forest	0.56	Immature Mixedwood Forest
Immature Deciduous Forest	Immature Mixedwood Forest	0.60	Immature Mixedwood Forest
Mature Coniferous Forest	Mature Mixedwood Forest	0.87	Mature Coniferous Forest
Mature Coniferous Forest	Coastline	0.74	Coastline
Mature Mixedwood	Roads	0.58	Mature Mixedwood Forest
Mature Forest	Roads	0.58	Roads
Mature Forest	Coastline	0.67	Coastline
Flyways	Intermittent Streams	0.56	Flyways
Intermittent Streams	Coastline	0.64	Coastline
Water Edge	Coastline	0.60	Coastline
Stand Edge	Coastline	0.55	Coastline

Appendix K. Top generalized linear mixed models of each model set at the intermediate (500 m) landscape level with their degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion corrected for small sample size (AICc), difference in AICc from top model (Δ_i), Akaike weight (w_i). Best models were derived by constructing global models of each model set and dropping parameters based on AIC until the lowest AIC is achieved. Results from the best model explaining bat activity (number of bat recordings per site) in Gros Morne National Park, Newfoundland are shown. Site was used a random effect and an offset variable was used to account for the number of survey nights. Species interactions were used to account for differences between *Myotis lucifugus* (reference level), *Myotis septentrionalis*, and unidentified bat recordings and interactions are indicated with an "x." Significant variables ($p < 0.05$) are indicated in bold.

Best Model Set	df	logLik	AICc	Δ_i	w_i(AIC)	Estimate	SE	z-value	*p-value*
Forest Age	**10**	**-854.31**	**1729.38**	**0**	**0.63**				
(Intercept)						-0.172	0.232	-0.743	0.458
Disturbed Landcover						0.383	0.175	2.187	**0.029**
Mature Forest						-0.152	0.211	-0.722	0.471
Myotis septentrionalis						-0.092	0.179	-0.511	0.609
Unidentified						1.516	0.164	9.239	**< 0.001**
Year: 2018						-0.580	0.161	-3.597	**< 0.001**
Mature Forest x *Myotis septentrionalis*						0.553	0.182	3.046	**0.002**
Mature Forest x Unidentified						0.345	0.163	2.110	**0.035**
Forest Age & Stand Type	**10**	**-855.67**	**1732.11**	**2.73**	**0.16**				
(Intercept)						-0.155	0.230	-0.672	0.502
Disturbed Landcover						0.387	0.171	2.259	**0.024**
Mature Coniferous Forest						-0.048	0.203	-0.236	0.813
Myotis septentrionalis						-0.102	0.180	-0.568	0.570
Unidentified						1.508	0.165	9.154	**< 0.001**
Year: 2018						-0.587	0.162	-3.612	**< 0.001**
Mature Coniferous Forest x *Myotis septentrionalis*						0.445	0.176	2.529	**0.011**
Mature Coniferous Forest x Unidentified						0.238	0.161	1.477	0.140
Non-Forest	**11**	**-855.04**	**1733.0**	**3.61**	**0.10**				
(Intercept)						-0.161	0.226	-0.714	0.475
Scrub Cover						0.354	0.191	1.857	0.063
Myotis septentrionalis						-0.084	0.177	-0.474	0.635
Unidentified						1.510	0.162	9.311	**< 0.001**
Transmission Line						0.295	0.171	1.727	0.084
Barren						-0.303	0.163	-1.861	0.063
Year: 2018						-0.540	0.161	-3.343	**< 0.001**
Scrub Cover x *Myotis septentrionalis*						-0.452	0.176	-2.564	**0.010**
Scrub Cover x Unidentified						-0.238	0.146	-1.634	0.102
Forest Stand Type	**7**	**-859.45**	**1733.28**	**3.90**	**0.09**				

(Intercept)						-0.148	0.230	-0.642	0.521
Disturbed						0.361	0.166	2.173	**0.030**
Myotis septentrionalis						-0.076	0.181	-0.421	0.674
Unidentified						1.499	0.166	9.028	**< 0.001**
Year: 2018						-0.576	0.163	-3.523	**< 0.001**
Linear Features	**12**	**-855.83**	**1736.76**	**7.38**	**0.02**				
(Intercept)						-0.151	0.231	-0.651	0.515
Flyways						0.249	0.212	1.173	0.241
Myotis septentrionalis						-0.077	0.176	-0.438	0.661
Unidentifeid						1.501	0.162	9.247	**< 0.001**
Intermittent Streams						-0.161	0.203	-0.794	0.427
Year: 2018						-0.575	0.161	-3.575	**< 0.001**
Flyways x *Myotis septentrionalis*						-0.337	0.187	-1.801	0.072
Flyways x Unidentified						0.052	0.165	0.312	0.755
Intermittent Streams x *Myotis septentrionalis*						0.389	0.173	2.250	**0.024**
Intermittent Streams x Unidentified						0.294	0.165	1.786	0.074

Appendix L. Top generalized linear mixed models of each model set at the broad (2,000 m) landscape level with their degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion corrected for small sample size (AICc), difference in AICc from top model (Δ_i), Akaike weight (w_i). Best models were derived by constructing global models of each model set and dropping parameters based on AIC until the lowest AIC is achieved. Results from the best model explaining bat activity (number of bat recordings) in Gros Morne National Park, Newfoundland are shown. Site was used a random effect and an offset variable was used to account for the number of survey nights. Species interactions were used to account for differences between *Myotis lucifugus* (reference level), *Myotis septentrionalis*, and unidentified bat recordings and interactions are indicated with an "x." Significant variables ($p < 0.05$) are indicated in bold.

Best Model Set	df	logLik	AICc	Δ_i	w_i(AIC)	Estimate	SE	z-value	*p-value*
Linear Features	**12**	**-837.7**	**1700.5**	**0.00**	**0.997**				
(Intercept)						-0.272	0.225	-1.206	0.228
Roads						0.030	0.218	0.138	0.891
Myotis septentrionalis						-0.264	0.174	-1.517	0.129
Unidentified bat						1.541	0.151	10.208	**< 0.001**
Streams						-0.216	0.202	-1.071	0.284
Year: 2018						-0.518	0.153	-3.384	**< 0.001**
Roads x *Myotis septentrionalis*						-0.872	0.215	-4.049	**< 0.001**
Roads x Unidentified bat						-0.450	0.158	-2.848	**0.004**
Streams x *Myotis septentrionalis*						0.758	0.160	4.725	**< 0.001**
Streams x Unidentified bat						0.406	0.149	2.724	**0.006**
Forest Age & Stand Type	**10**	**-845.8**	**1712.3**	**11.74**	**0.003**				
(Intercept)						-0.233	0.226	-1.030	0.303
Disturbed						0.488	0.171	2.851	**0.004**
Mature Mixed Forest						-0.370	0.209	-1.774	0.076
Myotis septentrionalis						-0.103	0.175	-0.589	0.556
Unidentified bat						1.540	0.159	9.680	**< 0.001**
Year: 2018						-0.565	0.157	-3.603	**< 0.001**
Mature Mixed Forest x *Myotis septentrionalis*						0.854	0.185	4.629	**< 0.001**
Mature Mixed Forest x Unidentified bat						0.635	0.169	3.765	**< 0.001**
Non-Forest	**13**	**-844.4**	**1716.0**	**15.46**	**0.000**				
(Intercept)						-0.238	0.223	-1.068	0.285
Wetland						-0.402	0.209	-1.922	0.055
Myotis septentrionalis						-0.115	0.171	-0.675	0.500
Unidentified bat						1.574	0.156	10.107	**< 0.001**
Scrub cover						0.333	0.201	1.651	0.099
Residential						-0.448	0.184	-2.428	**0.015**
Year: 2018						-0.581	0.155	-3.759	**< 0.001**

Wetland x *Myotis septentrionalis*						0.698	0.177	3.944	**< 0.001**
Wetland x Unidentifed bat						0.392	0.167	2.344	**0.019**
Scrub x *Myotis septentrionalis*						-0.896	0.189	-4.733	**< 0.001**
Scrub x Unidentified bat						-0.401	0.147	-2.724	**0.006**
Forest Age	**16**	**-843.4**	**1720.7**	**20.19**	**0.000**				
(Intercept)						-0.252	0.227	-1.112	0.266
Disturbed						0.554	0.195	2.835	**0.005**
Regenerating						0.385	0.196	1.965	**0.049**
Myotis septentrionalis						-0.060	0.176	-0.342	0.732
Unidentified bat						1.573	0.161	9.760	**< 0.001**
Immature Forests						0.187	0.237	0.788	0.430
Mature Forest						-0.224	0.213	-1.051	0.293
Year: 2018						-0.597	0.157	-3.798	**< 0.001**
Regenerating x *Myotis septentrionalis*						-0.433	0.179	-2.415	**0.016**
Regenerating x Unidentified bat						-0.193	0.150	-1.288	0.198
Immature Forest x *Myotis septentrionalis*						-0.434	0.188	-2.312	**0.021**
Immature Forest x Unidentified bat						-0.276	0.176	-1.571	0.116
Mature Forest x *Myotis septentrionalis*						0.609	0.191	3.190	**0.001**
Mature Forest x Unidentified bat						0.500	0.171	2.914	**0.004**
Forest Type	**10**	**-852.5**	**1725.8**	**25.30**	**0.000**				
(Intercept)						-0.169	0.225	-0.752	0.452
Disturbed						0.475	0.173	2.747	**0.006**
Mixedwood Forest						-0.225	0.212	-1.064	0.287
Myotis septentrionalis						-0.112	0.179	-0.629	0.530
Unidentified bat						1.500	0.163	9.230	**< 0.001**
Year: 2018						-0.578	0.160	-3.603	**< 0.001**
Mixedwood Forest x *Myotis septentrionalis*						0.559	0.189	2.965	**0.003**
Mixedwood Forest x Unidentified bat						0.410	0.171	2.405	**0.016**