Habitat use by Common Nighthawks (*Chordeiles minor*) in Canada's boreal forest

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SUPERVISORY AND EXAMINING COMMITTEE

Gabriel Josiah Foley, candidate for the degree of Master of Science in Biology**,** has presented a thesis titled, ***Habitat Use By Common Nighthawks (Chordeiles minor) in Canada's Boreal Forest,*** in an oral examination held on October 11, 2018. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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Abstract

Diurnal aerial insectivores, a guild of birds related by foraging behaviour, are declining rapidly across North America but the reasons for the decline are unknown. One of these guild members, the Common Nighthawk (*Chordeiles minor*), may have substantial but undocumented populations in Canada's boreal forest. Any differences between Common Nighthawk population trends in the boreal forest compared to more southern populations may help determine why aerial insectivore populations in general are declining. Wildland fires, common in the boreal forest, transform closed habitat into the open habitat Common Nighthawks prefer. Therefore, I assessed nighthawk abundance in northwestern Ontario in recently burned forest (~5 years since a fire) compared to unburned boreal forest. Based on survey data, Common Nighthawks were significantly more abundant in burned boreal forest than unburned forest, and the probability of detecting birds decreased with distance from a burn. Nighthawks were not more associated with riverine areas than other areas in my study area. I also evaluated forest attributes that may affect local nighthawk abundance. Lesser canopy cover and the number of logs in recently burned forest are likely important factors in habitat use by Common Nighthawks, but these factors are dependent upon the scale used for the evaluation.

Common Nighthawks, like other nightjars, often sit on gravel roads at night where they are at risk of being struck by passing traffic, but neither the reasons behind their use of roads nor the frequency of traffic strikes are known. I found no significant vegetation structure variable that predicted nighthawk site use on roads. Further, neither nearby Common Nighthawk abundance nor nearby potential roost availability predicted presence. However, the overall frequency of Common Nighthawks on roads was significantly correlated with lunar phase, which suggests that Common Nighthawks (subfamily Chordeilinae) use roads as a foraging site like other nightjars (subfamily Caprimulginae). The low vehicle-induced mortality I observed likely results from the low traffic rate at my study site, thus the use of gravel roads by Common Nighthawks in the boreal forest, assuming similar levels of traffic, does not appear to be a substantial conservation threat.

Acknowledgements

I am the sole author on this thesis, but that authorship belies the contributions of many other people. Without their input, this research would never have been realised. First and foremost, my thanks go to my supervisor, Mark Brigham, for his support, his guidance, and for the lab environment he has fostered. His involvement was essential to the production of this text, but also to shaping me as a scientist. Under his watch, I have learned to value the question before the species, that science is messy and conducted by regular people, and that one should never, ever use ‘utilize’. The Brigham lab itself has contained outstanding people who have ineffably contributed to the way that I now think, and who defined my term in the lab. Andrea Sidler had a tremendous influence on my research, my methods, the ideas I formulated, and was responsible for many unforgettable laughs. I owe Janet Ng much more than just my thanks for her development of the nighthawk capture method, and I am grateful to Elly Knight for her untiring enthusiasm, her expertise and thoughtfulness, and her collaborative resolve. Kevin Hannah developed the initial research question, provided funding, and was a pleasure to work with. Goldcorp’s Musselwhite Mine, Mitacs, the University of Regina, and the Inland Bird Banding Association all provided essential contributions. I am grateful to my field assistants Abbi MacDonald and Alyssa Stulberg for their attention to detail and their positive attitudes. Finally, I would like to thank Andrew Cameron, Mark Vanderwel, and Harold Weger for their comments on my research and my writing.

Dedication

I dedicate my thesis to science and to conservation, the two things I learned the most about while studying, the two things I had most in mind while writing, and the two things I hope this document impacts most.

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CHAPTER ONE: GENERAL INTRODUCTION

Habitat may be defined as “the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism” (Hall et al. 1997). Habitat use is the innate and learned choices an animal makes about what habitat to use (Hutto 1985, Block and Brennan 1993). These choices happen at multiple temporal and spatial scales, such as between seasons or between days, or the used land cover type versus a specific foraging site (Johnson 1980, Hutto 1985). Habitat that is acceptable to an organism varies in quality, and this variation in quality has a substantial impact on an organism’s fitness (Van Horne 1983, Block and Brennan 1993, Hall et al. 1997). Without acceptable habitat, an organism will be unable to survive and reproduce. Understanding what habitat an organism uses is critical to understanding their life history, ensuring their conservation, and conducting further field research.

The boreal forest is an understudied, vast Holarctic region characterized by harsh winters and short, productive summers. It is a region supporting timber and mining industries, helps regulate atmospheric carbon dioxide levels (D’Arrigo et al. 1987), and is the site of reproduction for 1-3 billion birds each year (Wells et al. 2014). Many parts of the boreal are geographically remote, with few roads and settlements; access to most of it is difficult and expensive. Compared to other more accessible locations, much less animal-focused research has been done in the boreal region. To properly manage the boreal forest and the animals within, the acceptable habitats of the animals must be quantified and understood.

Among the animals reproducing in the boreal forest are a guild of birds called aerial insectivores. This guild is comprised of multiple taxa grouped together not by taxonomy, but rather by the behavioural similarity of catching insects in the air. In the boreal, aerial insectivores include flycatchers (Tyrannidae), swallows (Hirundidae), and nightjars (Caprimulgidae). Continent-wide, aerial insectivores are declining faster than any other group of birds in North America (North American Bird Conservation Initiative Canada 2012). The reasons for this decline remain unknown (Smith et al. 2015), but are unlikely to be the result of a single factor (Michel et al. 2016). Potential drivers include pesticide use (Nocera et al. 2012, Hallmann et al. 2014) and decreased or asynchronous insect populations (Nebel et al. 2010, Nocera et al. 2012), climate change (Ambrosini et al. 2011, García-Pérez et al. 2014), and land use changes (Rioux Paquette et al. 2014).

The Common Nighthawk (*Chordeiles minor*; hereafter, nighthawk; Figure 1) is an aerial insectivore putatively declining across its range at 6.6% per year (COSEWIC 2007) and has been listed as Threatened in Canada (*Species at Risk Act* 2002). However, anecdotal evidence suggests substantial populations exist in the boreal forest. Due to the general remoteness and inaccessibility of the boreal forest, these populations have yet to be studied. Understanding the population size, stability, and demographics of boreal nighthawks may not only help conserve this species but may also shed light on some of the factors behind

Figure 1. A Common Nighthawk (*Chordeiles minor*) roosting on a corral gate in southern Saskatchewan.

the guild wide decline of aerial insectivores. If nighthawk populations in the boreal are faring better than southern populations, it may be possible to determine causal factors behind aerial insectivores' decline that are geographically restricted. These localised factors may have a greater influence on aerial insectivore population trends than other non-localised factors. Additionally, learning what habitat nighthawks use will directly affect their conservation by allowing preferred habitat to be appropriately managed and future population research to be optimally located, furthering their conservation.

My project's primary objective was to understand what habitat nighthawks use in the boreal forest. I used vegetation association as a correlate for habitat use (Hall et al. 1997). I examined this at three different spatial scales (first, second, and third order, *sensu* Johnson 1980) by relating abundance to vegetation characteristics. I also specifically evaluated nighthawks' nocturnal use of an anthropogenic habitat (gravel roads) and the mortality risk associated with proximity to traffic on these roads.

Throughout their continent-wide range, nighthawks are typically found in open habitat such as grasslands, beaches, or cleared forest (Brigham et al. 2011). In particular, short vegetation appears to be important (Pidgeon et al. 2001, McLachlan 2007, Ng 2009). During the day, individuals typically roost on bare ground, on logs, or in trees (Rust 1947, Fisher and Fletcher 2004). However, almost nothing is known about their habitat preferences in the boreal forest. Wildland fires, which occur frequently in the boreal forest, create large, open areas with short vegetation and are potentially suitable nighthawk habitat

(Hagar et al. 2004). I selected a recent, high-severity burn in the boreal shield ecozone (in northwestern Ontario) as my study site. I conducted abundance and vegetation surveys from June – August 2015-2016, coinciding with nighthawks' reproductive period. I also captured nighthawks and outfitted them with radio transmitters, allowing me to track individuals to roost sites. These data allowed me to determine nighthawk habitat use at three different scales based on vegetation characteristics.

The order Caprimulgidae, in which are found both the nighthawks (subfamily Chordeilinae) and true nightjars (subfamily Caprimulginae), is composed of crepuscular and nocturnal aerial foragers. The species in both subfamilies are known to sit on roads at night, but traditionally were thought to do so for different reasons. Nightjars use roads for thermoregulation (Camacho 2013) and as foraging site (Jackson 2009). The reasons for road use by nighthawks are less clear, but Poulin et al. (1998) speculated they may be used as bachelor roosts; however it is not clear why a road would be a suitable bachelor roost. The idea that nighthawks and nightjars use roads for different reasons is based on little more than assumptions surrounding the two subfamilies' foraging behaviour differences. Therefore, I evaluated thermoregulation and foraging as two potential explanations for the use of roads by nighthawks. I used roost surveys to determine where nighthawks were on the road and how they were positioned in relation to the road verge. I also used vegetation surveys to determine the vegetation characteristics near to where nighthawks were on roads and thermochrons to evaluate on- and off-road temperature differences.

Understanding the habitat nighthawks use in the boreal sheds light on a poorly studied member of a quickly declining guild of birds. Having this information may help conserve nighthawks by specifying the habitat they need and how to manage for it as well as increasing our knowledge of their basic biology. My results also create a springboard for future research on their population size, trends, and demographics in a vast, understudied ecosystem, which could potentially provide insight into the steep declines currently experienced by aerial insectivores both in the boreal and other regions.

CHAPTER TWO: COMMON NIGHTHAWKS USE RECENTLY BURNED AREAS IN BOREAL FOREST HABITAT

Introduction

Related only by their foraging behaviour, aerial insectivores (birds that catch and eat flying insects while themselves flying) are declining in North America. The aerial insectivore guild includes swifts, swallows, flycatchers, and nightjars. Bats are not typically included due to a lack of population trend data to quantify bat-specific declines. Unfortunately, the reasons behind this guild-level decline are unclear but are likely large-scale, complex, and common to most of the guild members (Smith et al. 2015, Michel et al. 2016). Mechanisms likely include flying insect declines (Hallmann et al. 2017), pesticide use (Nocera et al. 2012, Hallmann et al. 2014), habitat changes (Paquette et al. 2014), and climate change (Ambrosini et al. 2011, Fraser et al. 2012). Common Nighthawks (*Chordeiles minor*; hereafter nighthawk), are an aerial insectivore which occurs across most of the North American continent. They have putatively experienced steep population declines of 6.6% per year across their range (COSEWIC 2007, Sauer et al. 2017). However, they are difficult to sample because they are cryptic, mostly inactive when conventional bird surveys are conducted, and much of their range is remote and simply has not been surveyed. Therefore, the estimated rate of decline may not apply to all populations.

Nighthawks have been listed as Threatened in Canada under SARA (*Species at Risk Act* 2002). Breeding Bird Survey (BBS) data indicate that they have been declining steadily for several decades across the surveyed portion of their range (Sauer et al. 2017). However, anecdotal evidence suggests this may not be the case in Canada's boreal forest. BBS data have been collected across North America since the 1960s and are commonly used to estimate bird population trends. BBS uses road-based point counts beginning at dawn and lasting until mid-morning to allow observers to count birds during their reproductive period. However, the locations of BBS routes are biased towards populated areas with more roads and surveyors, so remote areas, such as the boreal forest (a large, coniferous forest interspersed with patches of deciduous trees), are poorly sampled. Additionally, nighthawks are only active during a short period at the beginning of the BBS survey period and are exceptionally difficult to detect when inactive. However, they are easy to detect when active because they produce frequent, loud, simple calls and there is little acoustic competition during their activity period. This means that crepuscular rather than early morning surveys should sample a population accurately. Finally, nighthawks historically nested in urban centers on flat gravel-covered rooftops, but the replacement of gravel with tar on most flat roofs has removed suitable urban nesting habitat for nighthawks. As a result, these formerly common and highly visible urban populations of nighthawks are all but gone, reinforcing the perception among many that the population as a whole has undergone a large decline. In some areas of their range this is the case, but perhaps not in the boreal forest.

The large size of the boreal forest (approximately half of Canada's landmass) coupled with high densities of nighthawks ostensibly occurring there might mean that the species' population remains large enough to instigate a rethinking of the classification of their conservation status. Learning how nighthawks are faring in the boreal forest may also enhance our understanding of the causes behind the trend in their population in other locations, thus providing a more accurate overall perspective about their conservation status. However, a more thorough reassessment of their status requires data on population trends and fitness, and these data cannot be collected without first understanding the habitats that nighthawk use and thus those where population studies should be focused.

Nighthawks are typically found in open habitats such as grasslands, beaches, or rocky outcrops (Brigham et al. 2011) and use these habitats for foraging, roosting, and nesting. As such, it follows that during their reproductive period, nighthawks in a forest-dominated ecosystem would preferentially defend territories in open areas within that habitat (Hagar et al. 2004). Wildland fires, fires occurring in vegetation or with natural fuels (National Wildfire Coordinating Group 2017), create open areas and are part of the boreal forest’s natural succession process. This leads to my hypothesis, partly derived from anecdotal observations: that nighthawk abundance will be higher in recently burned, open forest areas compared to closed, undisturbed forest. Therefore, I used targeted surveys to assess nighthawk abundance and presence probability in recently burned boreal forest (~5 years since a fire) compared to unburned forest. I also measured the vegetation characteristics of these two habitat types to quantitatively assess habitat openness and nighthawks’ use of it. Based on anecdotal reports and my own observations in the field, I also assessed whether nighthawks occurred around rivers more often than would be expected randomly.

Habitat use is a multi-scale behaviour (Johnson 1980, Mac Nally and Quinn 1998, Heisler et al. 2017), so I evaluated nighthawk habitat use at three different scales following Johnson (1980): 1) first order, hereafter landscape scale (i.e. burned or unburned forest), 2) second order, hereafter territory scale (i.e. where a nighthawk performed a breeding display), and 3) third order, hereafter roost scale (i.e. where a nighthawk was found inactive during the day). At each scale, I measured three variables: 1) canopy cover (i.e. the amount of air space occupied by trees), 2) bare ground (i.e. the amount of space on the ground unoccupied by plants), and 3) number of logs (i.e. reflecting the number of potential roost sites available). I hypothesized that 1) less canopy cover would provide easier and safer flight opportunities because there are fewer obstacles for nighthawks to avoid, 2) more bare ground would provide more potential nest and roost sites because there is space for a nest and better visibility for predator detection, and 3) more logs would provide more roost sites for nighthawks because logs provide a) an elevated site with increased visibility for detection of predators or b) backing to avoid detection by predators (Wang and Brigham 1997).

Materials & methods

Study site

My study was situated in the boreal shield ecozone, which, combined with the boreal plains ecozone further west, forms Canada's boreal forest. The boreal shield covers nearly 200 million hectares from northern Saskatchewan to Newfoundland. It is characterized by long, harsh winters and short, productive summers. The dominant trees include the coniferous white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*), and the deciduous trembling aspen (*Populus trembuloides*) and white birch (*Betula papyrifera*). The mixed (coniferous/deciduous) habitat is maintained by regular natural disturbances such as insect outbreaks or stand-replacing fires. Wildland fires have regular and short rotations in the boreal forest (Lyon et al. 2000) and are predicted to increase with climate change (Flannigan et al. 2009). These disturbances remove the longer-lived conifers and provide opportunity for the pioneering aspen and birch to invade.

My specific study site was situated in northwestern Ontario's Unorganized Kenora District (Figure 2) near Goldcorp's Musselwhite Mine (52.611500 -90.366400). In 2011, a large (141,000 ha), severe fire (where high severity = long-term effects on the plants and ecosystem from the fire; Saab and Powell 2005) burned around the mine site. Although severity varied somewhat (as is typical of wildland fires), the fire near the mine was mostly stand-replacing; only the wettest areas appear to have been burned less severely. I conducted bird abundance surveys along the gravel road leading to the mine (Figure 3). Immediately south of the mine, 34 km of that road had burned forest on both sides and the remainder of the road (175 km) was surrounded by unburned

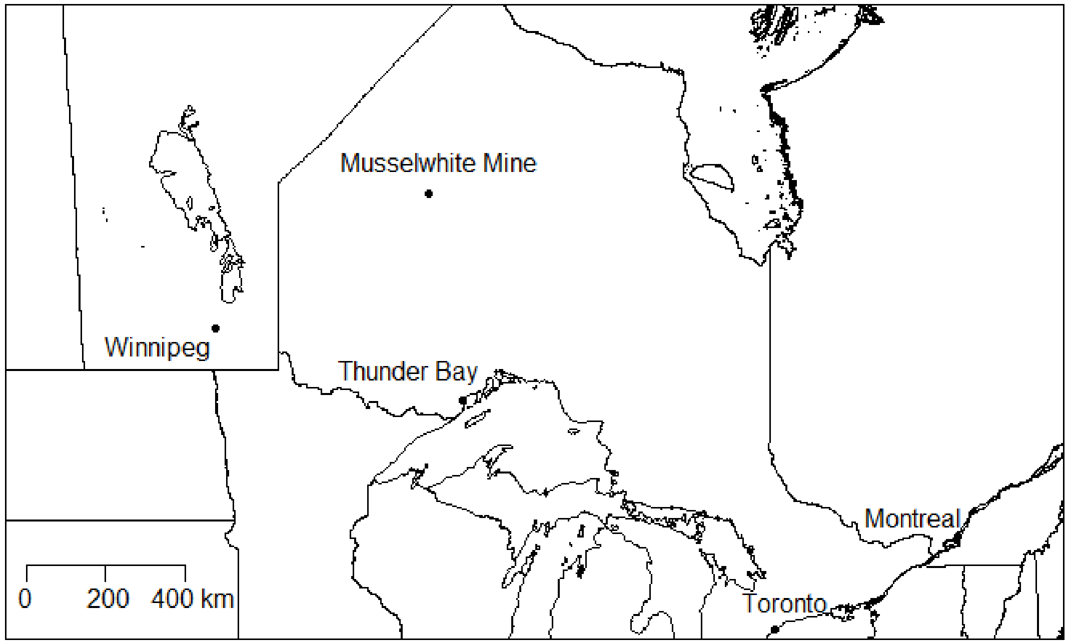

Figure 2. The study site was in boreal shield forest in northwestern Ontario immediately south of Musselwhite Mine.

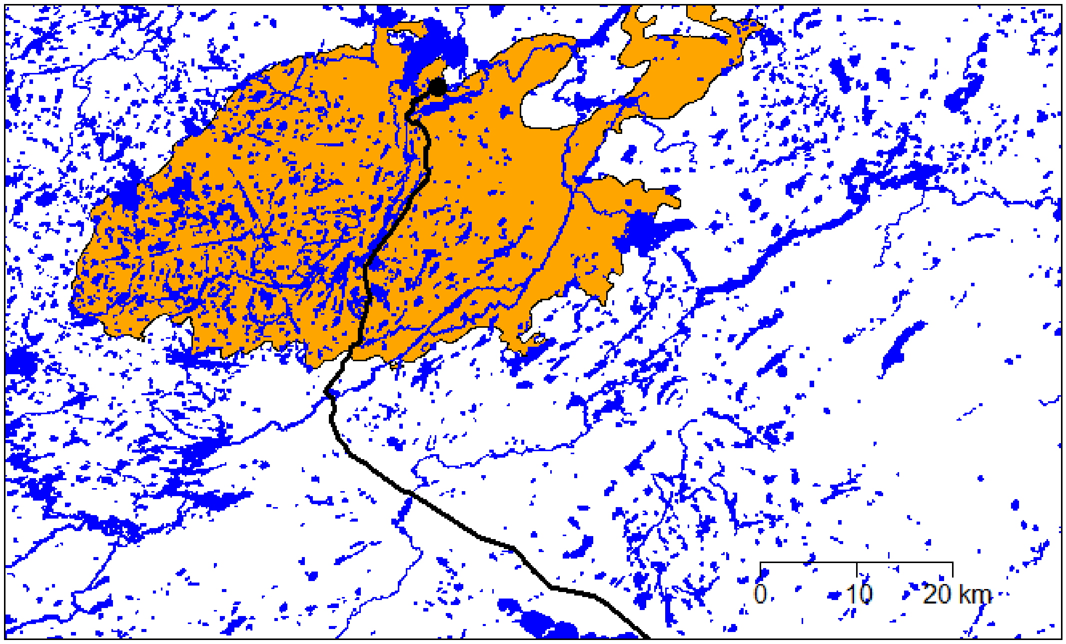

Figure 3. Study site. Surveys were conducted for 68 km on the road leading south from Musselwhite Mine (represented by the black dot). The extent of the 2011 fire is outlined in orange.

forest. I selected this site because the road provided access to a typically hard-to-access ecosystem and I wanted to investigate habitat use by individual nighthawks (GJF unpublished data). Due to logistic constraints, this finer-resolution picture of habitat use required focusing on a single site, rather than multiple sites.

Abundance surveys

I conducted on-road abundance surveys (point counts) from early June until early August each night in 2015 and twice weekly in 2016. Point counts were only undertaken when weather conditions were conducive (i.e., low wind, low precipitation). I chose the starting point and direction randomly. Point counts began 30 min before sunset and ended 120 min after sunset and I included all nighthawks detected visually and acoustically. I recorded approximate distance (> or < 100 m) and cardinal direction to the detected bird. I undertook 47 dawn point counts in June 2015 that began 120 min before sunrise and ended 30 min after sunrise. However, I encountered a low number of birds, so I did not continue them. In 2015, each point count lasted for five minutes but for six minutes in 2016. I changed the length of time to allow my survey methods to conform with the Canadian Nightjar Survey Protocol (Knight et al. 2016). Point count sites were spaced 500 m apart to reduce the likelihood of double-counting birds and I was conservative with recording detections. If I thought it was possible a detection had been recorded earlier (e.g. coming from a similar direction) then I did not record the detection. In 2016 I also recorded the occurrence of nighthawk breeding displays, steep dives that produce a low 'boom' sound from the wings. I surveyed burned and unburned forest equally in terms of the number of point counts. I surveyed burned forest the first night, followed by unburned forest on the next night. I defined burned forest as areas within the limits of the 2011 fire with charred, dead trees and new woody plant growth. I repeated this pattern for the duration of the summer. Surveying both burn types on the same night was less efficient than alternating nights given the lengthy distances between burn types. On most nights, I completed 12 point counts. In 2015, I performed 635 point counts over the summer while in 2016 I performed 170. Animal Use Protocol #15-02 was granted by the University of Regina's President's Committee on Animal Care on February 26, 2015 for this project from March 1, 2016 – March 1, 2019.

I did not calculate detectability because accurately estimating distance to a nighthawk is difficult. Many detections were acoustic only (no visual sighting) and distant (>100 m), and nighthawks often fly high (>100 m). Thus, accurate distance estimation would require an estimation of both height and distance, often based only on acoustic cues. Because of this, I concluded that accurate distance estimation was not feasible, and without this an accurate detectability estimate is not possible.

Vegetation surveys

I completed vegetation assessments at sixty-eight vegetation survey points at one km intervals along the road, thirty-four in burned and thirty-four in unburned areas of forest. Vegetation survey points coincided with every second bird point count. Burned and unburned areas were adjacent to each other and I conducted vegetation surveys in each area up to the boundary separating the areas. Each survey point consisted of four 5 m radius plots forming the corners of a 160 m x 100 m rectangle. The rectangle's 100 m sides were parallel to the road and two points were sited on each side of the road (Figure 4). In each 5 m plot, I measured percent ground cover, number of logs, and canopy closure. I visually estimated percent ground cover within a 1 x 1 m quadrat at the 5 m plot's center. Logs provide potential roosts for nighthawks, and so I measured characteristics of the logs I thought would be important to roosting nighthawks. I defined

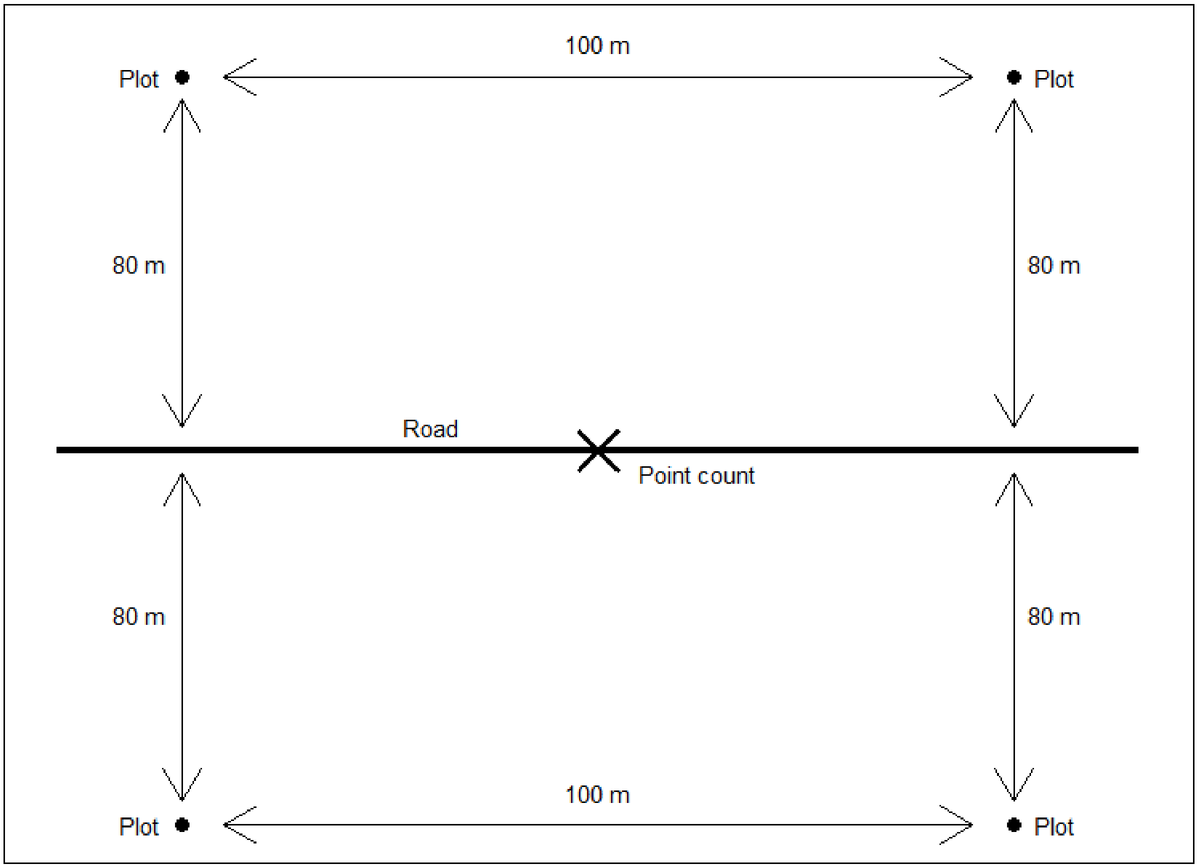

Figure 4. Vegetation survey design. Each vegetation survey point had four survey plots, two on each side of the road. The plots were 100-160 m apart and 80 m from the edge of the road and coincided with every second bird point count location.

logs as >60 cm long, >10 cm maximum diameter, <75% decomposed, and I counted all logs within each plot meeting these criteria. I estimated canopy closure with a sighting tube (Ganey and Block 1994, Korhonen et al. 2006) made of a hollow, L-shaped cardboard cube with a mirror fixed diagonally at the corner of the L, forming a rudimentary periscope. In the center of the mirror was a small "X". If the "X" was covered by the reflection of vegetation, I recorded a 1 for canopy closure. If uncovered, I recorded a 0. I measured canopy closure at the four corners of each plot's 1 x 1 m quadrat. I estimated canopy height based on a height estimate of a tree that appeared representative of the surrounding canopy. To estimate height, I moved on level ground as far away as possible while still being able see the top of the tree. I measured the distance to the bottom of the tree with a 50 m tape measure and the angle to the top of the tree with a Suunto MC-2 compass. I then calculated tree height using trigonometry (distance*(tan*θ)).

I evaluated nighthawk presence or abundance at three different scales (landscape, territory, and roost scale). The landscape scale encompassed the entire study area and compared use of burned and unburned forest. The territory scale was a location that a nighthawk was found performing a display at. The roost scale was a site where a nighthawk was found sitting during the day. At the landscape scale I defined a detection as any visual or acoustic detection of a nighthawk during a point count, while at the territory scale, I defined an occurrence as a nighthawk performing a breeding display and at the roost scale, I defined an occurrence as a nighthawk sitting at a location during the day. At a landscape scale, I used nighthawk abundance to estimate habitat use, while at territory and roost scales I used presence probability to assess habitat use. This is because nighthawks occurred, by definition, at 100% of territory and roost sites (e.g. a nighthawk roosting in some location = a roost site), while point counts at the landscape scale may or may not have had detections (e.g. a point count could have 0-N detections). I found roost sites by tracking nighthawks carrying radio-transmitters (Holohil model BD-2T; 1.7 g) during the day while they were roosting. If roosting nighthawks were found inadvertently, these sites were also added to the analysis. I captured nighthawks for radio-tagging by using a mist-net at dusk with a decoy and a playback call. I placed the net in a location I had previously seen a male perform a breeding display. The decoy was black plastic cardboard with large, white throat, wing, and tail patches painted on. I paired territory and roost sites with random sites so I could compare characteristics of the habitat used with that with no known nighthawk use. I surveyed vegetation at the random sites immediately after sampling a territory or roost site and located random sites by using a randomly generated compass bearing and travelling a randomly generated distance ($\leq$400 m) in that direction, or until a clear habitat change occurred (e.g. jack pine forest changing into white spruce forest).

Analysis

First, I evaluated only vegetation characteristics between burned and unburned sites to define the vegetation differences between sites. Next, I compared nighthawk abundance between burned and unburned sites. Then, I assessed the distance of detections of nighthawks relative to the boundary between burned and unburned sites. I also examined the distance at which I detected nighthawks from the three rivers (Zeemel, Pipestone, and Pineimuta Rivers) that crossed the surveyed portion of the road. I compared these distances by measuring the straight-line distance from each detection to the closest river and to the closest of three randomly generated points. I then tested if there was a difference between the distance from rivers compared to random points. Finally, I evaluated the importance of vegetation characteristics in relation to nighthawk presence at the landscape, territory, and roost scales. I analyzed these data using generalized linear models (GLM) in R version 3.3.0 (R Core Team 2016) with base function *glm*. I tested significance for all models using an alpha value of 0.05.

I used a binomial distribution with a logistic link to compare vegetation characteristics in burned and unburned forest, and to test nighthawks' use of those characteristics. I chose a binomial distribution because the independent variable was either burned or unburned (i.e. 1 or 0). I used a Poisson distribution with a logarithmic link for evaluating abundance differences in burned and unburned forest. I chose a Poisson distribution because the independent variable (count data) was positive, had many zeroes, and was not overdispersed. I used a gamma distribution with an inverse link to test if nighthawks were detected more frequently closer to the burn boundary in unburned forest and to rivers in the study site. I chose a gamma distribution because the independent variable was positive and non-zero.

Results

Abundance

I detected a mean of 0.5 nighthawks per point count (406 nighthawks / 805 point counts). In burned forest, I detected a mean of 0.7 nighthawks per point count (297 nighthawks / 414 point counts) while in unburned forest I detected a mean of 0.3 nighthawks per point count (103 nighthawks / 391 point counts). I found that canopy cover was significantly higher in burned forest (Figure 5; z = -3.97; p = <0.001) but that neither the amount of bare ground (z = -1.43; p = 0.15) nor the number of logs (z = 1.49; p = 0.14) were significantly different in burned vs unburned forest. I modelled total nighthawk abundance as a function of habitat type (burned or unburned) and showed that nighthawk abundance was significantly higher in burned sites than unburned (z = -8.64; p = <0.001). I also evaluated whether nighthawks in unburned forest were detected more frequently near the boundary of the burn. I found that there was a significant difference (z = 4.20; p = <0.001). Nighthawks detected at point counts in unburned forest tended to be closer to the boundary of the burn (Figure 6), but nighthawks in burned forest were not more likely to be closer to the burn boundary. Additionally, many of the nighthawk detections appeared to be near rivers, so I tested *a posteriori* whether there was a clumping effect near any of the rivers that crossed the sampling area (Zeemel Creek in burned forest, Pipestone River and Pineimuta River in unburned forest), but I found no significant clumping effect (z = -0.70; p-value = 0.48).

Habitat attributes

I evaluated nighthawks' use of three habitat attributes (canopy cover, bare ground, and number of logs) at all three scales (landscape scale, territory scale, and roost scale). I found that at the landscape scale, canopy cover was a significant predictor of nighthawk detection (Figure 7; $z = -9.41$; $p = <0.001$), but neither number of logs ($z = 1.53$; $p = 0.13$) nor bare ground ($z = 1.67$; $p = 0.10$) were. At a territory scale, canopy cover was significant (Figure 8; $z = -2.33$; $p = 0.02$) but neither number of logs ($z = -0.03$; $p = 0.98$) nor bare ground ($z = 1.40$ $p = 0.16$) were. Despite nighthawks' preference for burned forest, breeding displays did occur in unburned forest, but the frequency of these displays diminished with distance from the boundary of the burn (Figure 9). At the roost scale, canopy height ($z = 0.89$; $p = 0.37$) was not significant, but the number of logs was significant (Figure 10; $z = 2.54$; $p = 0.01$), while bare ground was not ($z = 1.78$; $p = 0.08$). Canopy height was used instead of canopy cover at the roost scale because height and cover were moderately correlated (~47%). Roost sites were only sampled in 2016, and canopy cover was not measured in 2016.

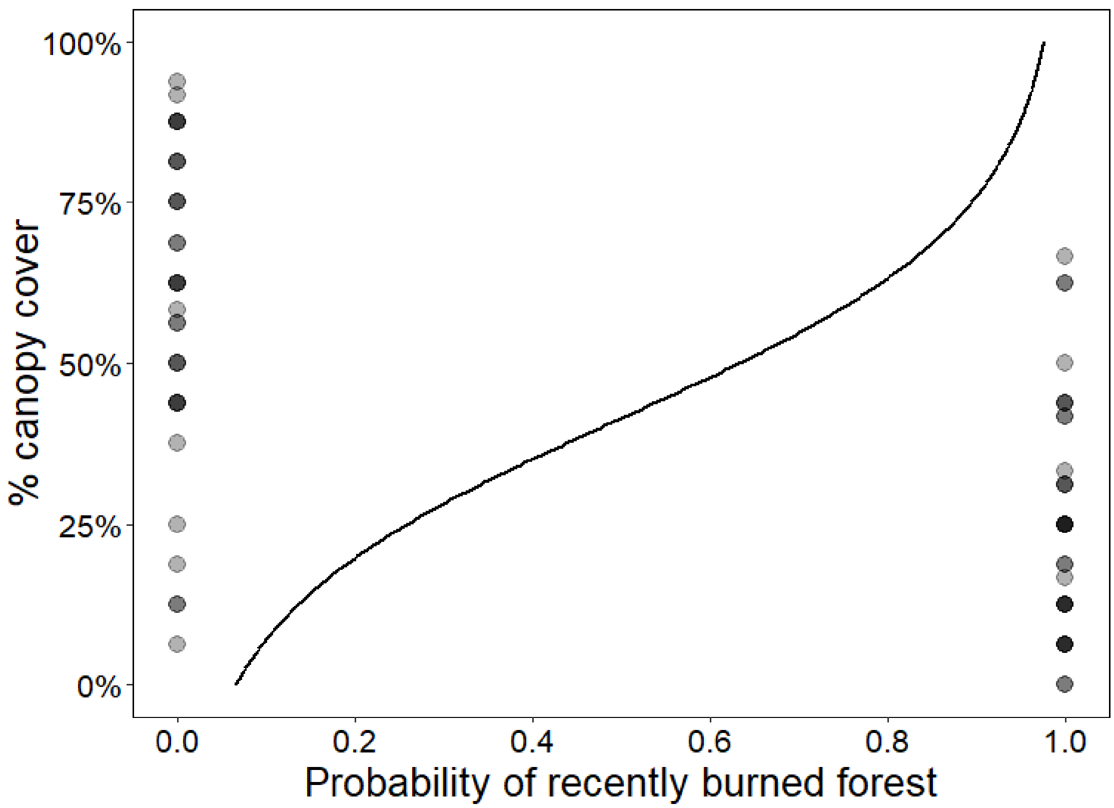

Figure 5. Forest was more likely to have recently experienced a burn as the percentage of canopy cover decreased.

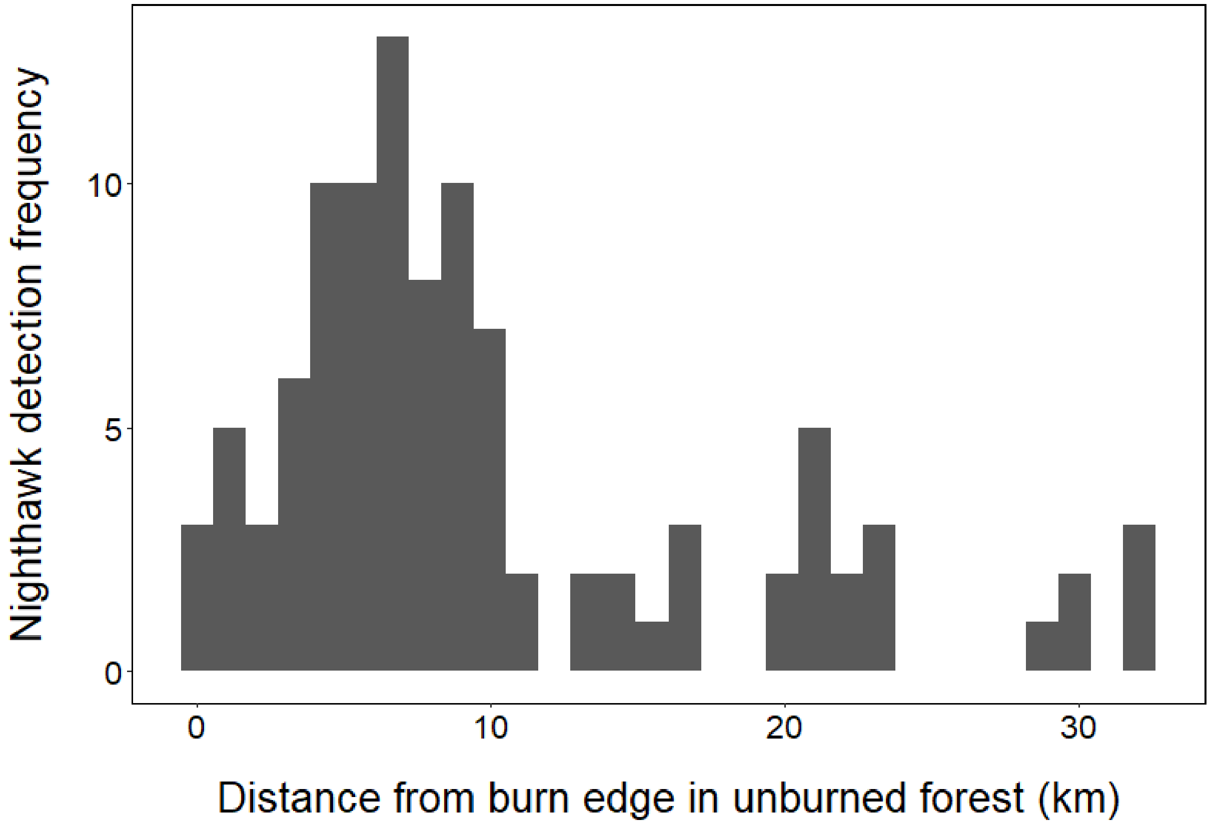

Figure 6. The number of Common Nighthawks detected in unburned forest decreased with distance from the edge of the recent burn.

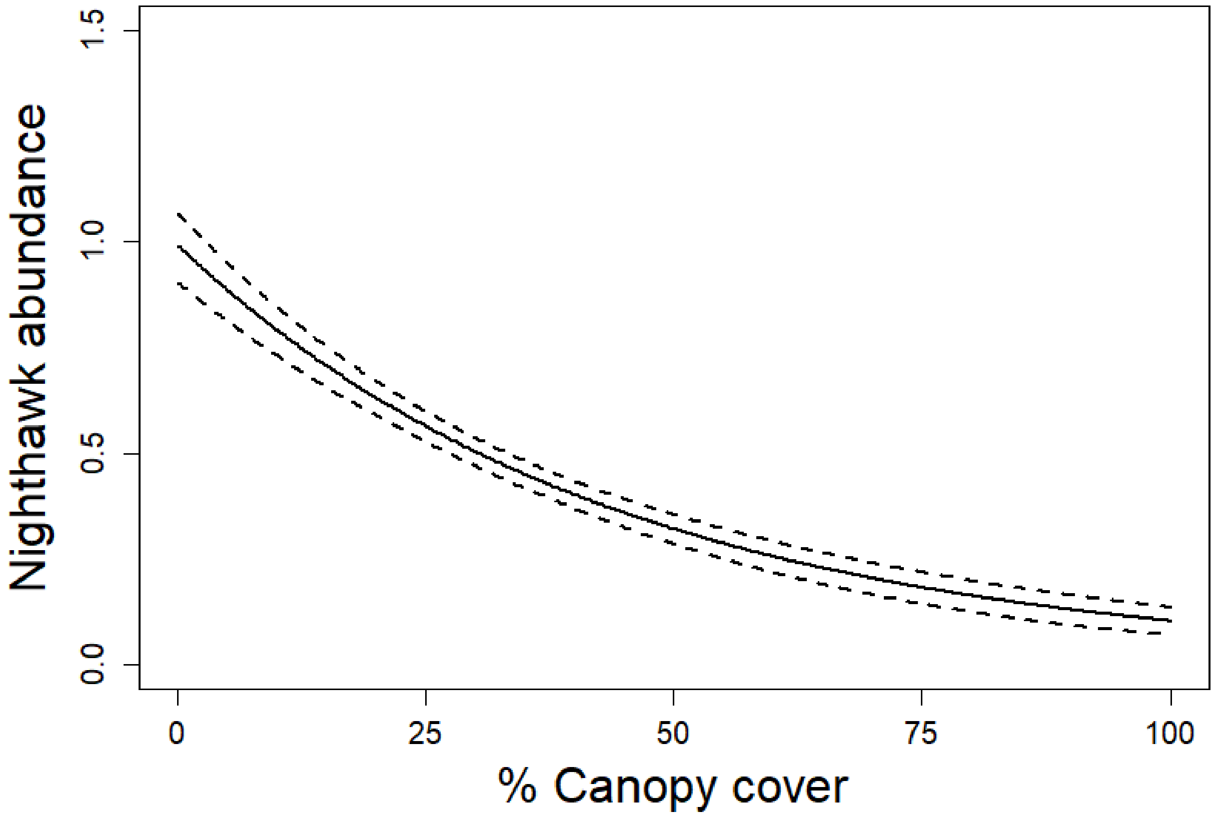

Figure 7. Common Nighthawk abundance at a landscape scale decreased as canopy cover increased. Solid line is abundance predicted from a GLM. Dotted lines are ± one standard error.

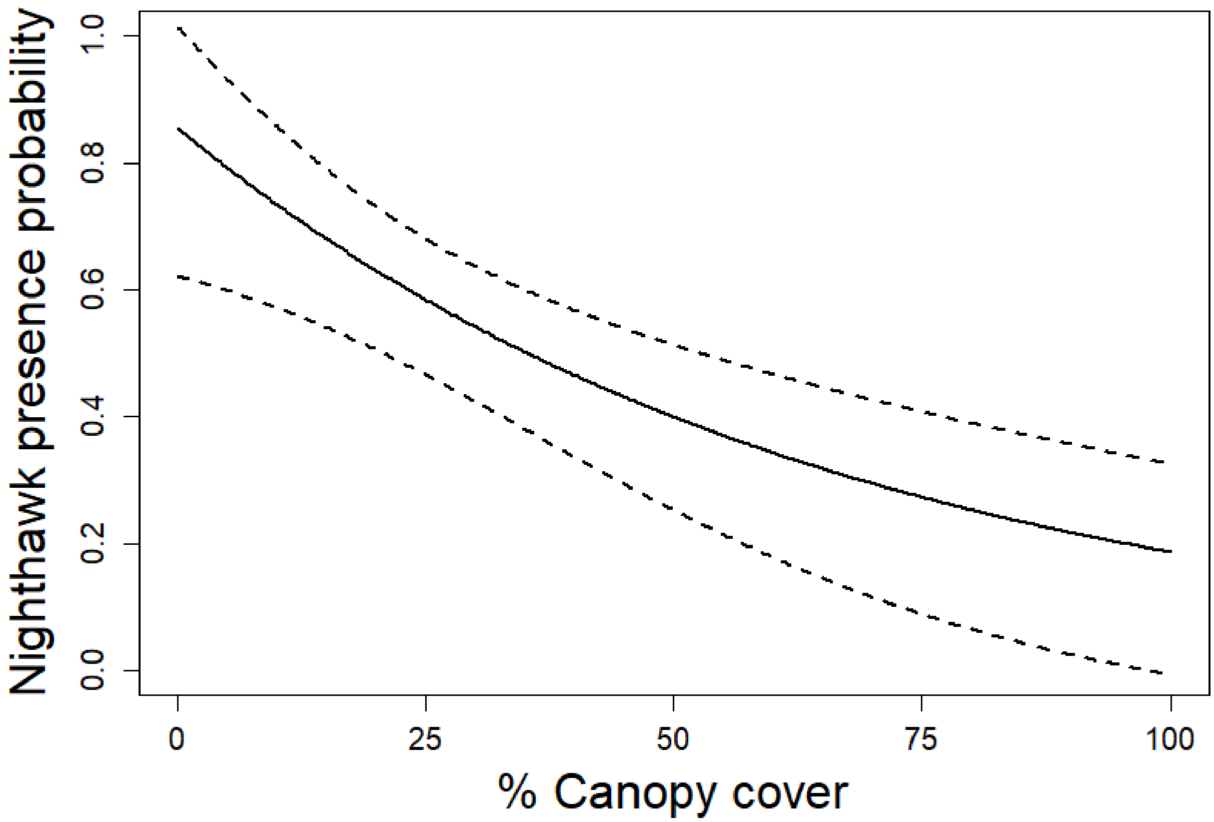

Figure 8. Probability of Common Nighthawk presence at the territory scale decreased as canopy cover increased. Solid line is presence probability predicted from a GLM. Dotted lines are ± one standard error.

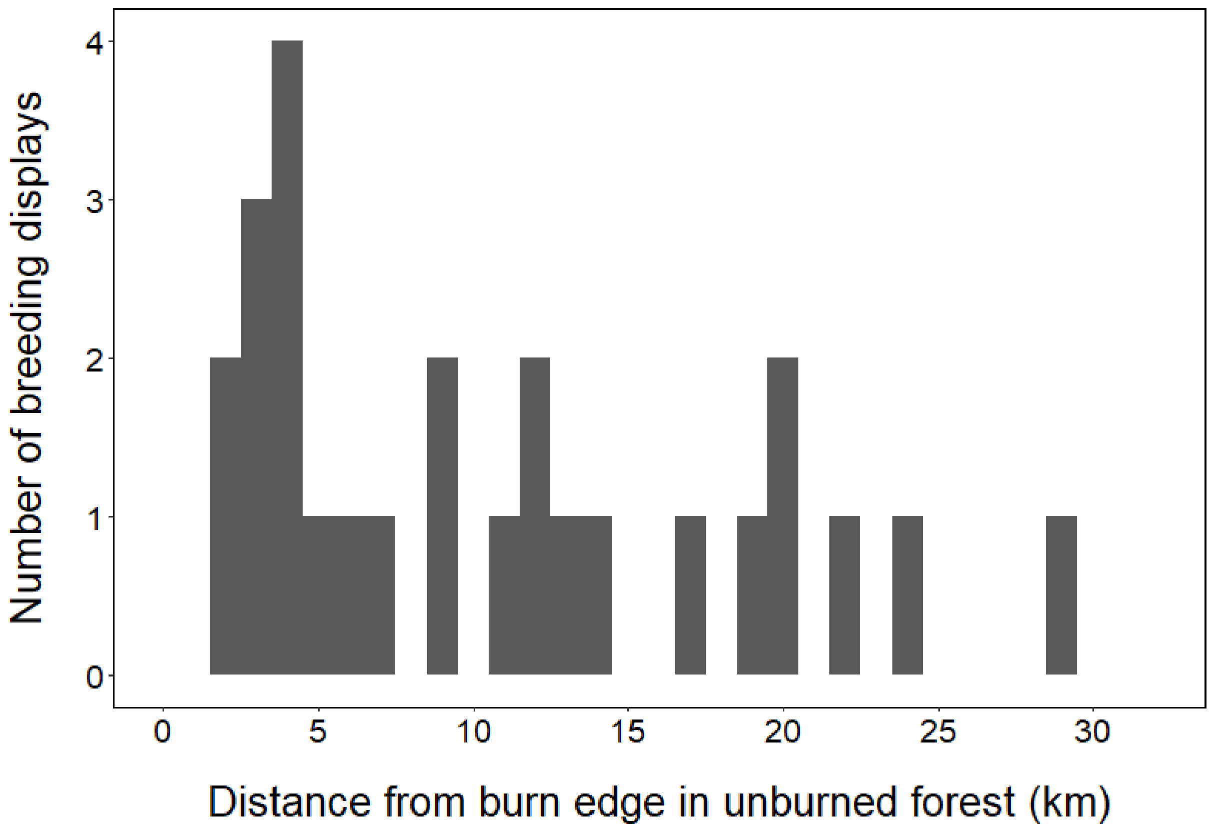

Figure 9. Number of nighthawk breeding displays detected in unburned forest decreased with distance (km) from the edge of the recent burn.

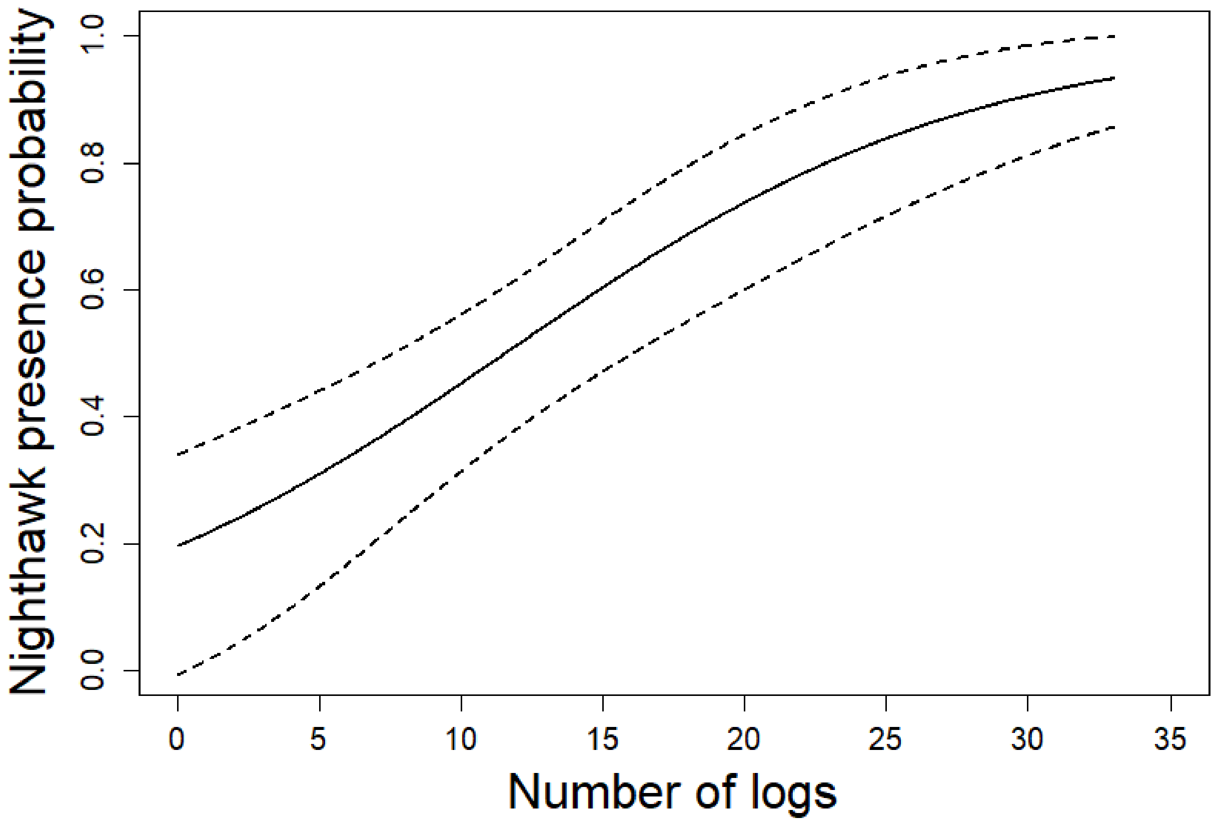

Figure 10. Probability of Common Nighthawk presence at the roost site scale increased with the number of logs present. Solid line is presence probability predicted from a GLM. Dotted lines are ± one standard error.

Discussion

As predicted, I found that nighthawks were more abundant in burned than unburned forest, but they still used unburned forest to some extent. Burned forest had less canopy cover at both the landscape and territory scales and low canopy cover was the only variable I measured that birds used. At the roost scale, it was the number of logs that was significant. Unexpectedly, there was no support for my hypothesis that bare ground was important for nighthawks, no matter the scale. Additionally, fewer nighthawks were detected further away from the burn and despite some anecdotal field observations, my analysis showed that they were not significantly more common around rivers.

Nighthawk abundance at my study site was 36% lower than abundance reported in former burns in the Yukon territory's boreal forest using similar survey methodology (Sidler 2017; 1.1 nighthawks per point count; 632 nighthawks / 724 point counts). In 2017, WildResearch volunteers conducted point counts across western Canada (British Columbia, Alberta, Saskatchewan, Yukon, Northwest Territories) and New Brunswick using similar survey methodology to mine. They found mean abundance was 29% lower than abundance at my study site (Knight and Noble-Dalton 2018; 0.5 nighthawks / point count; 858 nighthawks / 1,681 point counts). However, this abundance was across all surveyed regions and data were not parsed into boreal and non-boreal regions. These data suggest that nighthawk populations in the boreal are abundant. Past estimates of nighthawk population trends have been based primarily on Breeding Bird Survey data, which largely ignore the boreal forest. Due to the boreal's abundant nighthawk populations, future models of nighthawk population trends should incorporate boreal populations more explicitly.

I detected nighthawks much more often along the road I surveyed in areas where the forest had burned in 2011 than in areas that were unburned. Nighthawks are typically found on the ground in open habitat such as grasslands, beaches, or rocky slopes, likely because nighthawks have a relatively long wingspan (~19-20 cm; Brigham et al. 2011). Wildland fires remove many of the vegetative obstacles that exist in forested areas, transforming a closed forest into an open area with low canopy cover reflecting what is typically described as nighthawk habitat. Compared to forested areas, open areas have fewer obstacles and thus fewer hazards for nighthawks to avoid while initiating flight and landing. This preference for less canopy cover has been shown for other nightjars as well (Wang and Brigham 1997).

At both the landscape and territory scale, my results show that nighthawks use canopy cover and did not use either bare ground or number of logs. However, at a roost scale, the number of logs became important while bare ground and canopy height, the substitute variable for canopy cover in my 2016 vegetation surveys, were not significant. It is possible that canopy height is not an appropriate substitute for canopy cover, but roosting nighthawks are largely stationary. Easy access for departing and arriving at the roost site and a clear line of sight for detection of predators may be more important than the flying space needed for foraging. Most nighthawks I found roosting were on logs (75%), and anecdotally most flew a short distance once disturbed (< 50 m). Logs may be important for roost use because they provide an easy access point to land on and less obstructed visibility while roosting.

Although most nighthawk detections (74%) and breeding displays (68%) occurred in burned forest, there were still a substantial number of detections and displays by birds at point counts conducted in unburned forest. Detection and display frequency of nighthawks in unburned forest areas did decrease with distance from the boundary of the burned forest. These data indicate that while nighthawks were primarily found in open, burned habitat, unburned habitat was also used by these birds. Detections in unburned habitats may have been of nighthawks travelling from their territories in burned forest. Given the declining frequency of detections from the burn boundary, this likely accounts for some detections. However, the fact that I recorded breeding displays during point counts in unburned forest weakens this argument. More likely, nighthawks use unburned forest for nesting, roosting and feeding but in lower densities than in burned forest. Nighthawks use open areas with low canopy cover, but just how large these open areas need to be so they are useful to nighthawks is not known. Exposed bedrock, downed mature trees, riverbanks and lakeshores, and other features regularly create small open areas across the boreal region and these may provide areas that offer acceptable nest and roost sites.

It is possible that nighthawks were less detectable in unburned forest. The vegetation in unburned forest is denser than that in burned forest and this attenuates sound more. However, nighthawks were never directly observed flying below the forest canopy in unburned forest. All acoustic detections were of birds flying above the canopy where attenuation was unlikely to be an issue. Additionally, nighthawk calls are loud, distinct, and there is little acoustic competition at their peak activity time. Thus, I highly doubt that detection was worse in unburned forest.

While surveying nighthawks, I gained the impression that in the unburned forest nighthawks were more commonly detected near rivers, so I tested this *a posteriori*. Nighthawks have been known to travel substantial distances from roost (and presumably territory) sites to water (Brigham 1989, Brigham and Fenton 1991a) and appear to prefer foraging around waterbodies (Ng 2009). However, my quantitative analysis revealed no increase in abundance near any of the rivers that crossed the surveyed sites. This is likely because standing waterbodies were widespread and available throughout the study area. I did not test nighthawks' association with lakes because lacustrine systems were so abundant and nighthawks are so mobile that any association with them would have been difficult to assess given the data I had. An alternative explanation is that these birds are less reliant on water in the boreal forest. The research suggesting that nighthawks prefer foraging near water was conducted in dry areas with relatively little available water (i.e. Okanagan valley, prairie grasslands). These areas may generate a greater need for standing water to drink as well as the foraging opportunities provided (although no observations of nighthawks actually drinking were reported in these studies). In response to hot temperatures, nightjars evaporate water to regulate body temperature by using gular flutter. This is one of the most efficient means of evaporative cooling

(Howell 1959, O'Connor et al. 2017). Nighthawks drink by skimming low over water (Gross 1940), and may travel to waterbodies to replace body water. Boreal summers are typically cooler than sites where research has been undertaken previously, with mean maximum temperatures from June to August 2015-16 of 22.2 ºC at the study site, compared to 30.6 ºC in the Okanagan and 25.7 ºC in Saskatchewan (Environment Canada 2017) and similar day length (on June 21, study site = 16 hrs 38 mins; Regina = 16 hrs 27 min; Okanagan = 16 hrs 14 min). Therefore, it is possible that daily water requirements are lower in the boreal due to a reduced need to keep cool using evaporative water loss.

The hypothesis that nighthawks prefer burned sites because foraging is easier in more open areas assumes that nighthawks forage below the canopy in an unburned site. However, nighthawks likely avoid this cost by foraging above the canopy. This does assume that prey availability is not different between burned and unburned forest. Foraging above a closed canopy does occur, but likely at a lower rate than above open canopy, such as that found in a burned area. Therefore, either prey availability is higher in burned habitats, other behavioural requirements such as nesting or roosting are informing nighthawks' habitat choice, or foraging is indeed more difficult and perhaps riskier (e.g., collisions) in unburned areas.

It is possible that the habitat provided in burned forest leads to an increase in nighthawk prey availability. Knowledge of the community composition and abundance of boreal insects is limited (Spence et al. 1997), and not surprisingly given the enormous diversity present, the effects of fire on insects are mixed.

Fire likely increases the abundance of some (Fye 1972, Lyon et al. 1978, Mccullough et al. 1998, Morissette et al. 2002), but decreases the abundance of other groups/species (Holliday 1992, Mccullough et al. 1998) and these differences change with time following a burn event (Mccullough et al. 1998). Szaro and Balda (1986) found that insect abundance was lowest in recently harvested, more open forest habitats, but despite this, overall bird density increased with decreasing canopy cover. Aerial insectivores tend to increase in numbers in recently burned forest (Hutto 1995, Saab and Powell 2005, Smucker et al. 2005, Kotliar et al. 2007, Saab et al. 2007), but also increase following timber harvest (Szaro and Balda 1986, Parody et al. 2001, Hagar et al. 2004). This indicates that it is not necessarily a feature of the burn itself that attracts aerial insectivores, but rather the difference in structure, namely a decrease in canopy cover (i.e. a more open area). Most of these studies detected few or no nighthawks, which is not surprising given the timing of sampling. Nighthawks are difficult to detect unless surveys are timed to coincide with nighthawks' short crepuscular period of activity and most surveys, like the Breeding Bird Survey, are not conducted during this time. Nighthawks are generalist insectivores and target relatively large, abundant insects (Brigham 1990, Todd et al. 1998), so if other aerial insectivores are increasing it stands to reason that superior foraging opportunities for nighthawks exist following removal of canopy cover.

Nighthawks likely use patches of forest recently burned based on behavioural requirements other than just foraging, such as nesting or roosting. Nighthawks do not build a nest or even a scrape on the ground, but lay eggs directly on bare ground. Wildland fires, in addition to creating bare ground suitable for these kinds of nests, create open areas. Nighthawks also demonstrate some nest site fidelity (Dexter 1961, Brigham 1989) which may reflect the importance of a specific nest site, but this could equally be fidelity to a territory in addition to the nest site itself. Other nightjars (Caprimulgidae) also use bare ground as nest sites and are known to nest in forested areas, but unlike nighthawks, these birds have shorter, more rounded wings which are more suited to flight in less open, more "cluttered" habitats (Straight and Cooper 2012, Cink et al. 2017). Most of what is known about nighthawk roost use is related to their use of trees (Fisher et al. 2004) or gravel roof tops (Brigham 1989), but nighthawks also routinely roost on the ground (Rust 1947, Brigham 1989), meaning that the amount of bare ground might be expected to be important. In my study area, I found no evidence that bare ground was a significant factor for use at the landscape or roost site scale. This suggests that finding a patch of bare ground to sit or nest on is not difficult for nighthawks. Additionally, while nighthawks were less abundant in unburned forest, they still used this habitat and apparently also had territories there (based on the breeding displays recorded in unburned forest). Therefore, nighthawks may use small, open patches in unburned forest for nesting and roosting and then forage over the canopy in unburned forest, but they do so at a lower density than in large, open patches such as burned forest.

In conclusion, I hypothesized that nighthawks may use burned forest based on 1) the amount of bare ground, 2) the number of fallen logs, or 3) the amount of canopy cover. Bare ground provides nighthawks with a clear view of incoming predators, as well as space to lay their eggs. Fallen logs provide roost sites which allow birds to be above existing vegetation and increase the potential to detect incoming predators, and backing to reduce visual detection of nighthawks by predators (Wang and Brigham 1997). Decreasing canopy cover likely reduces the challenge of flying and foraging, particularly in low light conditions. I tested this association with low canopy cover at three different scales, including 1) landscape, 2) territory, and 3) roost scale. I found that nighthawks used burned forest more than unburned forest, and used less canopy cover at landscape and territory scales. At the roost scale, the number of available logs was important. Detections decreased with distance from the burn, but unburned forest is likely still useful for lower densities of nighthawks. Finally, there was no indication of an increased abundance of nighthawks near rivers.

My data reflect only one area of forest burned 4-5 years ago, therefore the application of this study to the entire boreal forest must be undertaken with caution. Nevertheless, my data provide an important starting point for understanding the habitat used by a little-known, putatively declining aerial insectivore. Each year, approximately 2.1 million hectares of forest burn in Canada (Natural Resources Canada 2018), suggesting high potential for plenty of suitable nighthawk habitat across the boreal. I predict that nighthawk density in the area will decrease as time progresses and the forest regrows (Hagar et al. 2004, Sidler 2017). Other factors that vary with each fire event, such as intensity or severity, will also impact the suitability of the burned forest as nighthawk habitat (e.g. a larger, hotter fire will create a more open area than a smaller, cooler fire). I found that canopy cover is the most important factor for nighthawk habitat use and have argued that this is because it enhances nighthawks' ability to fly and catch insects during times of the day with low light. This preference for open areas also suggests that areas recently logged, particularly clear-cut areas, will be perceived as good habitat by nighthawks. Although timber harvest and salvage logging (harvesting economically valuable trees after a fire) often remove snags from the landscape and this snag removal reduces bird density/diversity (Morissette et al. 2002, Koivula and Schmiegelow 2007), its effect on nighthawks should be limited because their life history does not require snags. Therefore, I recommend that 1) further research be conducted on nighthawk association with a) timber harvest and b) different fire regimes and 2) that managers keen on increasing or maintaining nighthawk populations consider a) evaluating the reduction or elimination of fire suppression in appropriate locations and or b) consider allowing sustainable timber harvest to occur. Managers should also keep in mind that these recommendations are for a single species only and must be evaluated within a comprehensive multi-species approach.

CHAPTER THREE: DO COMMON NIGHTHAWKS USE ROADS AS FORAGING SITES?

Introduction

Aerial insectivores are a guild of birds related not by taxonomy, but by behavioural similarities. Aerial insectivores forage in the air on flying insects and include taxa such as swallows (Hirundinidae), swifts (Apodidae), flycatchers (Tyrannidae), and nightjars (Caprimulgidae). Each of these taxa are experiencing steep population declines and together the guild is experiencing the steepest decline among Canada's bird guilds (North American Bird Conservation Initiative Canada 2012). The causes of this decline are unknown, but are likely large-scale, complex, common to each of the guild's taxa, and unlikely to be univariate (Paquette et al. 2014, Smith et al. 2015, Michel et al. 2016). Potential mechanisms include insecticides and declining insect populations (Nebel et al. 2010, Nocera et al. 2012, Hallmann et al. 2014, 2017), mismatched phenology and climate change (Ambrosini et al. 2011, Fraser et al. 2012, García-Pérez et al. 2014), and land use changes (Paquette et al. 2014).

Common Nighthawks (*Chordeiles minor*: Caprimulgidae; hereafter nighthawk) are aerial insectivores putatively declining at a rate of 6.6% each year (COSEWIC 2007, Sauer et al. 2017) and listed as Threatened in Canada (*Species at Risk Act* 2002). However, northern populations of nighthawks within the boreal ecoregion, a vast conifer-dominated forest, appear to be more abundant than southern populations (pers. comm. E. Knight, K. Hannah, A.

Sidler, GJF pers. obs.), particularly in recently burned areas (Sidler 2017, GJF chapter 1, E. Knight pers. comm., K. Hannah pers. comm.). Understanding nighthawk survival in the boreal, particularly anthropogenic induced mortality, is crucial to the management and protection of this at-risk species.

Many Caprimulgids are known to sit on roads at night (Quesnel 1986, Poulin et al. 1998, Jackson 2009, Camacho 2013). Within the Caprimulgidae, nighthawks form the subfamily Chordeilinae, while the subfamily Caprimulginae is composed of true nightjars (hereafter, nightjars). Although nightjars are known to use roads for thermoregulation (Camacho 2013) and foraging (Jackson 2009), the reasons why nighthawks frequent roads at night are unclear. Conventionally, naturalists have assumed that nighthawks were using roads to roost, where roosting is defined as settling in a location to sleep or rest. Poulin et al. (1998) speculated that nighthawks used roads as bachelor roosts, but this was based only on an absence of females and other behavioural observations. Even if true, this hypothesis provides little insight into why nighthawks would choose roads as night roost sites.

At first glance, thermoregulation seems to be a reasonable explanation for nighthawks' road use. Upon closer inspection, however, there appears to be an inconsistency between this theory and observations. Camacho (2013) found that nightjars used roads for thermoregulation. During cold weather they were found more often on asphalt roads, which were warmer than other available substrates. If nighthawks also used roads for thermoregulation, a similar pattern would be expected. Anecdotally though, nighthawks rarely, if ever, use asphalt roads to sit or roost on whereas they routinely use gravel roads. This incongruence makes a thermoregulatory explanation less likely.

Foraging has been ignored as an explanation simply because nighthawks do not typically forage at night. Nighthawks forage by ‘hawking’: capturing flying insects during non-stop flight, typically only at dawn and dusk (Brigham and Barclay 1992). Nightjars forage by ‘sallying’: waiting for flying prey to come close and then flying a short distance from a perch to catch it before returning to their perch, typically at dusk, dawn, as well as during the night. Nighthawk wings are relatively long and narrow, while nightjar wings tend to be shorter and broader. Long, narrow wings are better for sustained relatively fast flight, while short, broad wings are better for taking off from the ground and manoeuvring through clutter, reflecting the preferred feeding method of each subfamily. While hawking or sallying may be the preferred method of its respective subfamily, there is no good reason to believe that either subfamily is entirely restricted to that method. Nighthawks are known to extend their foraging period using artificial lights (Shields and Bildstein 1979, Foley and Wszola 2017), and this behavioural flexibility may extend to their choice of foraging method.

Flexibility in foraging behaviour is not unheard of. For example, Ratcliffe and Dawson (2003) found that little brown bats (*Myotis lucifugus*) and northern long-eared bats (*Myotis septentrionalis*), traditionally thought to be strict aerial foragers and surface gleaners, respectively, would engage in the opposite style of foraging behaviour associated with them (either aerial foraging or surface gleaning) when an opportunity was available.

The use of roads by both nighthawks and nightjars poses a potential mortality risk caused by passing vehicles (Jackson 2009, Camacho 2013). Determining the factors behind nighthawks' use of sites on roads, potential reasons for their use of roads, and quantifying mortality risk due to vehicles will collectively inform decisions about their conservation and management. Nighthawks, while the best-studied of North American Caprimulgidae, are still poorly understood compared to most birds. Learning more about their behaviour will serve to extend our knowledge of their basic biology and better inform management and conservation of a family with the unique niche of nocturnal aerial foraging, one they share only with bats.

I predicted that nighthawks would use roads in proportion to their general abundance near a road location at both coarse and fine scales (first and second order site use, *sensu* Johnson 1980) and when there were fewer potential roosts available nearby. I predicted that nighthawks would use sites for roosting with higher and denser verge vegetation because this should provide "backing" (an object that acts as a visual screen behind an animal) and be a potential aid for avoiding detection by predators (Wang and Brigham 1997). I predicted that on-road temperature would not affect their use of roads or their choice of specific sites along a road. I hypothesized that the frequency of nighthawks using the road would increase with lunar illumination because nighthawks may use roads as foraging sites, like nightjars. The uncluttered space of the road provides a clear view of the sky against which backlit insects can be more easily spotted, as well as room for birds to sally and capture prey. Finally, I predicted that nighthawk mortality on-road in my study site would be insignificant because traffic rates were low.

Materials & methods

Study site

My study site was in Canada's boreal forest, an ecoregion composed of the boreal shield and boreal plains ecozones, which together cover approximately one half of Canada's landmass. I conducted my research in the boreal shield, where mature forest is composed of coniferous trees such as white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*), while deciduous, pioneering trees such as trembling aspen (*Populus trembuloides*), white birch (*Betula papyrifera*), and willow (*Salix* sp.) colonize forest gaps. Canada's largest ecozone, the boreal shield covers almost 200 million hectares of the eastern half of the boreal ecoregion, ranging from Saskatchewan to Newfoundland. During its short, productive summers, the boreal forest is a destination for reproduction by hundreds of species of birds. Most of these species migrate to warmer climes after nesting to avoid the long, harsh winters that characterize the region.

My specific study site was in northwestern Ontario, near Musselwhite Mine (Figure 11). In 2011, a 141,000 ha fire burned south of the mine on either side of a gravel road that leads to it (Figure 12). While the fire's severity varied somewhat (as is common with wildland fires), the fire was mostly stand-

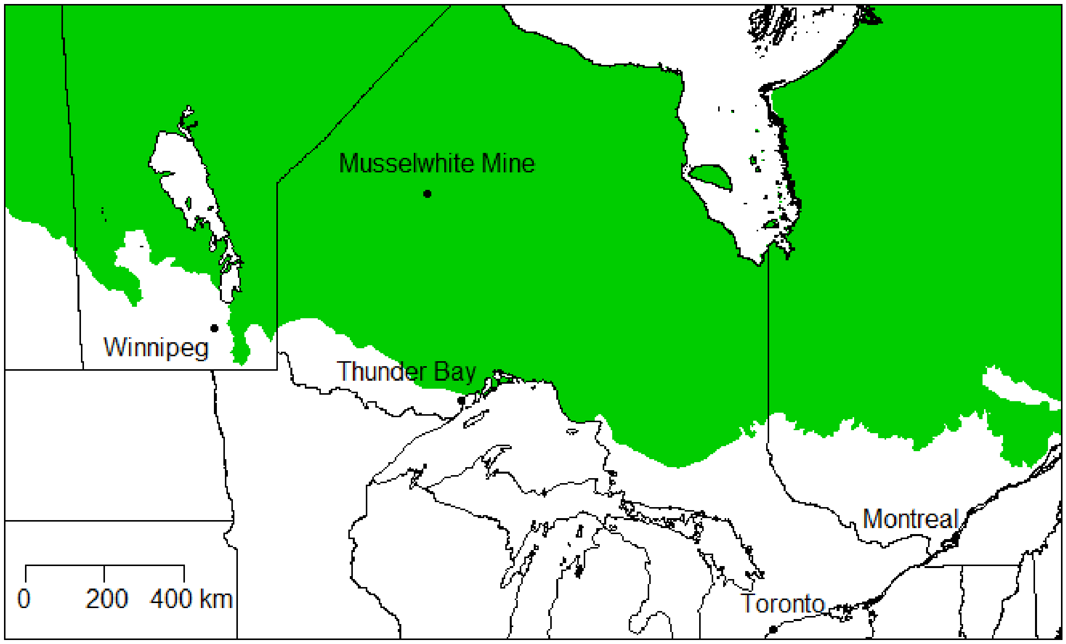

Figure 11. The study location was in northwestern Ontario, Canada, near Musselwhite Mine. The shaded green area is the extent of the boreal forest (both boreal shield and plains ecozones).

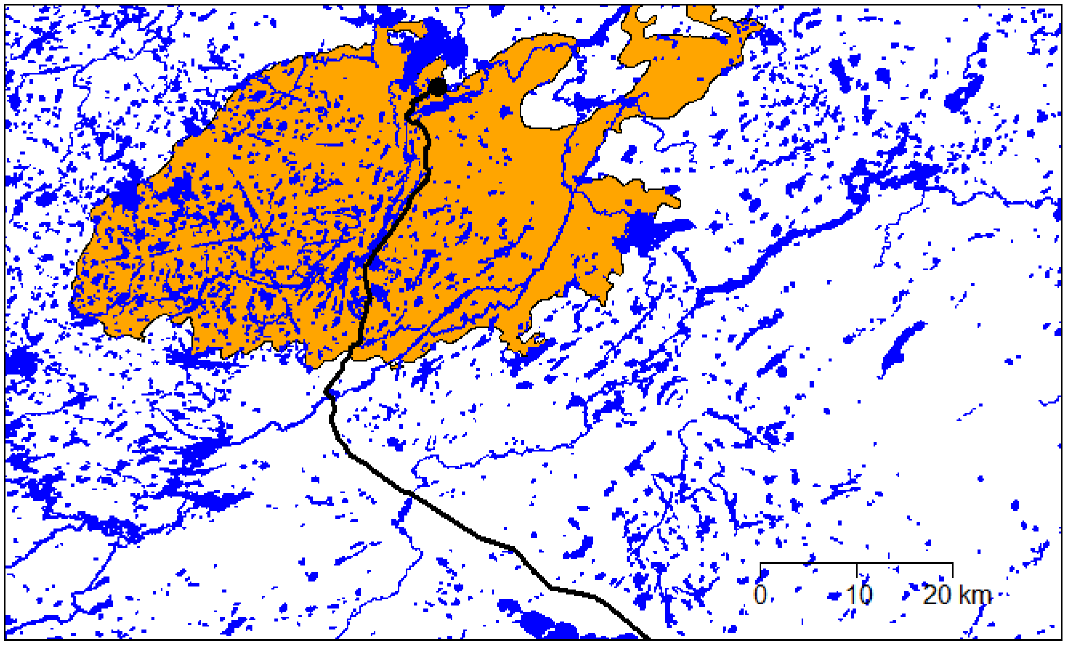

Figure 12. Research was conducted along the gravel road (black line) that terminates at Musselwhite Mine, Ontario, Canada, represented by the black dot. In 2011, a 141,000 ha stand-replacing fire (orange polygon) burned south of the mine on either side of the road.

replacing; only the wettest areas of forest did not burn. The private mine road traversing the burned area connects to a public road that continues southeast for approximately 200 km to the town of Pickle Lake. I conducted my research along 70 km of these two roads, from the mine entrance towards the southeast. I chose this site because anecdotal evidence suggested that nighthawks were more common in recently burned forest than in surrounding undisturbed forest.

Surveys

I conducted abundance surveys (point counts) from June to August in 2015 and 2016. In 2015, point counts (n = 673) were each 5 min long and conducted most nights, provided weather conditions allowed (i.e. low wind, low precipitation). In 2016, point counts (n = 96) were increased to 6 min to match the newly approved Canadian Nightjar Survey Protocol (Knight et al. 2016) and were conducted weekly. Each point count was 500 m from the previous one to reduce the chance of double-counting birds. The point count transects usually consisted of a dozen point counts. They were begun at a random point, moved in a random direction, and began approximately 30 min before sunset. I stopped surveying after approximately 120 min, when nighthawks were typically no longer active. Each transect was along the road in either burned or unburned forest habitat and the burn type I surveyed was alternated nightly. Burned forest was defined as areas with charred trees and new woody plant growth within the limits of the 2011 fire. I counted all nighthawks detected within the time limit, whether visually or acoustically.

In addition to point counts, I conducted nighthawk road use surveys from June to August 2015-16. In 2015, I performed these road surveys each night (n = 51 surveys) following the completion of the point count survey. In 2016, I reduced the frequency of road surveys (n = 17 surveys) to every third day for three reasons. First, in 2016, I only conducted point counts weekly. Second, I wanted to avoid habituating nighthawks to my vehicle and potentially influencing nighthawk mortality rates from nighthawk-vehicle collisions. Third, I wanted to sample at random times of the night, not just immediately after point counts were finished. Each road survey consisted of driving the length of the burned forest (34 km) section, typically 4-6 times, at ~30 km/hr and scanning with a Brinkmann Q-beam 800-2500-0 spotlight held out the driver’s window and aimed at the road edges. I did not survey the road in unburned forest because I never saw a nighthawk using the road in unburned forest, despite driving the road on 30 nights when returning from abundance surveys during the time nighthawks were most often on the road (23:00-1:00). I recorded the location of each nighthawk found sitting on the road, as well as the position relative to the road edge (perpendicular, parallel, or angled), the cardinal direction of the closest road edge and the direction the bird was facing, and the distance from the road edge (up to 5 m, which was the road center). Sex was determined when possible, but the diagnostic white throat patch and tail band on males was not always apparent before or as the bird flushed. By default, I began each road survey either from the mine entrance or from the location where the last point count was completed. During all driving whether at night or during the day, I searched the road for dead nighthawks. Lunar phase and cloud cover data were obtained from the Opapimiskan Lake Airport, situated at Musselwhite Mine. Animal Use Protocol #15-02 was granted by the University of Regina's President's Committee on Animal Care on February 26, 2015 for this project from March 1, 2016 – March 1, 2019.

I conducted a vegetation survey (n = 84) in August 2016 near to each clump of roost locations. I defined roost clumps as a group of roosts (group size = 1-14) within a 200 m radius with radii that did not overlap. Roost locations were often clumped together, so rather than survey vegetation at each individual roost site, I randomly chose one roost location from within each clump to serve as the vegetation survey location. Admittedly, this reduced my sampling power, but it was necessary to make sampling logistically feasible. While the locations of nighthawks on roads were recorded from June to August, the assessment of site characteristics was only conducted in August when vegetation would have been highest and densest. Each vegetation survey at a roost clump was paired with a vegetation survey at a random site along the road, chosen using a random distance and bearing from the paired site. All roost clump vegetation surveys were done in burned forest because no nighthawks were ever found roosting in unburned forest. Ditches along the road were unmaintained, so roadside vegetation was not cut or trimmed. At each vegetation survey point, I measured the height and density of roadside vegetation and the number of potential nighthawk roosts nearby. I used a measuring tape to measure vegetation height from the ground to the highest part of the plant (max = 2.5 m). I measured vegetation density by adapting the methods of Robel et al. (1970). I used a pole with nine markings spaced 10 cm apart and placed it in the roadside vegetation 1 m outside the road edge. I selected the side of the road to be surveyed by assigning to each survey point randomly generated numbers representing the east and west sides of the road. I viewed the pole from the center of the road and stretched a 5 m rope taut and level from the top marking on the pole to my eye to ensure consistency between measurements. From that position, I measured the lowest pole marking I could see. A visible marking lower on the pole (e.g. 9/9 markings visible) indicated lower vegetation density. I measured nighthawk roost availability by walking perpendicularly into the forest for 100 steps from the edge of the road. I assessed whether each place I stepped was a potential roost site. To reduce bias in where I stepped, I used a Suunto MC-50 compass set to a bearing perpendicular to the road. I followed that bearing meticulously and did not look at the ground until after I stepped forward. I defined a potential roost site as either a patch of bare ground at least 4 m^2 or a log >10 cm in diameter, >60 cm long, clear of branches for at least 60 cm, and <75% decomposed, and both had to be located at a spot with canopy cover <50%. All these criteria were estimated visually, and I was the only observer. This definition was derived from personal on-site observations and data from actual nighthawk roosts (GJF Chapter 1).

Surface temperature measurement

I used iButton thermochrons (Maxim model no. DS1921G) to measure surface temperature both on and off the road every 20 minutes. I placed thermochrons level with the soil surface in full sunlight and left them there from June to August 2016. I did not shield the thermochrons, but this was unnecessary because I was only interested in temperatures at night (Terando et al. 2017). Two thermochrons were placed on-road and two were off-road. The two off-road thermochrons were located near the two on-road sites, but several meters from the edge of the road and each pair of on-/off-road thermochrons was approximately 20 km apart. I selected the sites using a map of nighthawk road-use locations from the previous year. One pair of thermochrons was placed in a location commonly used by nighthawks, and the second pair in a location with no known use. The off-road microsites were chosen using the same potential roost location criteria described in the previous section; one was in a potential roost site, and one was not.

Scavenging experiment

I used quail carcasses to assess how quickly road-killed birds were scavenged at my study site. The adult quail, provided by Bryconn Development Inc., Edmonton, Alberta, Canada, were males extraneous to the farm's egg-laying operation and consequently euthanized and frozen. I performed two trials in June and July 2016, respectively. The first trial was begun in the morning (~10:00), while the second trial started in the evening (~19:30). I placed one quail every kilometer (Trial 1, n = 15 quail; Trial 2, n = 21 quail) along the road from a random starting point and alternated placing each one on the eastern or western edge or the center of the road. I returned every 12 hours for 60 hours to determine if carcasses had been removed.

Analysis

I tested whether the location of nighthawks on the road was related to their abundance by measuring the distance of each road detection and each point count detection to a single geographic point (the mine entrance). In other words, I measured how far each detection was from the mine entrance because if nighthawks simply used the road more where they were more abundant, then the mean distance of each group of detections (road use and point count) from the same point should be equal. I compared the distances of the road locations and point count locations to the mine entrance using a t-test. I only used point count detections from burned forest because I did not do road surveys in unburned forest.

I used a generalized linear model (GLM) with a binomial family and a logistic link to test whether any factors I measured associated with road use (i.e. vegetation height, density, and roost availability) were used by nighthawks. I used a binomial family because I was testing whether a nighthawk was present or not (i.e. 0 or 1) at a given roost site (i.e. roost vs. random). To evaluate roosting behaviour, I used a Chi-squared test to assess whether distance from the edge of the road and position relative to the closest road edge were significant. I used a GLM with a Poisson distribution and logarithmic link to assess whether lunar phase and cloud cover predicted nighthawk frequency on roads. Lunar phase was a quadratic term. I chose a Poisson family because the response variable was abundance data with no overdispersion. I used a t-test to examine the difference in temperature of on- and off-road surfaces. I only used temperatures recorded from 22:00-5:00 in the analysis because this was the period when nighthawks were observed using roads; the earliest observation of a bird roosting was ~22:30 while the latest was ~4:30. I used a Kaplan-Meier survival analysis ($q = d / d + l$; where q = survival rate at time i, d = number of deaths at time i, l = number survived) to calculate the removal rate of quail from the road. I used base packages in R version 3.3.0 and employed an alpha = 0.05 for all statistical tests.

Results

I predicted that nighthawk abundance based on point count data would reflect road use locations at a fine scale (defined as third order use, *sensu* Johnson 1980) and therefore I would find no difference between point count and road use locations. I found there was a significant difference between road use and point count locations ($t = 2.37$; $df = 540$; $p = 0.02$; Figure 13). Therefore, the hypothesis that road use location at a fine scale was related to nighthawk abundance was not supported. In other words, more point count detections at a given fine scale location did not also mean more nighthawks would be found

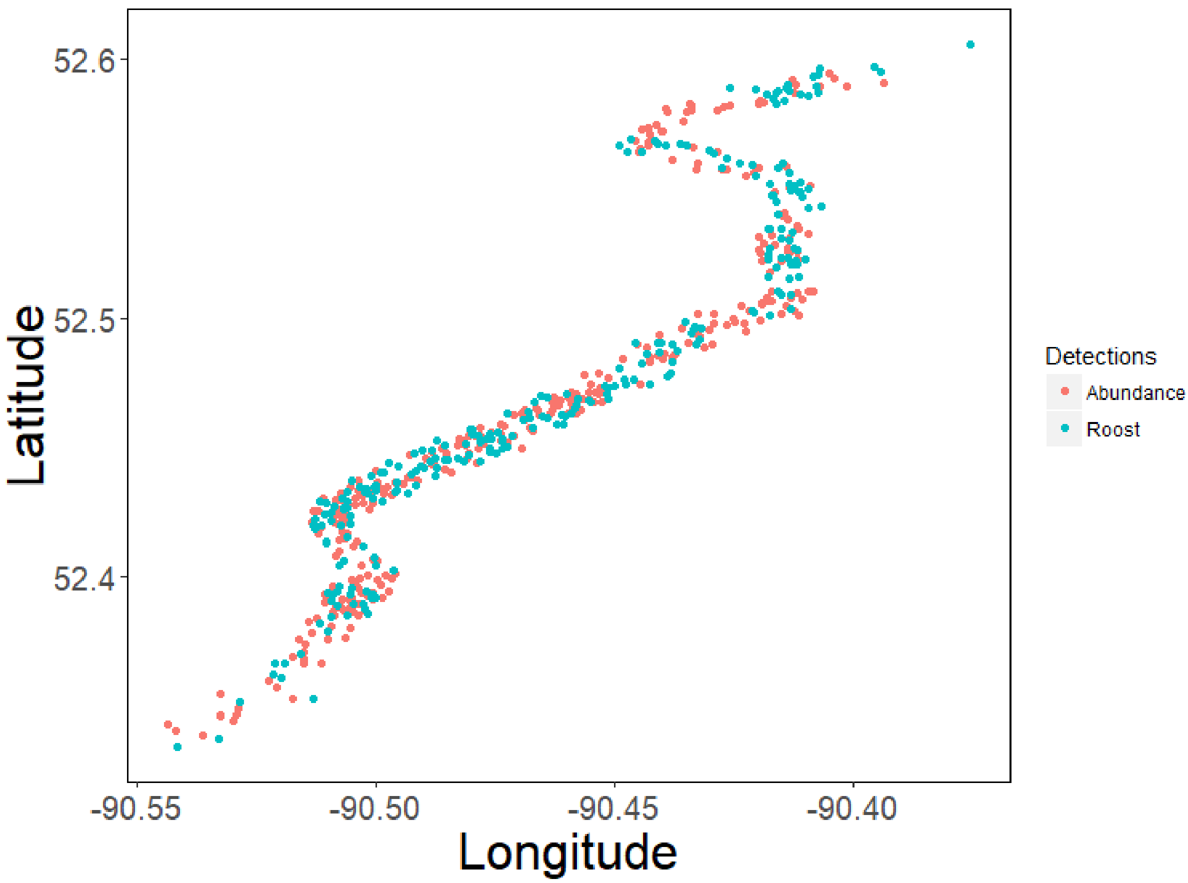

Figure 13. Detections from abundance and roost surveys along a road in burned forest. Each circle indicates a single nighthawk detection. Red circles are detections from abundance surveys and blue circles are from roost surveys.

using the road in that area at night. I also found that none of the site use factors I tested were significant, including vegetation height (z = 1.76; p = 0.08), density (z = 0.96; p = 0.34), and the availability of off-road roosts (z = 0.03; p = 0.97). While vegetation density and roost availability did not affect the probability of nighthawk presence at all, presence probability did appear to increase with vegetation height (Figure 14). Nighthawks on the road were significantly more often less than 1 m from the road edge than any other distance (X-squared = 8.21; df = 1; p = 0.004; Figure 15). I found that 63% of nighthawks on the road (n = 117 nighthawks) were less than 1 m from the edge of the road. Nighthawks were also significantly more likely to be sitting perpendicular to the road, facing towards the center of the road (X-squared = 113.7; df = 2; p = <0.001; Figure 16). I found that 81% (n = 108 nighthawks) of nighthawks were oriented perpendicular to the road and only 15% faced towards the vegetation. The number of nighthawks found roosting on any given night was significantly correlated with lunar phase (z = -2.30; p = 0.02; Figure 17), but not cloud cover (z = -0.001; p = 1.00) or year (z = -0.10; p = 0.32). The more illumination the moon provided, the more likely nighthawks were to be on the road. There was a significant difference between the means of nighttime (22:00-5:00) on- and off-road surface temperature (t = 20.47; df = 4594; p = <0.001; Figure 18). On-road surfaces were always warmer, both surface temperatures declined at a similar rate overnight, but there was no difference between roost and non-roost areas.

Of the birds on the road I could sex, more were males than females (9 females, 25 males) and 78% of the females were observed on the road in June

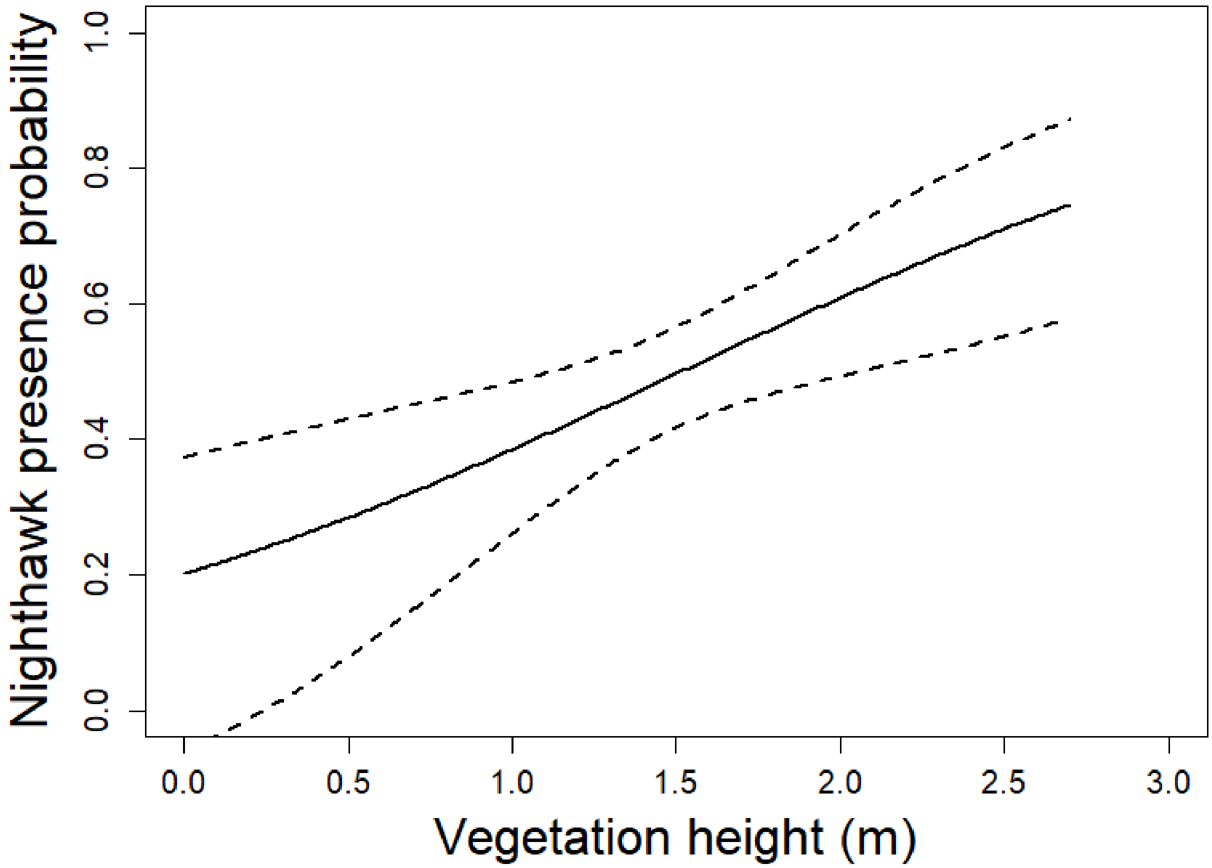

Figure 14. The probability of nighthawk presence appears to increase with vegetation height (m), although the relationship was not significant.

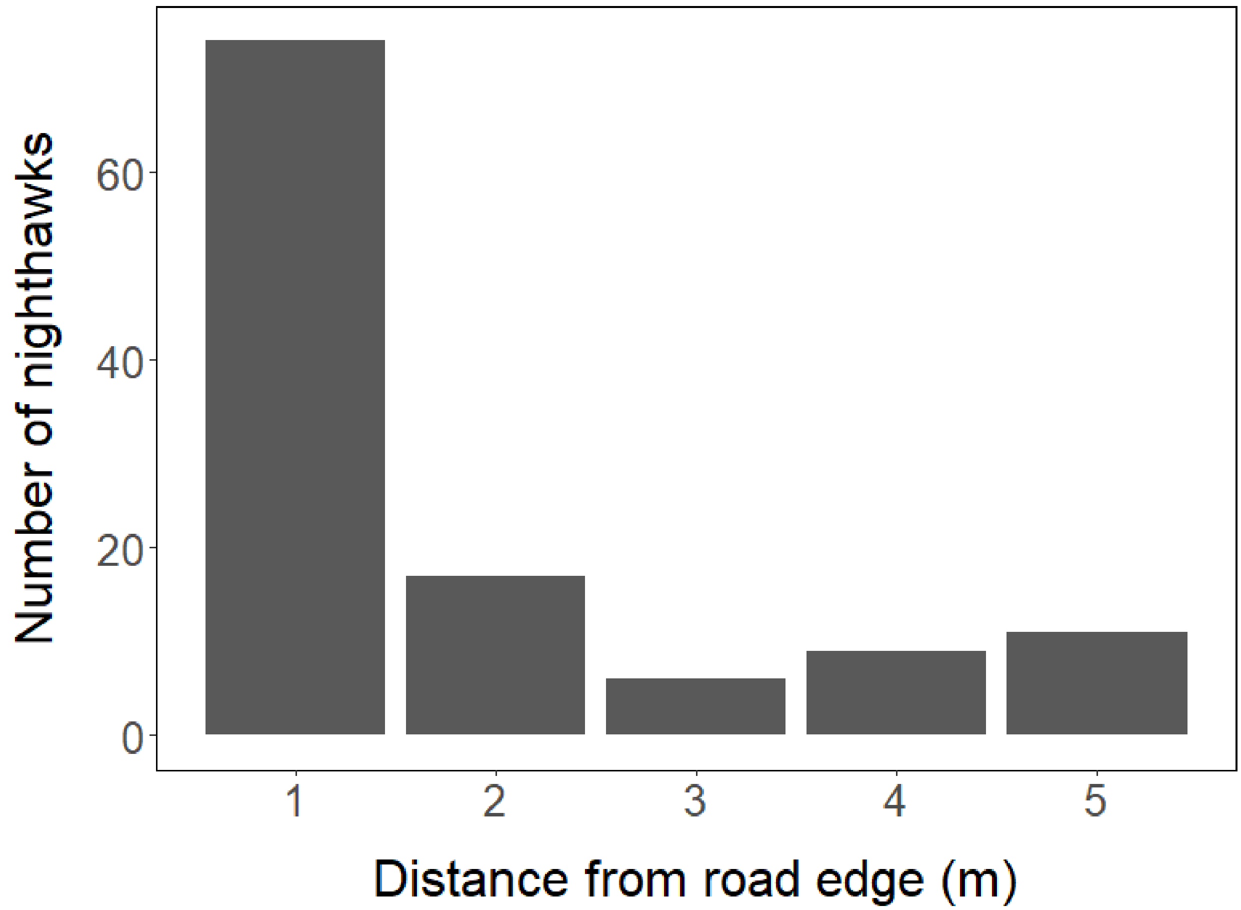

Figure 15. Nighthawks were found significantly more often <1 m from the road edge (5 m = road center).

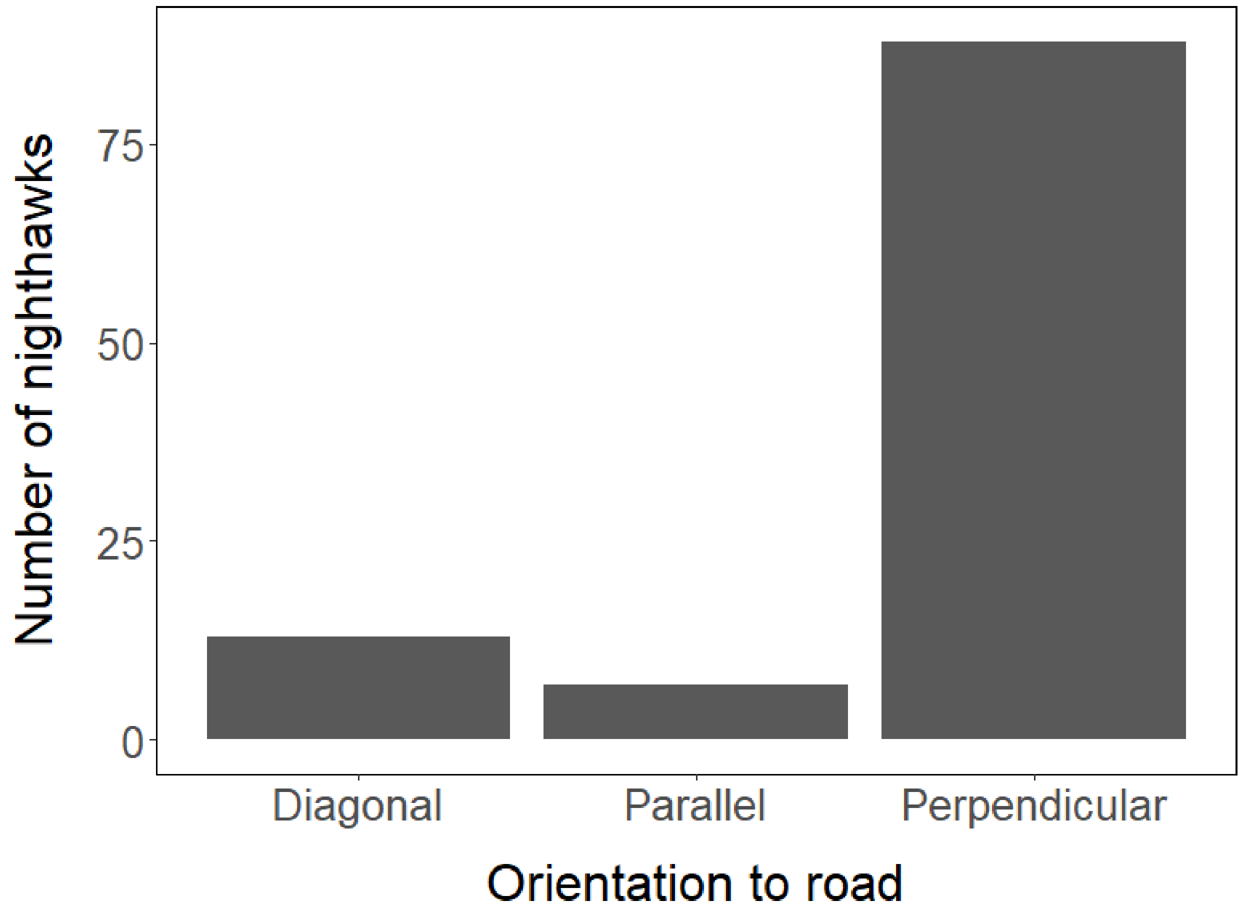

Figure 16. Nighthawks were found significantly more often sitting perpendicular to the road than diagonal or parallel.

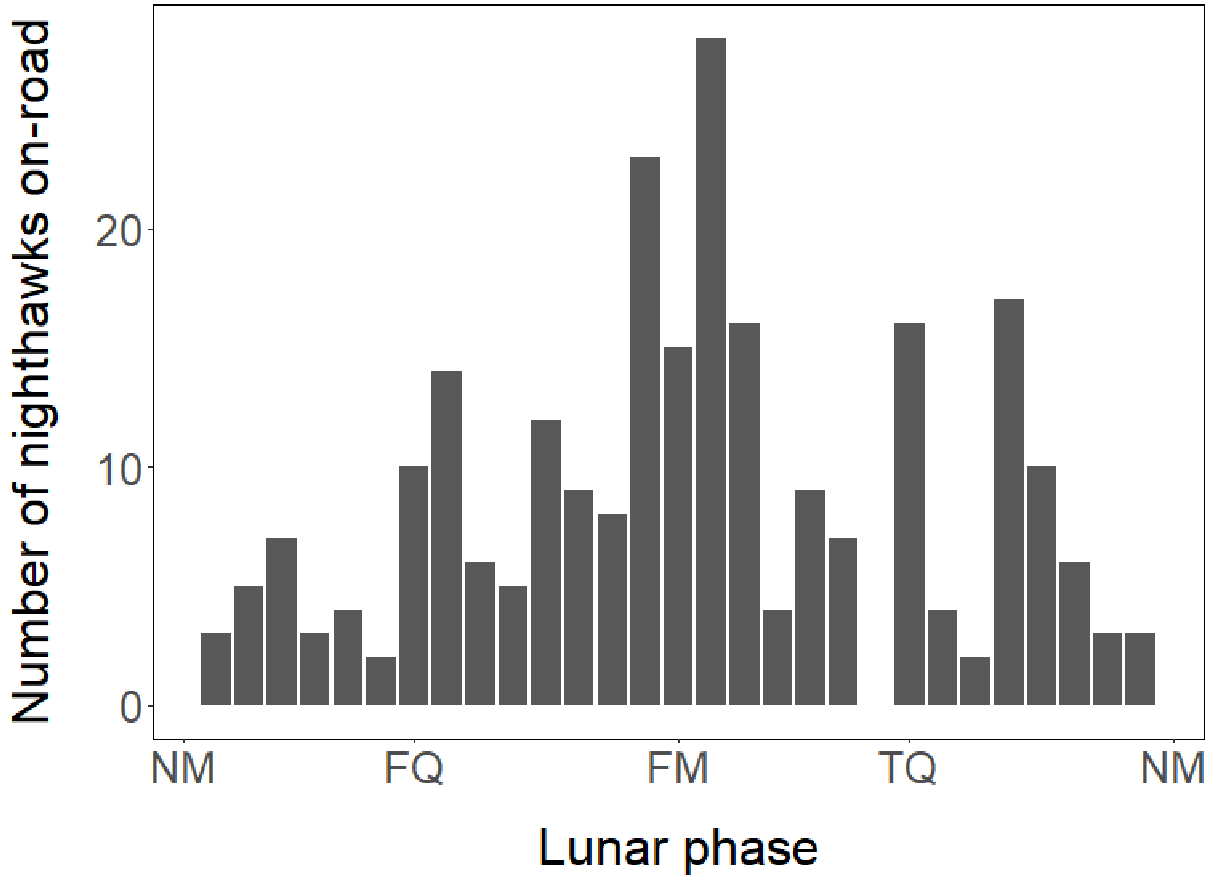

Figure 17. Nighthawks are more likely to be found on the road if the lunar phase is closer to a full moon (2015-2016). NM = new moon, FQ = first quarter, FM = full moon, TQ = third quarter. Data are from 2015-2016.

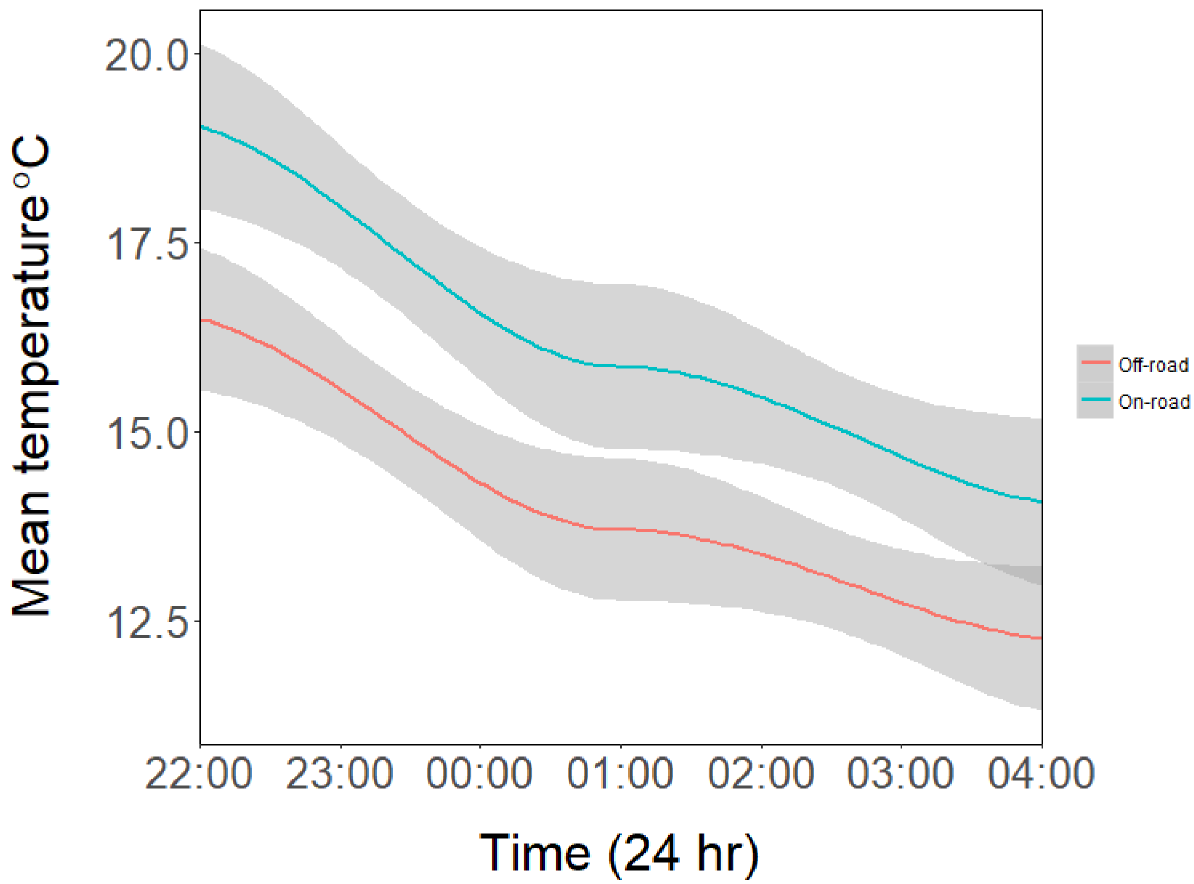

Figure 18. The mean road surface temperatures on- and off-road declined at similar rates overnight, but off-road temperatures are consistently cooler. Temperature was measured June – August 2016.

when egg laying occurs. The remainder were seen in the first two weeks of July. Twice, I observed a nighthawk sitting on the road and sally ~1 m to capture a moth. I also made five observations of grit ingestion, and all these observations were of females and occurred within a two-week period in mid-June (June 10 – June 23). Females comprised 58% of the sexed individuals seen on the road in June, but only 9% thereafter. With a 1:3 female to male ratio, the probability of seeing only females ingesting grit was 0.1% and unlikely to be random.

The road I surveyed was a private access road, so I used the vehicle entry log kept by Musselwhite Mine in 2015 to determine traffic rates. I did not include in the traffic data my use of the road because both the frequency and speed (~30 km/hr) of my driving were highly atypical for the road. There was an average of 8 vehicles per day (n = 398 vehicles) on the dates I conducted surveys (n = 52 days) but only 29 of those vehicles, or 0.6 per day, travelled the road between 22:00-5:00 hr (the time when nighthawks used the road). In 2015 there was a mean of 3.2 nighthawks using the road per day and in 2016 there was a mean of 3.7 nighthawks per day (cumulative mean of 3.5 nighthawks/day). In each year, I recorded only one vehicle-caused nighthawk road mortality. I also quantified the likelihood of a road-killed bird not being detected due to scavenging. I found that at my study site there was a mean 60.0% probability that a dead bird would be scavenged. Within 12 hours of placement there was a 44.4% removal rate, which increased to 69.4% by 24 hours and 91.7% by 60 hours (Figure 19). I drove the road at least once per 24 hours on 91% of the days I was on-site (n = 110 days), at least once per 48 hours 7% of the on-site days, and at least once per 60 hours

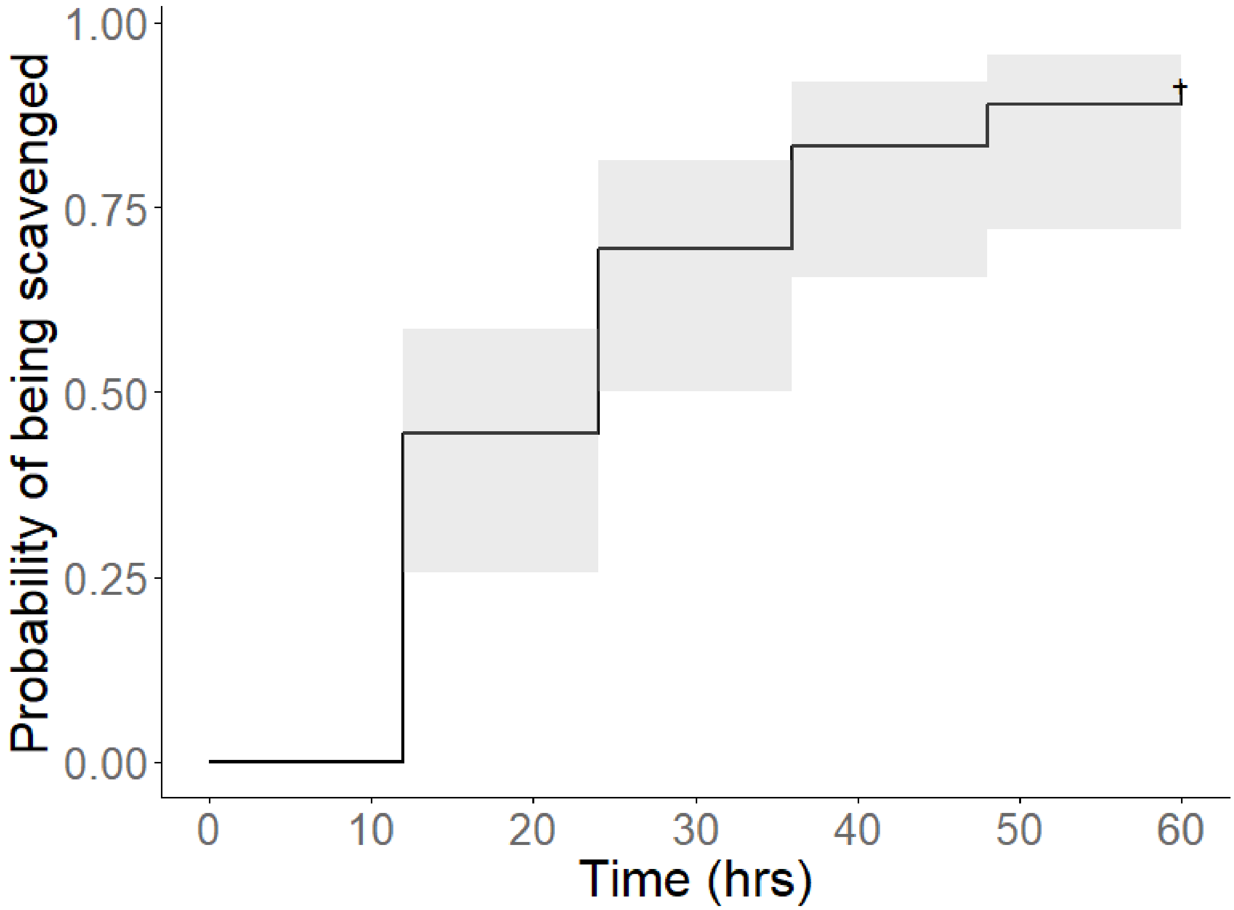

Figure 19. The probability of a road-killed bird being scavenged increases from 44% after 12 hours to 92% after 60 hours. Greyed area indicates 95% confidence interval. Horizontal dash indicates a censorship event (when an individual survives beyond the end of the survey; censored = 3; n = 36).

2% of the days on-site. As a result, I had a 71% overall probability of missing road killed nighthawks. Correcting for undetected road-killed birds due to scavengers removing the carcasses, I estimate that 1.7 birds were killed by passing vehicles each year (detected deaths + (miss probability * detected deaths)). This results in a mortality risk of approximately 1% per vehicle passing during their road use period ((nighthawk mortality per night / mean nighthawks on road per night) / passing vehicles during activity period).

Discussion

I found no evidence that any of the vegetation parameters I measured significantly predicted nighthawk occurrence. While not significant, nighthawk presence did increase with vegetation height at a rate that is likely biologically significant. At sites with no vegetation, nighthawks are predicted to occur approximately 20% of the time, but this increased to nearly 70% of the time when verge vegetation was 2.5 m tall. Taller vegetation may be used by nighthawks as backing to reduce detection by visually-orienting predators (Wang and Brigham 1997). An important caveat is that I only conducted vegetation surveys in August 2016, but I recorded nighthawk road locations from June to August 2015-2016. The verge vegetation was not the same height or density in June as it was in August, but the relative height and density differences were likely still similar at each stage of growth.

The fine scale sites (third order use, *sensu* Johnson 1980) used by nighthawks were not predicted by the local abundance of birds based on my point count data. In other words, just because an area had more nighthawks did not also mean a nearby road section would be used more by nighthawks at that fine scale. However, this does not apply to coarse scale site use (first order use, *sensu* Johnson 1980). No nighthawks were found using the road in unburned forest where nighthawk abundance was also significantly lower (GJF chapter 1). Therefore, while at coarse scales site use was associated with abundance, at fine scales nighthawks must have used sites based on some unmeasured criteria or else used sites at random. It is certainly possible that nighthawks used sites randomly but determining this would require data on individual use to separate site use from site fidelity. It is also unclear if nighthawks travelled to sites, resulting in higher use at these sites, or if nighthawks local to the sites used them more often relative to nighthawks near other less used sites.

Nighthawks may receive thermoregulatory benefits from roosting on the road if surface temperatures on-road are warmer than off-road (Camacho 2013). Temperatures both on- and off-road declined steadily overnight, but on-road temperatures were always warmer. While my iButton data support this, this explanation as the sole explanation is not entirely convincing. Anecdotally, nighthawks are seldom, if ever, recorded on paved roads, which would provide greater thermoregulatory benefits than gravel roads (Camacho 2013). Additionally, of the nighthawks detected on randomized transects, 68% were detected roosting on the road between 23:00 and 1:00. During the most energetically demanding period of the day – the pre-dawn hours – nighthawks tended to move elsewhere to roost. These observations do not support the idea that thermoregulation is the main reason for road use by nighthawks.

Other potential uses of roads include landing there to ingest grit (small stones used in digestion) or dust bathing (Poulin et al. 1998). I did not witness any dust-bathing, but I did observe five instances of nighthawks ingesting grit. Grit ingestion has been observed regularly in nightjars (Jenkinson and Mengel 1970), despite grit being used less frequently by insectivores than granivores (Gionfriddo and Best 1996). Females may supplement the calcium reserves needed for egg development through grit ingestion (Turner 1982, Barclay 1994). Incubation is carried out primarily by female nighthawks (Tomkins 1942, Rust 1947, Brigham 1989), and is the likely explanation for the skewed sex ratio observed later in the season. The timing of my observations of grit-ingestion coincides with the egg-laying period of local nighthawks (Brigham et al. 2011), indicating females may be using gravel roads as a source of grit to supplement calcium reserves.

Female nighthawks appear to use the road for grit early in the season. Presumably, after their eggs have been laid they are too preoccupied with incubation to continue using the road. Male nighthawks, on the other hand, continue to use the road all summer, and there is little evidence to indicate they are attracted there by the availability of grit (Poulin et al. 1998, Jackson 2009). Poulin (et al. 1998) speculated they used it as a roost site for bachelor males, but this also seems an unlikely explanation. First, nighthawks raise a single clutch each season, therefore the potential fitness reward of staying at their reproductive site diminishes quickly as the season progresses, yet males continue to use the road. Second, nighthawks used the road more in the early parts of the night (68% between 23:00-1:00). If they were just roosting (i.e. resting or sleeping), there should be no temporal clumping; they should be present all night long. Third, the locations of nighthawks on the road were not correlated with nearby roost availability. If nighthawks were using the road to roost on, fewer might be expected on roads in areas with more potential off-road roosts nearby. On the other hand, if they are using the road for a different reason, such as grit-ingestion or foraging, the number of nearby roosts should make no difference. Fourth, the locations of nighthawks on the road were not correlated with point count abundance. The road's surface temperature is likely to be consistent. If nighthawks were using road locations solely based on temperature and temperature was consistent across the surface, abundance would be expected to predict location. Finally, using a road as a roost site should be beneficial during the day as well as the night. Even if traffic caused nighthawks to leave a roost on the road for an off-road site, similar detection rates of on-road birds early in the day and early in the night would be expected. This is not the case; I never found any nighthawks on the road during the day and, while the phenomenon of nighthawks using roads at night is well-known to those familiar with the birds, nighthawks on roads during the day has, to my knowledge, never been reported.

Aldridge and Brigham (1991) calculated that Nighthawks' short, crepuscular foraging period does not allow them to meet their daily energetic requirements, unless this requirement is overestimated or their capture success rate is greater than 100%. The use of torpor would reduce energy requirements but, while capable of heterothermy, nighthawks do not appear to use it commonly in the wild (Firman et al. 1993, Fletcher et al. 2004). This led Aldridge and Brigham (1991) to speculate that nighthawks may be capturing multiple prey items per attack. A third possibility, however, is that nighthawks are obtaining additional food outside of the typical foraging period. Traditionally, the natural history of these birds has considered their foraging period to be limited to crepuscular periods, the time immediately before and after dusk, and again at dawn, unless extended by their ability to forage under artificial lights (Shields and Bildstein 1979, Foley and Wszola 2017). Nighthawks' standard foraging strategy of hawking prey relies on sufficient light, and the sensitive *tapeta lucida* in their retinas (Nicol and Arnott 1974) probably prevents them from foraging diurnally, unless cloud cover sufficiently reduces solar insolation. Nightjars are similarly unable to forage diurnally, but their sallying technique reduces their reliance on ambient light levels. Unlike nighthawks, moonlight appears sufficient for their needs (Mills 1986, Jetz et al. 2003a, Jackson 2007, Smit et al. 2011).

Nighthawks and nightjars are morphologically similar, the most apparent difference being their wing shape. Despite this difference, nighthawks may not actually be limited to a hawking foraging technique. After their crepuscular foraging bout is completed, nighthawks may extend foraging by sallying. To my knowledge, this foraging method has not been reported for nighthawks. Most observations of foraging nightjars occur because nightjars call and forage simultaneously, alerting a potential observer to their whereabouts. Nighthawks also call and forage concurrently, but apparently only while airborne. After darkness has grounded them, calling ceases. If they can continue foraging by sallying, their silence would make them far less detectable than nightjars.

Nightjar activity is known to be correlated with the lunar cycle; nightjars are more active the closer the moon is to complete illumination (Mills 1986, Brigham 1992, Brigham et al. 1999, Jetz et al. 2003b, Ashdown and McKechnie 2008, Woods and Brigham 2008, Jackson 2009, Smit et al. 2011). Nightjars are also known to use roads as sallying locations because the wide, open space of the road provides a clear sky backdrop against which to backlight insects (Jackson 2009). I found that the numbers of nighthawks using the road was positively correlated with increasing lunar illumination. In other words, the more lunar light, the more nighthawks I found on the road. Shortly after their crepuscular foraging bout was over, nighthawks were also found on the road more often (23:00-1:00). This mirrors the peak foraging period of nightjars (Jackson 2009, Smit et al. 2011) and when insects are typically most abundant at night (Racey and Swift 1985). I found that most nighthawks were less than 1 m from the road edge and even more were both perpendicular to the road and facing away from the roadside vegetation, another behaviour nearly identical to nightjars who forage from roads (Quesnel 1986). Finally, I directly witnessed two nighthawks sallying from the road to capture moths – items normally considered to be consumed more by nightjars (Brigham and Barclay 1992). Despite previously published suggestions that nighthawks' foraging period is strictly crepuscular regardless of the lunar cycle (Aldridge and Brigham 1991, Brigham and Fenton 1991b, Brigham and Barclay 1992, Brigham et al. 1999), I argue that nighthawks are using roads to extend the foraging period by sallying, a foraging technique usually associated with nightjars. Additionally, nighthawks foraging on roads receive a thermoregulatory benefit because on-road temperatures are consistently warmer than off-road.

I did not find any correlations between nighthawk road site use and vegetation, but nighthawks may be using road sites based on prey availability or sky visibility. I did not collect data on either prey abundance or sky visibility, so any further hypotheses are limited to speculation. Sites that nighthawks are using as sallying sites should have a clear view of the sky to better observe backlit prey items. The open spaces created by the recent burn has allowed pioneering and fire-reliant plants to experience intense but low regrowth, potentially reducing sky visibility off the road. Nighthawk frequency should increase with greater sky visibility, until the arc of sky visible from the nighthawk's location reaches 90 degrees (Jackson 2009). If greater than 90 degrees of the sky is visible, nighthawks may be less inclined to use a site because of the lack of backing and an increased risk of predation.

Nighthawks foraging on roads are exposed to the risk of being killed by vehicles. Due to low traffic rates on the road I surveyed, the mortality risk was low. Due to the low traffic rates, vehicles typically travelled down the center of the road while nighthawks almost always sat near the edge. Nighthawks tend to rely on their camouflage to avoid detection by predators and so do not typically move when vehicles pass. This behaviour, coupled with center-driving vehicles, likely reduces the risk of being struck. On a busier road, not only does the chance of being struck increase, but the mortality rate probably also increases because drivers are less likely to drive down the center of the road. This study was localised and, due to logistics, sampled an exceedingly small portion of the boreal forest. If the limitations of this study are kept in mind, these results may be cautiously extrapolated to other boreal locations. Many roads in the boreal likely have similar rates of traffic to the road I surveyed. More highly travelled roads are often paved. Nighthawks do not appear to use paved roads, further reducing their exposure to traffic-related mortality. Therefore, it does not appear that vehicles are a significant source of nighthawk mortality in the boreal forest.

In conclusion, at fine scales nighthawks did not roost on roads near to where they were more abundant, but at coarse scales site use was related to abundance. Nighthawks did not use road roosts based on vegetation density or potential roost availability nearby. The probability of their presence at a site did increase albeit not significantly with vegetation height. This was probably biologically significant because taller vegetation likely acts as a barrier to visual detection by predators for nighthawks sitting in front of it. Road surface temperature was higher than the temperature off-road, but the timing of road-use by nighthawks indicates thermoregulation may not be their primary reason for road use. There is little to indicate that nighthawk mortality due to vehicle strikes in the boreal forest is a threat to their conservation. Roads provide a substrate for nighthawks to ingest grit at, particularly for females during the egg-laying period, and a site to potentially extend the foraging period by sallying, a behaviour not previously reported.

CHAPTER FOUR: GENERAL CONCLUSION

Aerial insectivores are a group of birds related by their foraging behaviour and not taxonomy. Across North America, they are declining as a group. These declines are the steepest currently being experienced by any functional bird group (North American Bird Conservation Initiative Canada 2012). The factors driving these declines have yet to be fully determined (Smith et al. 2015, Michel et al. 2016), although pesticide use (Nocera et al. 2012, Hallmann et al. 2014), climate change (Ambrosini et al. 2011, García-Pérez et al. 2014), and land use changes (Paquette et al. 2014) all appear to be involved. If a location with a stable population of aerial insectivores exists, then learning how potentially responsible factors differ there will narrow down the factors that are actually responsible for the decline of aerial insectivores. Thus, research on this group in areas where they are currently common has conservation merit.

Common Nighthawks (*Chordeiles minor*; hereafter, nighthawk) are a Threatened aerial insectivore (*Species at Risk Act* 2002) reportedly declining at 6.6% per year (COSEWIC 2007). In the boreal forest, however, anecdotal evidence suggests that populations are larger than elsewhere within their range.

Within the boreal forest, there exists the potential of a nighthawk population large enough to change their overall conservation status in Canada. Furthermore, the boreal population may be more stable than elsewhere in their range. Quantifying the size of this population and its demographics is essential to understanding the veracity behind these anecdotes. These studies can only occur once the habitat nighthawks use is identified so that the research can be conducted in the right locations. The nature of habitat use by nighthawks in the boreal is currently unknown, and my project sought to fill this knowledge gap.

I examined habitat used by nighthawks in the boreal forest. I evaluated this at three scales (first, second, and third order, *sensu* Johnson 1980) by using abundance and vegetation surveys. I also studied why nighthawks chose to sit on gravel road surfaces at night and evaluated the mortality risk of this choice. My results lay the foundation for future population and demographic research, increase our knowledge of nighthawks' basic biology, and provide relevant information for current conservation and management of nighthawks in the boreal.

I used bird abundance and vegetation surveys to assess nighthawks' habitat use. I selected a study site in an area where there was a recent, severe wildland fire in northwestern Ontario's boreal forest. I found that at a first order, landscape scale, nighthawks were significantly more abundant in burned than unburned forest. At the landscape as well as second order, territory scale, canopy cover was an important predictor of nighthawk presence and abundance. At the third order, roost scale, I found that the number of logs available was an important predictor. Surprisingly, I found that regardless of the scale used, bare ground was not an important factor for predicting where I would find nighthawks.

I examined nighthawks' use of gravel roads by conducting roost and vegetation surveys and deploying thermochrons to assess the temperature of on- and off-road sites. I quantified the mortality risk nighthawks were exposed to on the road by recording all road-killed nighthawks. I determined the detection probability of these dead nighthawks by undertaking a scavenger efficiency experiment. I found that nighthawk road use was unrelated to abundance at third order, or fine scales, but was strongly related to their abundance at first order, or coarse scales. I concluded that nighthawks do not sit on the road for thermoregulatory purposes. Instead, I proposed that nighthawks used the road as a foraging site like other nightjars (subfamily Caprimulginae; Jackson 2009), a behaviour not previously observed or reported. Finally, I determined that the mortality risk to nighthawks by traffic using the road was low.

The results of my project provide information on where nighthawks are found in the boreal forest, and more specifically the vegetation variables associated with nighthawk presence at multiple spatial scales. My results led me to postulate reasons for why nighthawks are found on gravel roads at night and what the mortality risk of this choice is. These results may be cautiously extrapolated to the rest of the boreal forest, but care must be exercised and the limitations of this study kept in mind. Due to inadequate knowledge of boreal nighthawk populations and the logistical difficulties of sampling the boreal forest – a remote, inaccessible location – my study site was limited to a single burn and was small, especially when compared to the massive area covered by the boreal shield ecozone.

Future research should confirm my results at other sites to ensure that extrapolation to the boreal region is appropriate. In particular, the use of habitats of different wildland fire ages and severities should be evaluated (see Sidler 2017). Further studies confirming nighthawk foraging behaviour on roads and the importance of these anthropogenic sites, particularly if nighthawk abundance changes with distance from a road, would be useful. These studies would show the level of bias road-based surveys, the most common survey method, have on nighthawk abundance estimates. Where nighthawk road use occurs, experimental manipulation of road verge vegetation may help understand the microsite characteristics used by both foraging nighthawks and nightjars, and this knowledge may be applicable to both on- and off-road sites.

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