

**Common Nighthawk (*Chordeiles minor*) habitat associations and activity patterns
in the northern boreal forest**

A Thesis

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Andrea Sidler, candidate for the degree of Master of Science in Biology, has presented a thesis titled, ***Common Nighthawk (*Chordeiles minor*) Habitat Associations and Activity Patterns in the Northern Boreal Forest***, in an oral examination held on November 20, 2017. 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

Understanding how organisms interact with their environment is key to developing effective management strategies. Due to population declines detected in the southern part of their range, Common Nighthawks (*Chordeiles minor*) are listed as Threatened in Canada. Despite the northern boreal forest representing a significant portion of their breeding distribution, populations in these areas remain virtually unstudied and thus their numbers and biology are poorly understood. My study is one of the first to examine both temporal and spatial aspects of habitat associations for breeding nighthawks in the northern boreal forest.

In the boreal region, fires create open habitats in an otherwise densely forested landscape. Considering nighthawks typically prefer open habitat, I assessed nighthawk abundance relative to forest age and vegetation characteristics to better understand spatial habitat associations in the northern boreal forest. I conducted evening roadside surveys and vegetation assessments along 20 different survey routes in 2015 and 2016, in the Yukon Territory, Canada. Nighthawks (both breeding and non-breeding individuals) were positively associated with open habitat at both the landscape and, within that, at the territory scale. At the landscape scale, I detected more individuals in early successional, post fire habitat compared to older, more densely vegetated forests. At the territory scale, nighthawks were negatively associated with denser tree canopy cover and greater cover by low shrubs. As well, I detected more birds on nights with colder temperatures and on nights with higher values of moon illumination. Given the association of this species with open habitats, land managers should be aware that the availability of early

successional, post fire habitats may play a key role in the maintenance of populations of Common Nighthawks across the boreal region.

Northern latitudes are characterized by a large variation in summer photoperiod, which has the potential to impact the activity patterns of these crepuscular birds. Because of this, the current Canadian National Nightjar Survey Protocol, which targets populations at southern latitudes, may be ineffective to accurately monitor northern populations. My goal was to assess nighthawk activity at northern latitudes and to provide recommendations for a targeted monitoring protocol, in the event that the current protocol was not suitable to accurately monitor these populations. I deployed autonomous recording units to record calling activity throughout the summers of 2015 and 2016, in the Yukon Territory, Canada, to better understand how temporal changes in ambient light and temperature impacts nighthawk activity. Daily activity period approximately reflected the length of civil twilight (sun 0-6 degrees below the horizon) and was constrained by nautical twilight (sun 7-12 degrees below the horizon) as nights grew darker. Calling activity was higher over the evening civil twilight period than the morning period. During the evening twilight window which my study targeted, nighthawks were more likely to call at low temperatures during low-light conditions and at higher temperatures during brighter conditions. Seasonally, calling activity increased during the first week of June and remained elevated until the first week of July. My data suggest that the recommended sampling times outlined in the Canadian National Nightjar Survey Protocol align with peak activity periods of nighthawks in our study area and that therefore this protocol should be used for future monitoring of northern nighthawk populations.

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DEDICATION

I would like to dedicate this thesis to my wonderful and ever-supportive parents and brother. I could not have done any of this without you – thank you for being such an encouraging and inspiring family! I am grateful for the many fun and exciting hours we spent adventuring outdoors together as this instilled in me a true passion for the natural world which led me to where I am now. Mom, dad: Thank you for unknowingly setting me on this journey many, many years ago, when you introduced me to my first nighthawk before my very first day of school. I truly appreciate all the support you give me.

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Next family trip: Nighthawks in Brazil?

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1.0 – GENERAL INTRODUCTION

1.1 BACKGROUND

A central focus of ecology is to examine the factors which influence an organism's pattern of space use. Organisms must cope with both temporal variation and spatial heterogeneity in their environments as the arrangement of resources, spatial attributes and conditions change not only through space but also through time. As organisms concentrate their activities in areas that lead to the greatest potential for a fitness (reproductive success) advantage, fluctuations in environmental heterogeneity can elicit behavioral responses and changes in space use from both temporal and spatial perspectives (Price et al. 2013). For instance, temporal fluctuations in photoperiod (changes in daylength) can trigger the onset of avian migratory movements (Agarwal et al. 2015) and variation in precipitation (moisture) can influence nest site locations and ultimately reproductive success (Crowe and Longshore 2013). Similarly, spatial heterogeneity in vegetation structure can influence the amount of cover available in which to hide from predators which, in turn, affects species space use patterns (Torre and Díaz 2004). Further, geographic features (water bodies, mountains) have the potential to act as spatial barriers, or corridors (valleys), for species dispersal thereby affecting species distributions (Wiens 1989). Given these interacting processes, both temporal variation and spatial heterogeneity must be considered when evaluating a species space use pattern (Southwood 1977, Wiens 1989, Virkkala 1991, Block and Brennan 1993).

Patterns of space use are fundamentally related to the concept of habitat use (Block and Brennan 1993, Boyce and McDonald 1999). Although the term habitat is

commonly used in scientific literature, it is defined a variety of ways by different individuals and therefore its' precise meaning is ambiguous (Block and Brennan 1993, Hall et al. 1997, Krausman and Morrison 2016). To explore this ambiguity, Hall et al. (1997) collected data from the literature and concluded that habitat terminology was used vaguely in 40 out of 47 papers they reviewed. For instance, published papers used the term "habitat" to mean vegetation association (Hall et al. 1997), vegetation structure (Frank and McNaughton 1992), substrate properties (Brown et al. 1994) and in some cases even stated that the concept was too complicated to define (McCoy and Bell 1991, Hall et al. 1997). As more ecologists are consulted to inform species conservation planning (e.g., Northern Spotted Owl (*Strix occidentalis caurina*); Thomas et al. 1990) it becomes increasingly important for terminology to be standardized, not only to produce reliable results but for effective communication of those results (Murphy and Noon 1991). Until terminology is standardized within the scientific community, researchers should make the effort to define habitat within the context of each project to enhance the ability of readers to interpret and communicate findings accurately.

In the context of my project, habitat refers to the sum of spatial attributes (e.g., vegetation cover and structure), temporal conditions and resources (e.g., food, water) an organism requires for survival, reproduction and population persistence (Block and Brennan 1993, Hall et al. 1997). The impact of these habitat components on the population dynamics of various species are well documented. For instance, the fitness of Eastern Bluebirds (*Sialia sialis*) increased with proximity to more open habitats such as grasslands and agriculture (spatial attributes; Jones et al. 2014). Red-breasted nuthatches (*Sitta canadensis*), which selected nest sites in areas with higher mountain pine beetle

abundance (prey) fledged a higher number of chicks when compared to conspecifics inhabiting areas with lower beetle abundances (Norris and Martin 2014). Further, decreased temperatures (temporal conditions) result in delayed egg laying and decreased clutch size of Zebra Finches (*Taeniopygia guttata*) meaning lower individual fitness (Salvante et al. 2007). Changes in the reproductive success of individuals will affect species at the population level, increasing either the probability of population persistence or extinction. Therefore, understanding habitat associations are important for conservation efforts as a species space use patterns, abundance and distribution are largely driven by the prevalence of suitable habitat conditions at any one time in a given geographical area (Watts 1991, Lombardi et al. 2003, Ye et al. 2013).

The processes (geological, seasonal, disturbance, climactic) that shape resource distributions and habitat attributes, operate at various resolutions ranging from geographically large scales to site specific ones (Kristan 2006). At the local scale, space use patterns of individuals and distributions of species are governed by patch level resource distributions, attributes and conditions such as nest sites, prey availability, micro-climates and cover (Virkkala 1991, Block and Brennan 1993, Digby et al. 2014). Patch level attributes are nested within broad scale spatial features (geography, forest stand composition and structure; Kristan 2006, Deppe and Rotenberry 2008) and temporal conditions (regional climate and seasonality; Norris and Marra 2007). Resources encompassed by these broad scale features and conditions, such as foraging sites, influence the distribution of species at the landscape scale (Price et al. 2013). In consideration of this, the resolution (local vs broad scale) at which habitat is assessed is crucial when describing species-habitat relationships (Wiens 1989, Jackson and Fahrig

2015). Thus, to gain a comprehensive and accurate understanding of the mechanisms driving a species pattern of space use it is important to assess space use at multiple scales of resolution and from both a spatial and temporal perspective (Virkkala 1991, Price et al. 2013).

Common Nighthawks (*Chordeiles minor*, hereafter nighthawks), are neotropical migrants which breed throughout Canada and the US. Little is known about breeding populations of these birds in the boreal forest as the majority of Canadian studies have taken place at southern latitudes e.g., in southern British Columbia (Firman et al. 1993) and southern Saskatchewan (Todd et al. 1998, Fisher et al. 2004, Ng 2009). Despite the boreal forest representing a substantial proportion of the species summer breeding distribution, and potentially harbouring a significant proportion of their population, nighthawks that live in this biome have remained virtually un-studied. The information that we do have about nighthawk abundance and distribution in the northern boreal forest comes from a limited number of roadside surveys (Environment Canada and McKnight 2016).

Understanding patterns of space use and habitat associations of nighthawk populations across all environments is relevant and timely as in 2007, the species was listed as Threatened in Canada due to data from southern locations indicating steep declines in numbers (COSEWIC 2007). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is currently re-assessing the status of the species and thus any insights into the life history of these birds will allow for a more informed decision regarding their conservation status in Canada.

As a result of their crepuscular (active at dawn and dusk) nature and cryptic plumage, which makes finding daytime roosts difficult, diurnal bird surveys tend to miss or at very least substantially underestimate the abundance of this species. These surveying challenges highlight the need for targeted research aimed specifically at nighthawks to elucidate further aspects of their ecology. My study will be among the first to explore activity patterns and habitat associations of nighthawks in the boreal forest using survey methods specifically targeting this species. My research aims to relate patterns of space and habitat associations of nighthawks in the northern boreal forest to both spatial and temporal habitat components (spatial attributes, conditions) across the landscape.

1.2 RESEARCH OBJECTIVES

The objectives of my research were to:

1. Assess habitat associations of breeding nighthawk populations in the northern boreal forest relative to spatial habitat components by testing the hypothesis that nighthawk abundance is related to habitat openness. Specifically, I explore whether nighthawks, which are generally associated with open areas (Poulin et al. 1996), tend to select open, post-fire habitat or more densely forested later successional habitat in the northern boreal forest.
2. Investigate if nighthawk calling activity varies with seasonal fluctuations in ambient light and temperature (temporal habitat components). In particular, to identify periods of peaking calling activity and to assess if these are limited to the civil twilight period (when the sun is between 0 – 6 degrees below the horizon). This information will inform the timing of future sampling efforts of nighthawk populations at northern latitudes.

The purpose of this introduction is to establish a link between the following two data chapters (chapters 2 and 3), which are designed as independent manuscripts to be submitted for publication. Due to this, there is some repetition of material presented in this chapter and the following two chapters. As the final manuscripts will be co-authored, “we” instead of “I” will be used throughout chapters 2 and 3.

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2.0 COMMON NIGHTHAWK HABITAT ASSOCIATIONS IN THE NORTHERN BOREAL FOREST

2.1 INTRODUCTION

Only by examining how organisms use their environment can we understand how ecological systems function. Patterns of space use are fundamentally related to the concept of habitat (Block and Brennan 1993). Habitat refers to the sum of spatial attributes, temporal conditions and resources (e.g., food, water) an organism requires for survival, reproduction and population persistence (Block and Brennan 1993, Hall et al. 1997). The study of habitat is biologically relevant as habitat quality is linked to individual fitness as well as to population success (Norris and Marra 2007, Ye et al. 2013).

Relating how the spatial arrangement of habitat attributes and resources influences the distribution, movements and dynamics of natural populations is an essential component of understanding species habitat associations. Factors determining which habitats that organisms are most closely associated with, are influenced by a range of processes (e.g., geological, seasonal, disturbance) operating at multiple spatial scales (e.g., region, landscape, territory; Johnson 1980, Block and Brennan 1993, Wells et al. 2011). A variety of studies have illustrated the importance of scale-dependent habitat associations in mammals (Johnson et al. 2002), birds (Bakermans and Rodewald 2006), reptiles (Compton et al. 2002) and insects (McIntyre 1997). Across scales, it is recognized that species habitat associations are positively linked to the spatial

distribution of resources (e.g., food) and vegetation attributes (e.g., shelter) across the landscape (Morissette et al. 2002, Leonard et al. 2008, Lemaître et al. 2012).

At the local scale, the activities of individuals and distributions of species are governed by patch level resources and attributes such as nest sites, prey availability, predator density and cover (Virkkala 1991, Block and Brennan 1993). Vegetation structure and composition play a crucial role in shaping the spatial arrangement of these resources and attributes and therefore in shaping habitat associations of species (Deppe and Rotenberry 2008). Patch level attributes are nested within broad scale spatial features such as geography, forest stand composition and structure (Kristan 2006, Deppe and Rotenberry 2008). Resources encompassed by these broad scale features, such as foraging sites (e.g., proximity to water for insectivores), influence a species distribution at the landscape scale (Price et al. 2013).

The surrounding landscape may be particularly important for far ranging species, such as migratory birds, which are thought to employ a multi-scale, top-down, approach towards habitat selection (Johnson 1980, Kristan 2006, Deppe and Rotenberry 2008). In this scenario, migrating birds arriving in an area would initially evaluate habitat based on large scale geographic features, followed by landscape matrix, habitat patch suitability and ultimately fine scale, within habitat patch features, such as potential nesting sites (Johnson 1980, Deppe and Rotenberry 2008). Further, area sensitive species, which require larger habitat patches, or landscapes with regularly occurring habitat patches to reproduce, frequently supplement habitat patch resources with those from outlying areas (Davis 2004). Therefore broad scale landscape features and the surrounding habitat matrix can significantly influence individual fitness and population recruitment

(Dunning et al. 1992, Whitaker and Warkentin 2010) for these populations. In consideration of this, the scale at which habitat is assessed is crucial when describing species-habitat relationships (Block and Brennan 1993, Cornell and Donovan 2010, Jackson and Fahrig 2015).

In areas not influenced by anthropogenic disturbance, fire is the primary driver of both local and broad scale spatial resource variation in the northern boreal forest (Wylie et al. 2014). Every 50-200 years (Bonan and Shugart 1989) forest fire events typically generate a new assembly of heterogeneous vegetation features across landscapes. Over time, this results in a variety of successional stages across a landscape that forest species have presumably evolved to exploit to varying degrees. Crucial life stages (e.g., breeding) of many boreal species, including birds (Haney et al. 2008), mammals (Fisher and Wilkinson 2005) and insects (Saint-Germain et al. 2008) have been shown to be closely tied to different successional stages. Thus it can be said, that boreal species habitat selection and associations are heavily influenced, at multiple scales, by the fire regime.

Common Nighthawks (*Chordeiles minor*, hereafter nighthawks), are neotropical migrants, typically associated with open habitats, which breed throughout Canada and the US. Little is known about populations of these birds in the boreal forest as the majority of Canadian studies have taken place at southern latitudes e.g., in southern British Columbia (Firman et al. 1993) and southern Saskatchewan (Todd et al. 1998, Fisher et al. 2004, Ng 2009). Despite the boreal forest representing a substantial proportion of the species summer breeding distribution, and potentially harbouring a significant portion of the population, nighthawks that live in this biome have remained

virtually un-studied. The information that we do have about nighthawk abundance and distribution in the northern boreal forest comes from a limited number of roadside surveys, the majority of which did not specifically target nighthawks (Environment Canada and McKnight 2016). Understanding habitat associations of nighthawk populations across all environments is relevant and timely as in 2007, the species was listed as Threatened in Canada due to data from southern locations suggesting steep declines in numbers (COSEWIC 2007). COSEWIC (Committee on the Status of Endangered Wildlife in Canada) is currently re-assessing the status of the Common Nighthawk. Any new insights into the life history of these birds will allow for a more informed decision regarding their conservation status in Canada.

Common Nighthawks construct scrape nests directly on the ground, primarily in open or sparsely vegetated areas (Poulin et al. 1996). Further, nighthawks commonly forage on Coleoptera (beetles; Todd et al. 1998), specifically pyrophilous members of this group of insects attracted to heat and smoke, which increase in abundance following fires (Saint-Germain et al. 2008). The creation of open, post-fire habitat should, therefore, increase potentially limiting ground nesting sites and foraging opportunities for these ground nesting aerial insectivores. Thus, we would expect nighthawks to be positively associated with recently burned, open sites in the midst of a densely wooded landscape such as the boreal forest.

As a result of their crepuscular (active at dawn and dusk) nature and cryptic plumage, which makes finding daytime roosts difficult, diurnal bird surveys tend to miss or at very least severely underestimate the abundance of this species. In addition, as nighthawks regularly leave territories to commute to distant foraging areas (Ng 2009),

identifications based on the *peent* calls (in flight call) or visual sightings do not provide a precise understanding of how the habitat underneath an individual is used. For example, detection may occur over a breeding site, over a foraging site or while the bird is commuting between the two. By specifically documenting the number of wing-booming (territorial display performed over breeding territory), as well as *peenting*, birds we can begin to understand what habitat breeding nighthawks are most likely to be associated with. These surveying challenges highlight the need for targeted research aimed at nighthawks to examine their ecology in the boreal forest. Our study is among the first to examine habitat associations of nighthawks in the northern boreal forest using survey methods designed specifically for the species.

Our goal was to increase our understanding of nighthawk habitat associations in the northern boreal forest by determining if nighthawks select more recently burned, open areas or more densely forested later successional habitat. We achieved this by conducting nighthawk surveys in areas with different aged forests and assessing abundance relative to vegetation characteristics (fine scale) and relative to forest age (broad scale, fire regime). This information will help us to understand habitat associations, in particular the importance of recently burned sites, to nighthawks breeding in the northern boreal forest.

2.2. METHODS

2.2.1 Study Area

Our study was conducted in south-central Yukon Territory. Individual field sites were located in the boreal cordillera ecozone which is a semi-arid (< 300 mm precipitation/year), mountainous region characterized by short summers and extended winters (Environment Canada 2010, Wylie et al. 2014). Non-alpine, boreal forest stands are typically conifer dominated and primarily composed of white (*Picea glauca*) and black spruce (*Picea mariana*), interspersed with lodgepole pine (*Pinus contorta*). Trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are scattered throughout, forming pockets of mixed and deciduous only stands.

2.2.2 Study Design

Site selection --- To capture differences in vegetation as result of the fire regime, we used the Yukon's fire history GIS layers (Geomatics Yukon 2010) to categorize nine forest-age classes (age class: 0-5, 6-10, 11-15, 16-20, 21-30, 31-40, 41-50, 51-60, >61) based on years since fire. We selected these categories to ensure that sampling accounted for the rapid vegetation changes and seedling recruitment following a burn event (age class: 0-5, 6-10, 11-15, 16-20; Johnstone and Chapin 2006), the gradual vegetation changes and the transitional stage between deciduous and conifer dominated stands typically occurring at 50-60 years post fire (age class: 21-30, 31-40, 41-50, 51-60) (Strong 2009) as well as the later successional stages (age class: >60). Using ArcGIS, we randomly generated survey starting locations from within each of these nine forest-age classes (Figure 2.1).

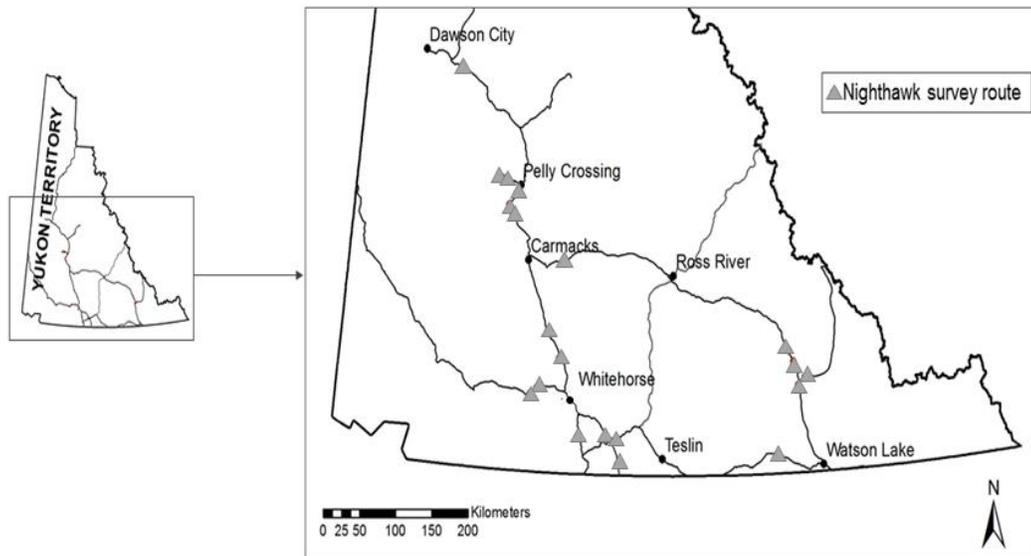


Figure 2.1 Study area in the south-central Yukon. Grey triangles indicate nighthawk survey route locations. Ten routes were surveyed in 2015 and 10 different routes in 2016. All locations were randomly selected using ArcGIS.

The Yukon’s limited road network constrained us from sampling all age classes equally. Thus, depending on road accessibility, we conducted 1-4 survey routes per forest-age category. To ensure independence between sites, all survey routes are separated by a minimum of two kilometers. Survey coordinates were loaded into a handheld GPS unit to locate sites in the field.

Survey layout: Nighthawk surveys --- We surveyed twenty, 9 km long survey routes from 7 June – 31 July in 2015 and 7 June – 1 August in 2016. Each route consisted of 19 point count stations located 500 m apart (Ministry of Environment-Lands and Parks Resources Inventory Branch 1998). Each route was surveyed by two surveyors, beginning 500 m apart and travelling in opposite directions, one on a bicycle (route length: 3.5 km) and

one in a vehicle (route length: 5 km). Weather permitting, all routes (with the exception of one) were surveyed twice, with approximately three weeks between survey periods. To reduce bias, the survey direction for each route was reversed during the subsequent survey e.g., the last bike point count location on the first survey was used as the starting bike point count location on the second survey.

Survey layout: Vegetation assessments --- We expected forest structure, particularly percent cover, to be an important habitat attribute for nighthawks as they have a large wingspan and dense vegetation may prevent them from accessing ground nesting sites or foraging effectively. Thus, we undertook vegetation assessments that focused on assessing individual forest layers including, ground cover (e.g., rock, needles, dirt, leaf litter, lichen, moss), herbaceous vegetation (< 10 cm), low shrub (10 cm – 1 m), tall shrub (1 m -3 m) and tree canopy for percent cover.

We conducted four vegetation assessments for every 1 km of nighthawk survey route (at every second point count; Figure 2.2). Vegetation assessments were located 40 m away from the road right-of-way to ensure minimal impact on vegetation structure by the road. Individual vegetation assessments consisted of a 5 m radius plot, centered over a 2x2 m plot, in which we recorded percent cover of individual forest layers (Figure 2.3).

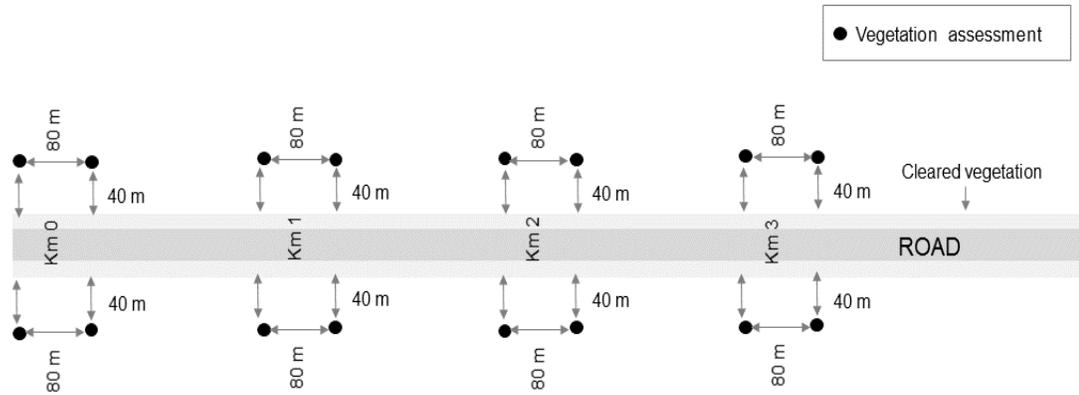


Figure 2.2 Layout of vegetation assessments conducted along each nighthawk survey route. Forty vegetation assessments were conducted for each 9 km route.

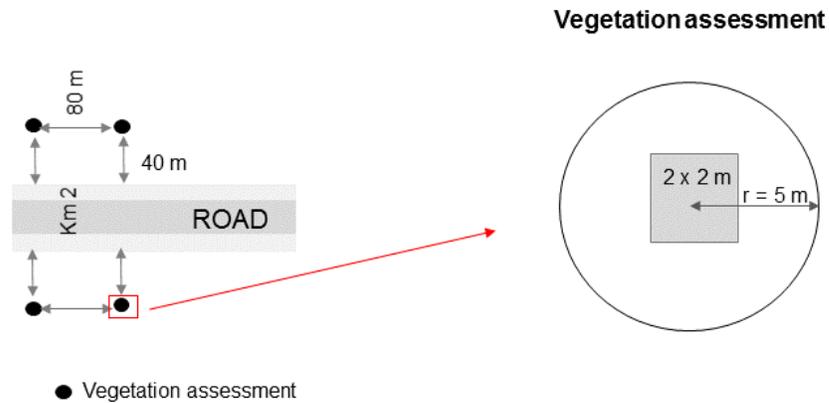


Figure 2.3 Layout of individual vegetation assessments. Ground and herbaceous vegetation cover were measured in the 2x2 m plot. Low shrub cover, tall shrub cover, tree canopy cover, and the number of logs were measured in the $r = 5$ m plot.

2.2.3 Data Collection

Nighthawk surveys --- Surveys were weather dependent and postponed during rain, when average wind speed was greater than 10 km/hr (too loud to hear birds calling in deciduous forests) or when ambient temperature was below 0° C. Surveys began 30 mins before sunset (Knight 2014). Information on daily solar/lunar cycles was retrieved from timeanddate.com for the specific location of the survey.

We conducted 10 mins of listening at each point count location. We listened silently for the first 6 mins and used a playback for the following 4 mins (Parker et al. 2007). The number of individual birds detected at each point count location was recorded. Detection type (physical sighting, *peent* call and/or boom display) was also noted for each individual bird. To avoid double counting an individual bird at two or more successive point count locations we payed close attention to the location and direction of detected individuals. When two birds on successive counts appeared to be calling from the same location, we did not count the second individual.

We also recorded data on environmental variables at the end of each sampling period including: lunar phase (retrieved from timeanddate.com), moon visibility (Table 2.1), average temperature, average wind speed (Kestrel 2000 Pocket Weather Meter), noise (Table 2.2) and cloud cover (Table 2.3). The number of passing vehicles was also recorded.

Table 2.1 Evaluation criteria for documenting moon visibility on nighthawk surveys (Knight 2014).

Code	Percent Moon Visible	Description
0	0% showing	No moon visible
1	1-25% showing	Moon partially visible
2	25-50% showing	Up to half the moon visible
3	50-90% showing	More than half of moon visible
4	>90% showing	Entire moon visible

Table 2.2 Evaluation criteria for documenting noise levels on nighthawk surveys (Knight 2014).

Code	Noise Level	Description
0	None	No effect of background on listening ability
1	Slight	Noise slightly affects listening ability (e.g., distant traffic)
2	Medium	Noise moderately affects listening ability (e.g., airplane, moderate local traffic)
3	Excessive	Noise seriously affects listening ability (e.g., continuous local traffic, frog chorus)

Table 2.3 Evaluation criteria for documenting cloud cover on nighthawk surveys (Knight 2014).

Code	Percent Cover	Description
0	0% cover	Cloudless sky; can see stars and moon clearly
1	< 25% cover	Mostly clear with scattered clouds
2	25% - 50% cover	Up to half the sky covered with clouds
3	50% - 90% cover	Dense cloud cover, but some patches visible
4	> 90 % cover	Entire sky clouded over

Vegetation assessments --- Visual estimates of percent ground cover and herbaceous vegetation (< 10 cm) were conducted in the 2x2 m plot. Low shrub (10 cm - 1.0 m) and tall shrub (1.0 m – 3.0 m) vertical cover were recorded in the 5 m radius plot using a visual obstruction technique similar to a Robel pole (Robel et al. 1970). We divided a three meter long pole into two vertical height classes by using blue (low shrub: 10 cm – 1.0 m) and red (tall shrub: 1.1 m – 3.0 m) tape markers placed at 10 cm increments along the length of the pole. A visual obstruction reading was taken by an observer from a

distance of 5 m. The observer crouched at a height of approximately 1 m for low shrub readings and stood at full height for tall shrub readings. The number of tape markers covered was recorded for each height class. Forest canopy cover (densiometer) was also recorded (r = 5 m plot). Nighthawks have been reported to roost on and place nests beside fallen logs (Poulin et al. 1996). As logs have the potential to be important habitat components for nighthawks, we recorded the number of logs (diameter > 15 cm, length > 1 m, decay < 0.5) found within in each plot (r = 5 m).

2.2.4 Statistical Approach

Statistical approaches to analyse data can vary considerably. A challenge across all approaches is variable selection (which variables to include in any particular model). At the onset of a project, researchers should develop an *a priori* hypothesis with the purpose of pre-selecting important, biologically relevant variables (based on prior knowledge) which will be used to model this hypothesis (Whittingham et al. 2006). Analytical techniques are then applied to models to explore significance relationships between variables. Although popular, analytical methods of variable selection can overestimate effect sizes, creating the potential for non-biologically significant relationships (Freedman 1983, Whittingham et al. 2006, Forstmeier and Schielzeth 2011). Further, when using an analytical variable selection approach, generally only one, or at most a few top models are presented in the results. These top models are commonly limited to depicting the most significant variables only, without making the reader aware of variables that were considered and discarded due to non-significant relationships.

An alternative variable selection approach is to refrain from using analytical methods for explicit model selection but rather to consider all relationships between pre-selected variables included in the *a priori* hypothesis. There are several advantages to using this approach. The overestimation of effect sizes are reduced resulting in model outputs that are more likely to reflect biological relationships (Whittingham et al. 2006, Forstmeier and Schielzeth 2011). This approach also supports a more exploratory aspect of data analysis as it considers the effects of non-significant variables, which while often overlooked, can lead to unanticipated yet important findings – particularly when the system has been the focus of little research. Further, disclosing all variables considered, enables others to replicate the work presented (Forstmeier and Schielzeth 2011).

Given that nighthawks are a highly understudied species, we took an exploratory approach to data analysis by refraining from using analytical model selection. We used p-values as a guideline for significance and presented all pre-selected variables which we investigated as our findings.

2.2.5 Statistical Analyses

Data processing --- All statistical analyses were completed in R 3.1.2 (R Development Core Team 2015). All survey data analyses were conducted using mean number of birds detected per point count. All data are presented as means with standard error ($\bar{X} \pm S.E.$).

Landscape scale --- We assessed nighthawk abundance relative to forest age (years since fire) to investigate if nighthawks are associated with burned areas across the landscape. Because nighthawks regularly leave their breeding territory to forage, habitats over

which birds are identified either visually or by call recognition may not be representative of breeding habitat. To examine the relationship between stand age and potential breeding habitat we also assessed the number of wing-booming (territorial display performed over breeding habitat) males detected in different aged forests. We hypothesized that the relative abundance of nighthawks and of wing-booming individuals would vary with forest age. We predicted that younger, more open forests would have a higher number of both individual calling nighthawks and wing-booming male detections, compared to older forests. We explored this relationship using a generalized linear model with a log link function to relate response to predictor variables. We used a negative binomial distribution (in the MASS package; Ripley 2015) to account for overdispersion in the data. We opted against using a Generalized Linear Mixed Model (GLMM), with route as a random effect, as our study design was such that we selected routes based entirely on forest age. We therefore wanted to explore the difference in nighthawk numbers and wing-booming males between routes/forest ages rather than accounting for this difference with a random effect. We used hanging rootograms (Kleiber and Zeileis 2016) from the countreg package (Zeileis and Kleiber 2016) and residual plots to visually assess model fit. We used the ggplot2 package (Wickham 2009) to generate graphs to illustrate how overall calling nighthawk and wing-booming male relative abundance varied with forest age.

To gain a basic understanding of the number of nighthawks found in different aged forests we calculated and graphed (gg2plot package; Wickham 2009) the mean number of nighthawks detected per point count for each forest-age category.

Territory scale --- We assessed nighthawk abundance relative to vegetation characteristics, using vegetation data collected at a scale approximately representative of (estimated) breeding territory size. Specifically, we hypothesized that nighthawk abundance would be affected by the amount of open space, as well as by potential roost sites, in an area. We predicted that areas with lower vegetation cover (better for aerial maneuvering), more exposed bare ground (increased potential nest sites) and a higher number of dead, horizontal logs (potential roost sites) would have a higher abundance of nighthawks when compared to more densely vegetated, log-free areas. To gain insight into how these vegetation characteristics affect the presence of both non-breeding and breeding individuals, we examined vegetation variables relative to both the total number of nighthawks detected and the number of wing-booming males recorded at each point count.

Initially, our goal was to include several measures of vegetation cover at different forest heights (i.e., ground, herbaceous, low shrub, tall shrub and tree canopy) and the number of logs as predictor variables in our models. However, our sample size was not large enough for a GLMM to support this number of variables and models did not converge. To decrease the number of predictors in the models, we identified the most correlated variables. Due to the lack of existing data on nighthawk vegetation associations, we were unable to base our decision of which correlated variable to retain on prior knowledge. Therefore, we believe that the benefit of objective analytical variable selection warranted the use of a Principal Component Analysis (PCA) biplot in this situation. We used the PCA biplot to select the variables with the greatest influence,

which we then included in our model. We decreased the number of predictor variables one at a time until the models converged.

Our final models contained ground cover, low shrub cover, canopy cover and number of logs as predictor variables. We ran two GLMMs (lme4 package; Bates et al. 2016), one with total nighthawks (point count⁻¹) and the other with the number of wing-booming individuals (point count⁻¹) as response variables. We used a negative binomial distribution to account for overdispersion in the data and a log link function to relate response to predictor variables. We specified route as a random effect to account for differences in the number of nighthawks between routes. We used the DHARMA package (Hartig 2016) to assess model fit based on standardized residual plots. To illustrate significant relationships between vegetation characteristics and relative nighthawk abundance, we plotted canopy and low shrub cover against nighthawk detections and against the number of wing-booming individuals detected (using the ggplot2 package; Wickham 2009).

Environmental conditions --- To ensure that we had conducted surveys when the detection of individual birds was not significantly hampered by environmental conditions, we explored variables that had the potential to limit an observers detection ability. We predicted that as noise, wind and the number of passing vehicles increased nighthawks, even if present, would become more difficult to detect, and thus would be recorded in lower numbers. We used the lme4 package (Bates et al. 2016) to run a GLMM which assessed the number of nighthawks detected relative to noise, wind and number of vehicles counted during each point count. As before, we specified a negative

binomial distribution, used a log link function to relate response to predictor variables and added route as a random effect. Using the DHARMA package (Hartig 2016), we assessed model fit based on standardized residual plots.

As avian activity is known to be influenced by a variety of environmental conditions we hypothesized that nighthawk activity could potentially be affected by temperature, wind speed, cloud cover, moon visibility (percent of the moon visible to the surveyor) and lunar phase (percent of moon illuminated). We predicted that nighthawks would be less active, and therefore detected in lower numbers, at cooler temperatures and higher wind speeds, as these conditions can constrain airborne insect (prey) activity (Boiteau et al. 2010, Arbeiter et al. 2016). Nighthawks are a visually orienting species and their activity is thought to be limited by light (Aldridge and Brigham 1991), therefore we predicted that increased cloud cover and lower values of moon illumination as well as moon visibility (i.e., darker conditions) would result in decreased activity and detection of individuals.

We excluded moon visibility from our analysis because we only saw the moon during 8% of all point counts. We felt this percentage was not representative of the lunar environment that airborne nighthawks would have experienced. Instead, we believe it was more likely to be an artifact of the physical structure (i.e., sub-grade roads, thick forests, mountainous area) of the survey environment rather than of the moon being truly obscured by clouds. We modeled the number of nighthawks detected (point count⁻¹) as the response variable, with temperature, wind speed, cloud cover and moon illumination as predictor variables. As before, we used a GLMM with a negative binomial distribution, a log link function and route as a random effect. We used the DHARMA

package (Hartig 2016) to assess model fit based on standardized residual plots. Using the ggplot2 package (Wickham 2009), we generated two graphs to illustrate the significant relationship between the number of nighthawks detected and 1) moon illumination and 2) temperature.

2.3 RESULTS

Nighthawk surveys were conducted over a total of 39 survey nights (19 nights in 2015, 20 nights in 2016). In 2015, during 356 point counts, we detected a total of 286 nighthawks and recorded 186 wing-booming individuals during these counts. In 2016, during 368 point counts, we detected a total of 346 nighthawks, including 170 wing-booming individuals.

Landscape scale --- Forest age was a predictor of nighthawk (estimate = -0.02, *S.E.* = 0.002, *z*-value = -11.05, *P*-value = <0.001) and wing-booming male (estimate = -0.02, *S.E.* = 0.002, *z*-value = -9.60, *P*-value = <0.001) relative abundance. Relative to older forests, younger forests supported a higher number of both total nighthawks as well as wing-booming males (Figure 2.4). Nighthawks were most abundant in forests under 20 years of age; the number of individuals detected per point count was three times higher ($\bar{X} = 1.54 \pm 0.20$) in these younger forests than in forests greater than 20 years of age ($\bar{X} = 0.52 \pm 0.17$) (Figure 2.5).

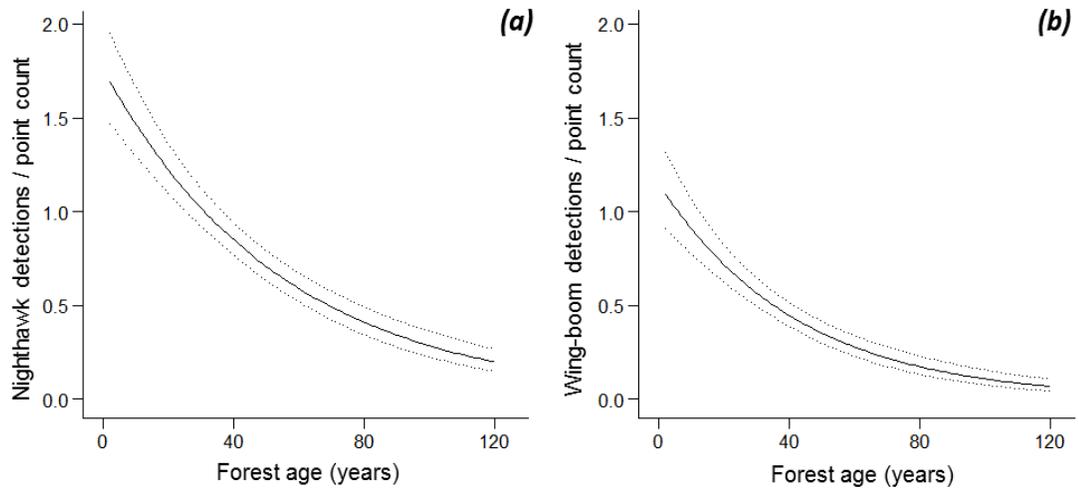


Figure 2.4 Detection of (a) total nighthawks and (b) wing-booming males (point count⁻¹) relative to forest age (95% confidence intervals) based on GLM predictions. Roadside surveys were conducted along twenty 9 km long routes, from 7 June - 31 July in 2015 and 7 June – 1 August in 2016.

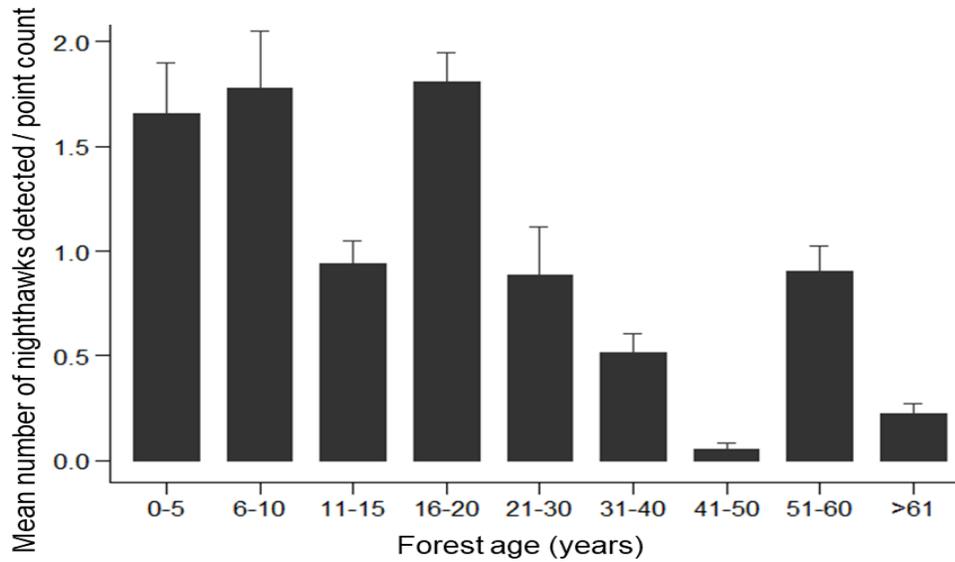


Figure 2.5 Mean number of nighthawks detected at each roadside point count station in each of nine forest-age categories (\pm standard error). Numbers include both calling and wing-booming individuals.

Territory scale --- The relative abundance of nighthawks was affected by both percent tree canopy cover and cover by low shrubs (Table 2.4). As predicted, fewer nighthawks were detected in areas with higher percent canopy and low shrub cover (Figure 2.6). The amount of exposed bare ground and the number of logs did not influence the number of nighthawks detected (Table 2.4).

Table 2.4 GLMM output relating relative nighthawk abundance to vegetation characteristics. Vegetation assessments were conducted at every 1 km along survey routes.

Model: detection ~ bare ground + canopy cover + low shrub cover + logs				
				<i>n</i> = 724
Model Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Bare Ground	0.002	0.002	0.87	0.39
Canopy Cover	-0.005	0.002	-2.49	0.01
Low Shrub	-0.007	0.002	-2.76	0.005
Logs	-0.008	0.01	-0.51	0.61

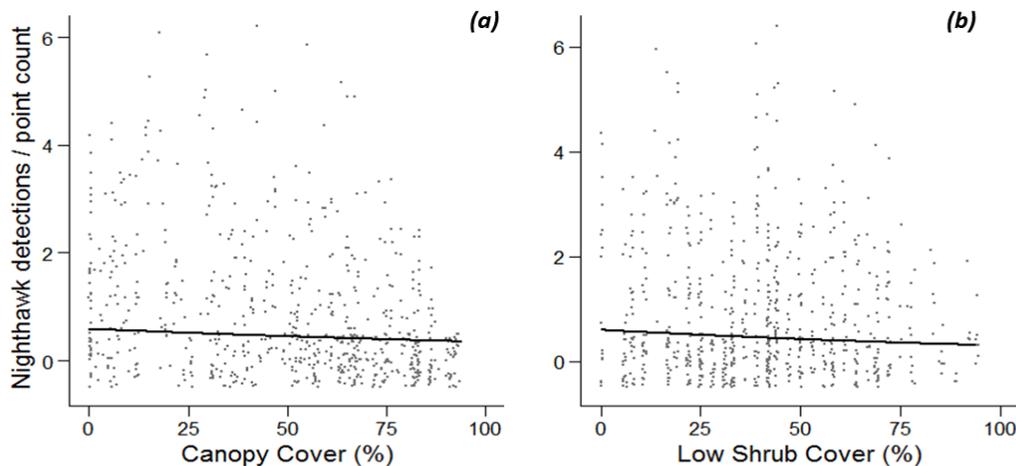


Figure 2.6 Plots of nighthawk detections (point count⁻¹) relative to (a) canopy cover and (b) low shrub (10 cm – 1 m) cover, based on GLMM model predictions. Vegetation assessments were conducted every 1 km along survey routes. Developing efficient methods for representing uncertainty parameters of negative binomial GLMMs (i.e., `glmer.nb` models) are currently underway. Uncertainty is illustrated by the grey dots which represent total survey data collected between 7 June - 31 July in 2015 and 7 June – 1 August in 2016. Specifically, each dot denotes the number of nighthawks detected at one roadside point count (dot spacing adjusted with: `position_jitter` (`width=.5`, `height=.5`)).

At sites where we detected nighthawks, the percent of wing-booming males was higher (63%, 256/404) in forests younger than 20 years of age when compared with forests older than 20 years (44%, 100/228). The number of wing-booms detected was influenced by the amount of canopy cover as well as low shrub cover (Table 2.5). As canopy and low shrub cover increased, we detected fewer wing-booming individuals

(Figure 2.7). The percent bare ground and the number of logs were not significantly related to the number of wing-booming nighthawks detected (Table 2.5).

Table 2.5 GLMM output comparing the relative abundance of wing-booming nighthawks to vegetation characteristics. Vegetation assessments were conducted every 1 km along survey routes.

Model: WBdetection ~ bare ground + canopy cover + low shrub cover + logs				
<i>n</i> = 724				
Model Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Bare Ground	<-0.001	0.003	-0.13	0.89
Canopy Cover	-0.01	0.003	-4.03	<0.001
Low Shrub	-0.008	0.003	-2.28	0.02
Logs	0.003	0.02	0.17	0.86

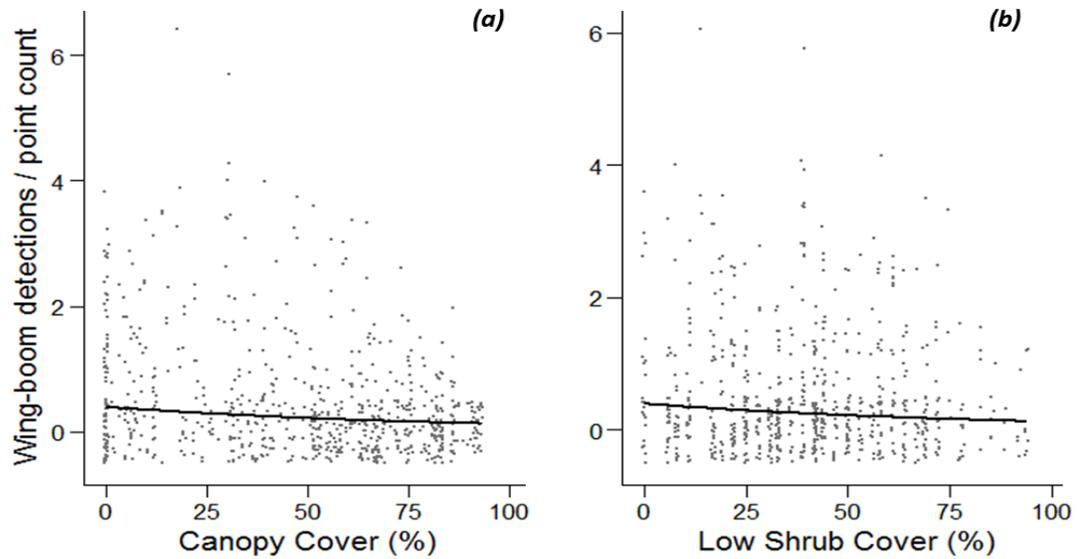


Figure 2.7 Plots of wing-booming nighthawk detections (point count⁻¹) relative to (a) canopy cover and (b) low shrub (10 cm – 1 m) cover, based on GLMM model predictions. Uncertainty is illustrated by the grey dots which represent total survey data collected. Specifically, each dot denotes the number of nighthawks detected at one roadside point count (dot spacing adjusted with: position_jitter (width=.5, height=.5)).

Environmental conditions --- The number of nighthawks detected was not significantly affected by noise, wind speed or the number of passing vehicles (Table 2.6). Although not significant, there were weak trends suggesting that as noise, wind speed and the number of passing vehicles increased, the number of nighthawks detected decreased.

Table 2.6 Model (GLMM) output examining the effects of noise, wind and number of vehicles on the number of nighthawks detected.

Model: detection ~ noise + wind + cars				<i>n</i> = 724
Model Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Noise	-0.02	0.07	-0.22	0.83
Wind	-0.06	0.03	-1.80	0.07
Number of Cars	-0.09	0.05	-1.79	0.07

Moon illumination and temperature (detection range: 2 – 20°C) influenced nighthawk activity throughout the survey seasons (Table 2.7). Overall, nighthawk detection increased as moon illumination increased (Figure 2.8). Nighthawks were detected in greater numbers at lower, rather than higher, temperatures (Figure 2.8). Of the 19 routes surveyed twice, we detected more nighthawks during the first set of surveys on 17 routes ($\bar{X} = 1.02 \pm 0.19$ detections per point count) when compared to the second set of surveys ($\bar{X} = 0.72 \pm 0.14$ detections per point count). We detected 40% of nighthawks on the five coldest routes ($\bar{X} = 9.12 \pm 0.30$ °C) and 32% on the five warmest routes ($\bar{X} = 13.18 \pm 0.29$ °C). Wind and cloud cover were not significantly related to nighthawk detection rates, however there was a trend toward increasing detections with increasing cloud cover (Table 2.7).

Table 2.7 GLMM output exploring the effects of temperature, wind speed, cloud cover and moon illumination (lunar phase) on the number of nighthawk detections (point count⁻¹).

Model: detection ~ temperature + average wind + cloud cover + moon illumination				
<i>n</i> = 724				
Model Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Temperature	-0.41	0.01	-4.89	<0.001
Average Wind	-0.08	0.03	-0.91	0.36
Cloud Cover	0.08	0.04	-1.99	0.06
Moon Illumination	0.01	0.003	3.07	<0.002

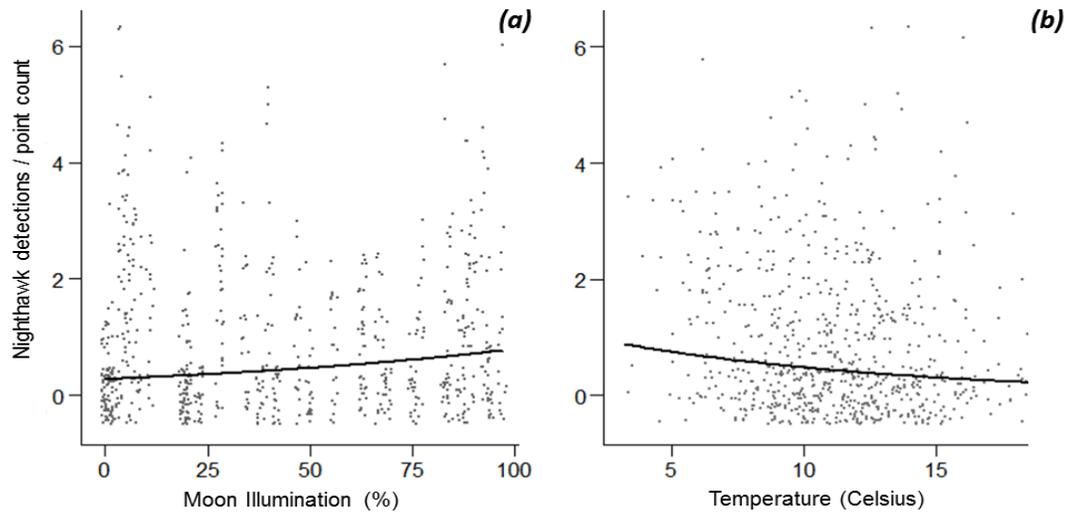


Figure 2.8 Plots of nighthawk detections (point count⁻¹) relative to (a) moon illumination (lunar phase) and (b) temperature, based on GLMM model predictions. Uncertainty is illustrated by the grey dots which represent total survey data collected. Specifically, each dot denotes the number of nighthawks detected at one roadside point count (dot spacing adjusted with: position_jitter (width=.5, height=.5)).

2.4 DISCUSSION

In the absence of anthropogenic disturbance, fire is the main disturbance and driver of spatial heterogeneity in the boreal forest (Wylie et al. 2014). Many boreal species are able to exploit different successional habitats and thus their abundance is closely related to the fire regime (Fisher and Wilkinson 2005, Schieck and Song 2006, Haney et al. 2008, Saint-Germain et al. 2008). We predicted that breeding Common Nighthawks in the northern boreal forest would be positively associated with post fire habitats as recently burned, open areas should have more potential ground nesting sites and foraging opportunities for these aerial insectivores. We identified that at both the landscape (forest age) and territory scale (vegetation characteristics), nighthawks were positively associated with more open habitat. Specifically, at the landscape scale we detected more total nighthawks, as well as wing-booming males (point count⁻¹), in younger, more open forests. At the territory scale, our data indicate that more open sites with decreased canopy and cover by low shrubs, regardless of forest age, had a higher relative abundance of both nighthawks in general and wing-booming males.

Landscape scale --- We found that nighthawk abundance was positively associated with younger forest stands. Schieck and Song (2006) suggested that many boreal bird species reached their peak abundance at a specific forest age. Our data show that nighthawk abundance peaks in forests that are younger than 20 years old as we had the highest rates of individual detections per point count ($\bar{X} = 1.54 \pm 0.20$) within this forest age range. Because nighthawks regularly leave territories to commute to distant foraging areas (Ng 2009), identifications based on the *peent* calls (in flight call) or visual sightings do not

provide a precise understanding of how the habitat underneath an individual is used. For example, detection may occur over a breeding site, over a foraging site or while the bird is commuting between the two. Therefore, to better understand how nighthawks use different aged forests as breeding habitat, we assessed forest age relative to the number of wing-booming (territorial display performed over breeding territory) males detected at each point count. As predicted, wing-booming males were positively associated with younger forests. At sites where nighthawks were detected, 63% of individuals in forests under 20 years old were wing-booming males, compared to 44% in forests that were older than 20 years.

It is possible that nighthawks prefer recently burned forests because open, post fire habitat presents increased foraging opportunities (McCullough et al. 1998). In fire driven ecosystems pyrophilous insects, which can detect heat and smoke, are attracted to post fire habitats (McCullough et al. 1998, Saint-Germain et al. 2008) resulting in increased insect abundance following burn events. White et al. (2015) proposed that the ephemeral increase in insect abundance following a burn event was linked to an increase in Olive-sided Flycatchers (*Contopus cooperi*). Our findings align with previous studies in the southern and western United States which found that birds belonging to the aerial insectivore guild, specifically those that capture insects through open air maneuvers, had the strongest positive response to post fire habitat (Hutto 1995, Kotliar et al. 2007, Russell et al. 2009). Additionally, many pyrophilous insects are common prey species of nighthawks, including beetles (Coleoptera), wood-boring wasps and ants (Hymenoptera; Todd et al. 1998). Considering that aerial insectivores are commonly reported to be associated with recently burned sites, we surmise that increased foraging opportunities in

these areas explains, at least in part, why we detected more nighthawks in younger forests.

Open habitat generated by fire also increases the availability and accessibility of ground nesting sites. As many ground nesting birds rely on the cover of foliage and shrubs to hide their nests, they have somewhat contrasting strategies for foraging (open areas) and nesting (low vegetation; Azeria et al. 2011). Thus individuals of these species may feed within burns and select habitats adjacent to burned areas for nesting (Azeria et al. 2011) or colonize low-severity burns or use burns following the reestablishment of grasses and shrubs (Hutto 1995, Kotliar et al. 2007). For instance, ground nesting Dark-eyed Juncos (*Junco hyemalis*) nested in low-medium severity burns while exploiting high severity burn patches for foraging (Kotliar et al. 2007). Nighthawks fulfill a unique niche among forest, ground nesting birds as they are able to take advantage of open, post fire habitat directly following a fire event. Similar to many shorebirds which nest on open beaches, nighthawks lay two eggs directly on patches of open ground (e.g., rock, dirt, gravel, lichen) and rely strictly on camouflage for protection (Poulin et al. 1996, Allen and Peters 2012, Lohnes 2010). Recently burned forests not only have many potential ground nesting sites but the more open forest stands also make these sites easier to access which further favors the use of younger, early successional habitats by nighthawks.

Burn severity is an important determinant of avian response to fire (Smucker et al. 2005, Kotliar et al. 2007) as it can cause significant variation in forest structure within the same burn. Given the perceived importance of forest structure to nighthawks, we recommend that future research should incorporate burn severity measures into study

design. Although we did not assess burn severity, the relationship we observed between forest age and relative nighthawk abundance indicates that these birds are able to take advantage of broad scale habitat conditions that occur in younger forests.

It bears mentioning, that despite being more common in younger forests, we did detect nighthawks throughout all forest ages. Naturally occurring wildfires were not suppressed in our study area (barring concerns for human safety). Thus our study area was composed of a landscape matrix with a variety of different forest ages and habitat types. This heterogenous landscape likely enabled breeding pairs to use localized open patches (e.g., pine clearings, rocky outcrops) for nesting, while commuting to more suitable habitat for foraging.

Territory scale --- We assessed habitat associations at the territory scale to gain a better understanding of which vegetation characteristics are good predictors of nighthawk abundance in the northern boreal forest. As predicted, we found that the relative abundance of both total nighthawks, and of wing-booming males, was negatively associated with percent tree canopy cover and cover by low shrubs, regardless of stand age.

Hutto (1985) proposed that migrating birds evaluate habitat using a hierarchical, top-down approach. For instance, a flying migrant would first perceive and assess potential breeding habitat based on broad scale geographical features, followed by forest structure and ultimately fine scale, within habitat patch characteristics (Hutto 1995, Norris and Marra 2007, Deppe and Rotenberry 2008). From a habitat selection perspective, tree canopy cover is presumably one of the first structural attributes that

nighthawks encounter and evaluate; this may help explain why it is influential in determining habitat associations. From a biological perspective, habitats associated with lower canopy cover are less cluttered and are likely important to nighthawks because they allow for more efficient aerial foraging and better access to ground nesting sites (when compared with more densely vegetated areas). Likewise, we found that habitats with less low shrub cover are preferred by nighthawks potentially because they have a higher availability of ground nesting sites. As nighthawks appear to consistently favor more open forest strata, and more open areas within these strata, our study highlights the overall importance of habitat openness to this species. It bears mentioning that evaluating nighthawk abundance relative to vegetation composition may further contribute to our understanding of habitat association as some bird species, which respond to habitat configuration at a large scale, respond more strongly to vegetation composition at finer spatial scale (Wiens and Rotenberry 1981).

Nighthawks may also favor open habitats due to potentially reduced predation risks associated with these areas. Small mammals such as rodents and mustelids which can depredate nests, are least abundant following burn events (as post fire habitats are often devoid of shrubby vegetation; Fisher and Wilkinson 2005). Red squirrels (*Tamiasciurus hudsonicus*), in particular, are a dominant nest predator in the boreal forest (Bayne and Hobson 2002). For example, a study in northern Saskatchewan found that egg survival rate of ground and shrub nests increased by up to 32% following the removal of red squirrels from an area (Bayne and Hobson 2002). While the female broken-wing display, intended to intimidate predators and draw attention away from the nest (Tomkins 1942), may be effective for larger carnivores (which also hunt adult

birds), it is likely to be less effective for smaller predators (which consume only eggs). Therefore, we speculate there may be a significant fitness advantage associated with nesting in open habitat types with few shrubs and a low abundance of small mammal predators. Conversely, nesting in open habitats (with decreased canopy and shrub cover), may make nests more visible to aerial predators such as corvids and owls. Although corvids are important nighthawk egg predators in urban settings, nest depredation in rural landscapes appears to be considerably lower, possibly owing to better camouflage due to natural substrates (Latta and Latta 2015). Gray Jays (*Perisoreus Canadensis*), Common Ravens (*Corvus corax*) and Black-billed Magpies (*Pica hudsonia*), the Yukon's main corvid species, are not associated with recently burned sites and thus we suspect they are unlikely to exert significant predation pressures on nesting nighthawks in our study area (Strickland and Ouellet 1993, Boarman and Heinrich 1999, Trost 1999). On three separate occasions (two routes) we observed (presumably) male nighthawks exhibiting aggressive mobbing behavior toward one Great Gray Owl (*Strix nebulosa*) and two Great Horned Owls (*Bubo virginianus*). In all three instances, owls were perched on the upper branch of a tree, slightly above average canopy height. Upon detection of the owl, nighthawks immediately began to circle and aggressively wing-boom over the owl while loudly *peenting* and making guttural croaking sounds. Within seconds, several other nighthawks joined, performing similar mobbing behavior. The nighthawks dispersed once the owl departed. Avian mobbing behavior is typically directed towards predators (Shedd 1982) thus, based on our observations, we conclude that large owls in the boreal forest are potentially important nighthawk predators. While nesting in open habitats makes the detection of females and chicks on the ground easier

for aerial predators our observations indicate that open habitat also allows nighthawks to better detect and deter aerial predators. Although speculative, we propose that nighthawks are more effective at defending nests against large carnivores (female display) and aerial predators (aerial mobbing) when compared to small mammals and that these predator-prey dynamics lead nighthawks to select more open, early successional habitats for nesting.

Contrary to our predictions, we did not detect a relationship between percent open ground and nighthawk abundance. Studies focusing on nest site characteristics have found that the amount of open ground at nest locations is significantly higher when compared to the surrounding habitat (Lohnes 2010, Allen and Peters 2012). Considering that we found no association with open ground, it is possible that this measurement is primarily relevant at the nest site scale rather than at the territory scale.

Previous studies which have collected data on nighthawk abundance, based on visual and *peent* call detections, have abstained from making inferences about breeding habitat associations because nighthawks may have been detected during foraging bouts outside their breeding territories. Unpaired males perform wing-boom displays over potential nesting areas to defend their territory from other males and to attract mates (Poulin et al. 1996); paired males center their wing-booms over nest sites (E. Knight, unpublished data). As wing-booms are concentrated over nesting areas, we assumed that wing-boom detections signify the presence of breeding habitat. We found similar relationships between the number of nighthawks detected based on *peents* and visual identification and the number of wing-booming males detected in relation to forest age

and across vegetation characteristics. Overall, our results indicate that nighthawks are detected in higher numbers closer to potential breeding territories. We suggest that despite these birds being a far ranging species, general inferences about breeding habitat associations in the northern boreal forest can be made based on regular abundance surveys (particularly when other data are not available). We predict, that this finding can be extrapolated to other forested habitats, where open areas surrounded by dense vegetation, would likely result in similar patterns of habitat association for nighthawks. As forestry practices create open areas, often resulting in habitat that is structurally similar to burned areas, this likely applies to regions of the boreal where timber harvesting has modified the landscape. However, we recommend that further research should be conducted in unforested habitats (e.g., grasslands) and other anthropogenically modified areas (e.g., towns), as factors aside from vegetation cover may be important drivers of nighthawk habitat associations in these habitats.

Environmental conditions --- We found that nighthawk detection across our study area increased at colder temperatures. This was unexpected, as more southern populations of nightjars (e.g., British Columbia) are thought to be inactive at cooler temperatures, perhaps because their insect prey decreases below 7°C (Ministry of Environment-Lands and Parks Resources Inventory Branch 1998). Northern species are typically adapted to, and thus better able to cope with, cooler climates (Bergmann 1848, Allen 1877, Koskenpato et al. 2016). This includes northern insects (nighthawk prey) which remain active at lower temperatures than southern conspecifics (Danks 2004). However, remaining active at lower temperatures is associated with the increased costs of

thermoregulation for many animals (Maggini and Bairlein 2013). Thus, the increase in activity we observed may, in part, be explained by increased foraging efforts required to sustain elevated costs of thermoregulation at colder temperatures.

We detected more nighthawks on our first set of surveys earlier in the summer than during our second set of surveys later in the summer. Our first set of surveys corresponded with the time of year when bird song generally reaches a peak as males use song to defend territories and to attract mates (Slagsvold et al. 1994, Amrhein et al. 2008, Catchpole and Slater 2008). Male nighthawks actively advertise breeding territories when they arrive in late spring and are therefore most likely to be detected in early summer. At our study site, this period of increased calling coincided with lower temperatures. This suggests that the preference for colder temperatures we observed may be partially explained by an overlap in timing between survey date and the time of year when males establish breeding territories. Thus, increased activity at cooler temperatures may be related to survey date as well as to metabolic requirements and a biological preference for cooler temperatures.

Contrary to Aldridge and Brigham (1991) who did not detect a relationship between nighthawk activity and moon illumination, we found that activity was positively associated with increased moon illumination. Higher activity on brighter nights is a well documented pattern for other North American (Woods and Brigham 2008, Cink et al. 2017) and African (Jetz et al. 2003, Ashdown and McKechnie 2008) nightjars. Furthermore, there is evidence to suggest that on brighter nights, when insect prey are more visible, foraging efficiency of sallying nocturnal nightjars is elevated, which likely accounts for the activity increase (Csada and Brigham 1992, Jetz et al. 2003, Woods and

Brigham 2008, Doucette et al. 2012, Cink et al. 2017). The foraging strategy of nighthawks, which capture insects on the wing during bout of continuous flight, differs from sallying nightjars which capture insects during short flights originating from a perch or the ground. We argue that increased illumination would make insects more visible, particularly against a backlit sky, and thus easier to capture for all visually orienting birds regardless of foraging strategy. Thus, similarly to sallying nightjars, increased foraging opportunities due to brighter conditions are likely to be advantageous to Common Nighthawks breeding in the boreal and may explain the positive relationship that we detected between moon illumination and activity.

One challenge of analyzing point count data is the uncertainty associated with zero-detections. This uncertainty stems from the inability to discern whether a zero-detection was recorded because there were no birds at a particular site (true zero) or because the observer was unable to detect the birds present at a particular site (false zero). Environmental conditions (e.g., weather) can diminish an observers ability to make detections resulting in the inflation of false zeros in a dataset, thereby biasing the results (Simons et al. 2007). To ensure that we surveyed during conditions when the detection of individual birds was not compromised, we assessed nighthawk detections (point count⁻¹) relative to variables which had the potential to limit our detection ability (i.e., noise, wind, cars). None of these variables were significantly related to the number of birds recorded (point count⁻¹) indicating that we conducted surveys when conditions were most suitable for detecting nighthawks.

Point count surveys are extensively used to monitor avian population trends. Despite the popularity of these surveys they have implicit biases (in addition to those discussed above) that must be taken into consideration when interpreting results. For instance, spatial differences in habitat structure and vegetation density influences sound attenuation and can result in variable detection distances for species between sites (Simons et al. 2007). However, as nighthawks typically call from well above canopy height and count stations were located centrally on a wide road/cleared right-of-way, we believe that spatial and vegetation differences between sites did not meaningfully impact nighthawk call transmission for our study. Further, variation or changes in observer hearing ability may produce trends in count data that are not representative of true population trends (Simons et al. 2007). Aside from observer biases, the presence of the road itself may influence the number of birds detected at a particular location (roadside bias). A recent study in the Northwest Territories demonstrated that for selected species, off-road population trend estimates deviated considerably from roadside survey trend estimates (Machtans et al. 2014). To reduce roadside bias, we attempted several off-road surveys early on in our study but quickly concluded, that given the difficult terrain, they were not a logistically feasible option. As current nighthawk population trends are primarily derived from roadside surveys (Environment Canada and McKnight 2016), despite the biases, we consider the data that we collected to be an important contribution towards increasing our understanding of nighthawks in the northern boreal forest.

2.5 MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Fire suppression is a common land management practice across much of North America. This practice can impact the value of forested areas from a social (recreational use), industrial (timber harvesting, resource extraction), global (carbon sequestration) and conservationist (wildlife management) point of view. Thus, land managers have the difficult task of balancing, often conflicting, ideas when it comes to managing forested areas. From a wildlife management perspective, suppression is not consistently the best approach as we have come to recognize the importance of naturally occurring fires on the ecology of species, particularly in fire mediated ecosystems (e.g., boreal forest; Brawn et al. 2001).

We detected nighthawks on 19 out of the 20 routes we surveyed, suggesting that despite declining population estimates for the species continent wide, albeit based largely on surveys from southern locations, this species is common in the northern boreal forest. Further, we found that breeding individuals were associated with recently burned, open habitat. Naturally occurring wildfires are not currently suppressed in the Yukon (barring situations with direct safety concerns for people). We argue that we consistently detected nighthawks for two main reasons: Firstly, because of the availability of early successional habitat which supported high numbers of breeding individuals. Secondly, birds nesting in older forests, were readily able to commute to open foraging areas as a result of the heterogeneous landscape - a less likely event in an even-aged, homogenous landscape. Given the importance of early successional habitats to breeding populations of Common Nighthawks, we recommend that land managers in boreal regions should aim for management plans which allow naturally occurring wildfire events to burn in

areas that are unlikely to present safety concerns to humans or be of high social and economic value. Conservation of post fire habitats will also benefit other important early-succession associated species (Brawn et al. 2001) such as Black-backed woodpeckers (*Picoides arcticus*; keystone architects; Martin et al. 2004, Nappi and Drapeau 2009) and snowshoe hares (*Lepus americanus*; keystone prey; Ferron and St-Laurent 2008) as well.

In locations where fire suppression practices are necessary, timber harvesting may produce alternative, open habitats which are structurally suitable for breeding nighthawks. A recent study by Farrell et al. (2017) found that nighthawk occupancy rates did not vary significantly between wetlands, recent burns (< 20 years old) and clear cut areas in northern Canada. However, as the insect community varies between clear-cuts and post-fire habitats (Chaundy-Smart et al. 2012), further research is needed to ensure that changes in prey availability do not result in these clear-cut areas being sink habitats for breeding nighthawk populations.

Water may be a crucial resource for nighthawks as the open space above water bodies typically has high concentrations of insects and thus may provide valuable foraging habitat for these birds. Previous studies indicate that water may be an important habitat attribute as nighthawks were commonly observed foraging near water (Ng 2009), drinking at still water bodies (Poulin et al. 1996) and had high occupancy rates in areas with open wetlands (Farrell et al. 2017). Future research should explore nighthawk abundance relative to the proximity to water and wetlands to evaluate whether habitats near these features support higher numbers of breeding individuals.

Given the limited information on the breeding biology of this species (Poulin et al. 1996, Perkins and Vickery 2007, Allen and Peters 2012, Kramer and Chalfoun 2012, Lohnes

2010), particularly in northern boreal forest, future studies should focus on examining nest site characteristics and nest success rates in this habitat. A large portion of the North American nighthawk breeding range is thought to be in the boreal region, thus understanding reproductive timing, rates and nest site selection in this habitat type are important prerequisites for the development of effective management strategies.

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3.0 LIFE IN THE TWILIGHT ZONE: COMMON NIGHTHAWK ACTIVITY PATTERNS IN THE NORTHERN BOREAL FOREST

3.1 INTRODUCTION

Understanding patterns of habitat and space use of organisms is biologically relevant as these patterns are closely tied to survival and reproduction. It is widely recognized that species occurrence and movements are related to life history characteristics and to the spatial distribution of habitat attributes and resources across the landscape (Morissette et al. 2002, Leonard et al. 2008, Lemaître et al. 2012). However, spatial heterogeneity alone is not sufficient to explain the daily, seasonal and annual activity patterns of organisms, as the arrangement of resources changes not only through space, but also through time (Block and Brennan 1993, Price et al. 2013, Georgiadis et al. 2014).

Temporal changes in an environment alter the conditions that an individual may experience at the same location and thus can affect how and when a particular area is used. Temporal variation can influence activity patterns as a result of changes in biotic factors such as predation risk (Woods and Brigham 2008) and prey distribution (Heurich et al. 2014), as well as through abiotic factors such temperature (Everall et al. 2015), light (Claretand and Anderson 1997), precipitation (Price et al. 2013) and noise (Bormpoudakis et al. 2013). Changes in species activity and movement patterns in response to temporal resource fluctuations are well documented in a broad range of taxa including, insects (Narendra et al. 2010), fish (Georgiadis et al. 2014), mammals (Musyoki and Strum 2016) and birds (Claretand and Anderson 1997). Consequently,

temporal variation in resource availability must be considered when evaluating space use patterns (Southwood 1977, Virkkala 1991, Block and Brennan 1993).

Changes in ambient light (photoperiod) are considered to be one of the most influential variables that produces temporal variation across the globe. Fluctuations in seasonal and daily light levels function as a global Zeitgeber, dictating the timing of essential biological processes for organisms worldwide (Aschoff 1954, Kelber 2005, Ware et al. 2012, Steiger et al. 2013). Because photoperiod predictably tracks time at both daily and seasonal scales, it is not surprising, that changes in ambient light are an important predictor of biological activity patterns ranging from those at a broad scale, e.g., breeding (Helm et al. 2009) and migration cycles (Gwinner 1996), to fine scale daily activities such as diurnal rhythms (Steiger et al. 2013) and roosting patterns (Kranz and Gauthreaux 1975).

Other sources of temporal variation, such as temperature, can interact with and fine-tune light cues thus acting as secondary means of modifying animals space use patterns (Fernandez-Duque 2003, Lehmann et al. 2012). For endotherms, temperature changes can directly affect space use by exposing organisms to conditions outside of their thermoneutral zone resulting in the modification of activity and other behaviors (Ashdown and McKechnie 2008, Aublet et al. 2009). This can influence the timing of reproductive events (Visser et al. 2009, Bian et al. 2014) and movement cycles (Georgiadis et al. 2014). Further, temperature fluctuations indirectly drive patterns of space use by modifying the distribution of resources across the landscape, such as vegetation cover (Soja et al. 2007), local temperature refuges (Dugdale et al. 2016) and foraging opportunities (Jetz et al. 2003, Heurich et al. 2014).

In addition to temporal variability of resources across environments, behavior and activity patterns of organisms are also influenced by life history characteristics. For example, Eurasian Lynx (*Lynx lynx*) exhibit sex-specific activity with males spending significantly more time per hour being active (walking, hunting, interacting) than females (Heurich et al. 2014). Furthermore, changes in behavior by the same individual over time can often be related to life stage. For instance, adult male Song Sparrows (*Melospiza melodia*) will aggressively sing to defend a spring territory whereas young males invest more energy in learning new songs rather than defending territories (Templeton et al. 2012). Additionally, reproductive stage is a predictor of vocal activity in many bird species (Catchpole and Slater 2008). Thus, when assessing space use, considering the effect of temporal variability in the context of a species life history can be crucial to developing a more accurate understanding of general activity patterns.

Temporal variation can elicit varying behavioral responses in organisms. These responses are often related to the active period of a species (e.g., diurnal, nocturnal, crepuscular). For instance, longer, warmer summer days may provide benefits to diurnal species, as time available for foraging increases (Steiger et al. 2013). In addition, warmer temperatures allow individuals to seek out areas within their thermoneutral zone, thus decreasing energy demands (Kobbe et al. 2014). For nocturnal species, longer days lead directly to shorter nights which means less time to forage and replenish energy reserves (Talerico 2008).

Ambient light is a particularly important resource for visually orienting crepuscular species as their daily activity period is often limited to just a few hours (Jetz et al. 2003). Both predictable (solar cycles) and unpredictable (cloud cover) light

fluctuations can influence an organism's space and habitat use. For instance, as the ability to visually detect prey or conspecifics changes, the dynamics of predator-prey interactions and intra-specific communication (Aldridge and Brigham 1991, Roth et al. 2003, Woods and Brigham 2008) also shift. Further, changes in calling frequency, foraging patterns and activity levels in response to variations in lunar cycles, cloud cover and ambient light are well documented for nightjars (Poulin et al. 1996, Jetz et al. 2003, Woods and Brigham 2008, Smit et al. 2011).

Thermal variation also plays an important role in the activity patterns of crepuscular species as temperature can decline rapidly following sunset – over the relatively short period during which crepuscular and nocturnal animals are active. Remaining active at lower temperatures can come with increased metabolic costs, as animals often use more energy to regulate elevated body temperature and activity levels (Maggini and Bairlein 2013). Changing thermal conditions can also affect the availability and abundance of prey species, particularly smaller bodied organisms which lose heat rapidly (e.g., insects (Danks 2004), rodents (Stawski et al. 2016)). Thus, like light, temperature can considerably impact patterns of space use by crepuscular species through changes in predator/prey dynamics (Jetz et al. 2003, Ashdown and McKechnie 2008).

Crepuscular species near the equator experience twilight lengths that differ by just a few minutes annually, however both twilight duration, and variability in that duration, increases at higher latitudes (Mills 2008). For instance, at latitudes greater than 53.5°, morning and evening twilight periods merge into one daily period around summer solstice (Mills 2008). These substantial changes in light conditions are likely to have a

considerable impact on the phenology of species found in these environments. In North America, the majority of studies which have assessed light and temperature effects in the context of activity patterns by wild populations have been conducted at more central latitudes where there is either a fairly constant day-night cycle (Bruni et al. 2014) or in the high arctic where there is continuous summer daylight (Underwood 1975, Steiger et al. 2013, Nilsson et al. 2015). Large seasonal variation in ambient light levels across the summer, and cool evening temperatures, are a distinguishing feature of northern latitudes between 60° and the Arctic Circle. This geographic range includes a large portion of Canada's boreal forest which is an important nursery-habitat for many of North America's breeding birds (The Boreal Avian Modelling Project 2011). To our knowledge, there has been no research which has attempted to quantify how changing photoperiod (i.e., light availability), in conjunction with temperature variation, impacts the activity patterns of a crepuscular species in northern boreal forest habitat.

Common Nighthawks (*Chordeiles minor*, hereafter nighthawk), are crepuscular, neotropical migrants which breed throughout Canada and the US. Little is known about the populations of these birds in the northern boreal forest as the majority of Canadian studies have taken place at southern latitudes e.g., in southern British Columbia (Firman et al. 1993) and southern Saskatchewan (Todd et al. 1998, Fisher et al. 2004, Ng 2009). Despite the fact that the boreal forest represents a substantial proportion of their summer breeding distribution, and potentially a significant proportion of their numbers, populations of nighthawks that live in this biome have remained virtually un-studied. The information that we do have about nighthawk abundance and distribution in the northern boreal forest comes from a limited number of roadside surveys, the majority of

which did not specifically target nighthawks (Environment Canada and McKnight 2016). Understanding activity patterns of nighthawk populations across all environments is relevant and timely as in 2007, the species was listed as Threatened in Canada, largely based on data for southern populations which suggest steep declines in numbers (COSEWIC 2007). COSEWIC (Committee on the Status of Endangered Wildlife in Canada) is currently re-assessing the status of the Common Nighthawk. Any new insights into the life history of these birds will allow for more informed decisions about this species conservation status in Canada.

Given that nighthawk activity periods appear to be primarily constrained by darkness (Aldridge and Brigham 1991), we expected elongated crepuscular hours to elicit a marked behavioral response as individuals take advantage of the increased time in which to fulfill foraging needs. By virtue of being at northern latitudes, nighthawk populations in Canada's northern boreal forest must contend with a shortened breeding season (Wylie et al. 2014) and may therefore, despite cooler night time temperatures, be particularly responsive to increased foraging opportunities allowed by long periods of twilight.

Current nighthawk sampling protocols recommend that surveying be undertaken during the crepuscular period, between sunset and nautical twilight (when the sun is between 0 and 12 degrees below the horizon; Ministry of Environment-Lands and Parks Resources Inventory Branch 1998, Knight 2016). As a consequence of northern latitudes' having a large variation in the length of the summer crepuscular period, including the complete absence of nautical twilight around solstice (Mills 2008), and low evening temperatures, these protocols may be ineffective for accurately assessing

nighthawk populations in the northern boreal forest. In consideration of the Threatened status of *C. minor*, the importance of developing an appropriate sampling protocol based on local peak activity periods cannot be understated.

The objective of our research was to assess whether nighthawk activity varies with ambient light and temperature levels and ultimately to identify periods of peak calling activity across the breeding season by northern nighthawks (using vocalizations as a measure of activity). We assessed this objective by investigating seasonal and daily activity patterns in relation to seasonal variations in ambient light and temperature. In addition to collecting data on peak calling periods, this study will expand our understanding of how fluctuations in temperature and ambient light levels across the summer impact the behavior of a crepuscular species.

3.2 METHODS

3.2.1 Study Area

Our study was conducted in south-central Yukon Territory. Individual field sites were located in the boreal cordillera ecozone which is a semi-arid (< 300 mm precipitation/year), mountainous region characterized by short summers and extended winters (Environment Canada 2010, Wylie et al. 2014). Non-alpine, boreal forest stands are typically conifer dominated and primarily composed of white (*Picea glauca*) and black spruce (*Picea mariana*), interspersed with lodgepole pine (*Pinus contorta*). Trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are scattered throughout, forming pockets of mixed and deciduous only stands.

3.2.2 Data Collection

Daily and seasonal calling activity --- Remotely located, Autonomous Recording Units (SM2+, Wild Acoustics Inc., hereafter known as ARUs) were used to collect data on nighthawk activity patterns and peak calling times. Following consultation with Canadian Wildlife Service biologists in Whitehorse, three ARUs were deployed within the study area (around Whitehorse, Yukon) at locations known historically to support high densities of nighthawks (Figure 3.1).

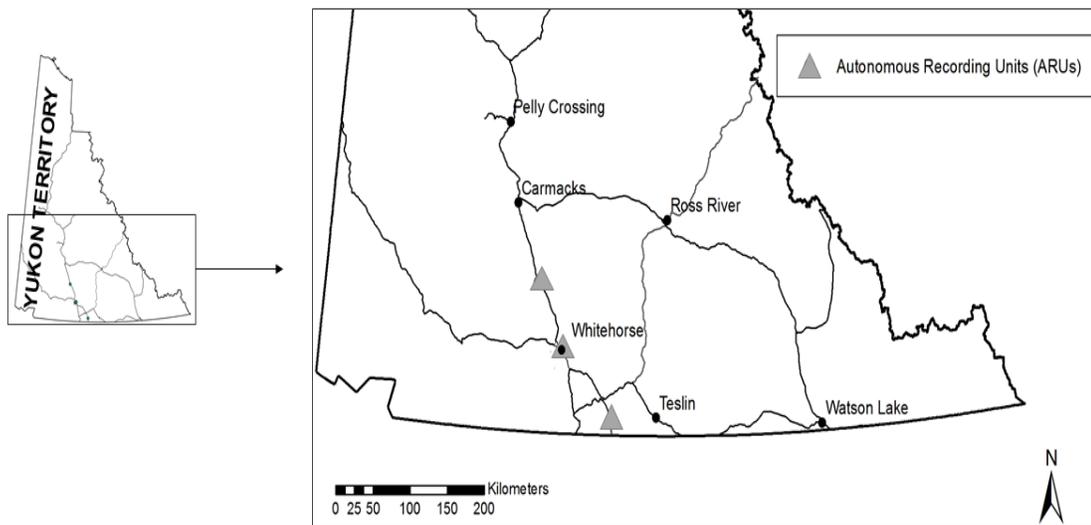


Figure 3.1 Locations of ARUs deployed from late May – late August in both 2015 and 2016 in the southern Yukon. These sites were selected given historical records for high nighthawk densities.

We deployed three ARUs to record nighthawk calls between late May and late August (Table 3.1) in 2015 and 2016. We attached the units to trees, approximately 2 m off the ground, at the edge of clearings to minimize the attenuation of sounds by

surrounding branches and vegetation. They were programmed to actively record from one hour before sunset until one hour after sunrise each night. The units were capable of calculating daily sunset and sunrise times based on geographical location. ARUs were visited approximately every three weeks to exchange batteries and download data.

Table 3.1 ARU locations and deployment schedule during summers 2015 and 2016.

Recorder name	Deployment dates 2015	Deployment dates 2016	Latitude, Longitude (DD)
Fox Lake	2 Jun - 27 Aug	20 May - 23 Aug	61.36732, -135.66873
Gray Mt	2 Jun - 22 Aug	20 May - 23 Aug	60.71594, -135.01112
Snafu	31 May - 27 Aug	23 May - 24 Aug	60.13520, -133.81165

Calling activity relative to ambient light and temperature --- A light logger (HOBO Pendant Temperature/Light Data Logger) was deployed alongside the Snafu ARU to allow us to directly assess the impact of ambient light levels on calling frequency. We mounted the logger, in an upright position, on a 2 m long pole in the center of the clearing adjacent to the ARU (to minimize the impact of shadows cast by vegetation). The logger recorded light levels at 10 min intervals throughout the day. Data were downloaded approximately every three weeks.

To assess the impact of ambient temperature on calling activity we deployed a temperature sensitive iButton (Maxim Integrated, Thermochron family, DS1921G) alongside the Snafu ARU. The iButton was placed in a mesh cloth casing and suspended in a white, styrofoam cup (to insulate it from and reflect direct sunlight). This device was

programmed to record temperature at 20 min intervals. Data were downloaded approximately every three weeks.

3.2.3 Statistical Approach

Given that nighthawks are a highly understudied species, we took an exploratory approach to data analysis (see Chapter 2;2.2.3 Statistical approach) by refraining from using analytical model selection. We used p-values as a guideline for significance and presented all pre-selected variables which we investigated as our findings.

3.2.4 Statistical Analyses

Data processing --- We used Cornell's Raven Pro software (Raven Pro 1.4 build 48), which displays sound files as visual representations known as spectrograms, to analyse ARU acoustic recordings. To decrease processing time, calls and wing-booms (male territorial display) in the first 5 mins of each half hour of the recording were visually identified and date/time stamped (hereafter, total calls). These data were subsequently transferred from Raven Pro selection tables into a MS Excel spreadsheet for tallying. Although less frequent, the relative proportion of wing-booms were in similar proportion to calls throughout the summer, therefore we present an analysis of the call data only.

All statistical analyses were completed in R 3.1.2 (R Development Core Team 2015). All data are presented as means with standard error ($\bar{X} \pm S.E.$). Unless otherwise noted, we analysed 2015 and 2016 data together to increase the sample size for each calendar night from three ARU recordings to six.

Daily calling activity --- We assessed daily calling activity relative to the sun's altitude (using sun altitude as an indirect measure of ambient light), between 7 June and 8 August, 2015 and 2016. Sun altitude (in degrees) is the measurement of the angle between the center of the sun and the horizon. Data from early June (1 June – 6 June) and mid-August (9 August – 15 August) were excluded to ensure our analysis targeted the time period which best captured the activity of resident breeding populations rather than the activity of potential migrants.

For each ARU recording night, we counted the total number of calls detected during each hour after sunset, beginning one hour prior to sunset and ending one hour post sunrise (to reflect the ARU recording schedule). We retrieved the median sun altitude for each ARU recording from timeanddate.com.

Specifically, we hypothesized that daily nighthawk calling activity would change with sun altitude throughout the summer. We expected that nighthawks would call most during civil twilight (the time when the sun is 0-6 degrees below the horizon) in a unimodal pattern. We explored this relationship using a generalized linear model with a negative binomial distribution (in the MASS package (Ripley 2015)) to account for overdispersion in the data. We used a log link function to relate response to predictor variables. We opted against using a generalized linear mixed model with location added as a random effect because our ARU location sample size was low ($n=3$). However, we did include location in our model to take into consideration that each of our ARUs collected data from different populations, likely each with a different number of individual nighthawks. We used hanging rootograms (Kleiber and Zeileis 2016) from the `countreg` package (Zeileis and Kleiber 2016) and residual plots to visually assess model

fit. We used the `ggplot2` package (Wickham 2009) to generate a graph illustrating the relationship between sun altitude and hourly nighthawk calling activity across the summer.

As light levels change drastically over the course of the summer, we further hypothesized that the influence of sun altitude on nighthawk calling activity would have a seasonal component. To explore this seasonal aspect of sun altitude we divided the summer into three light-periods (early, mid, late) based on length of night (time between sunset and sunrise). The median time between sunset and sunrise was approximately five hours (4 hrs 52 mins) during the early light-period, six hours (5 hrs 58 mins) during the mid light-period and seven hours (7 hrs 4 mins) during the late light-period.

We predicted that sun altitude would be a more important predictor of calling activity during late summer (late light-period), when the sun sank considerably further below the horizon and nights grew darker and longer, compared to early summer (early light-period). Sunset is a primary predictor of activity by crepuscular species, therefore we also hypothesized that time-of-night relative to sunset (measured as hour-after-sunset; e.g., 1 hr after sunset etc.) would predict nighthawk activity. We expected that during early summer, when there was little variation in sun altitude, time-of-night would influence nighthawk activity but this would become less important later in the summer, as the effect of sun altitude became more pronounced. To explore this relationship, we included hour-after-sunset and an interaction term between hour-after-sunset and sun altitude in our models. As above, we included a log link function and location as a covariate to take into consideration that our three ARUs were collecting data from different populations. We assessed early and late light-periods independently by creating

two models (early, late) in which we explored the seasonal effect of sun altitude and hour-after-sunset on nighthawk calling activity. We used the effects package (Fox et al. 2017) to generate plots which explore the interaction between sun altitude and hour-after-sunset.

The recently developed National Nightjar Survey Protocol (Knight 2016) recommends starting nighthawk surveys 30 mins before sunset. To assess the suitability of these guidelines, we related sun altitude to hour-after-sunset during the early light-period – the time during which nighthawk surveys are conducted. We did this by using the ggplot2 package (Wickham 2009) to generate a graph which illustrated calling activity relative to both sun altitude and hours-after-sunset.

Seasonal calling activity --- Based on anecdotal evidence, nighthawks arrive in the Yukon from late-May to early-June and remain until mid-August, thus our intention was to document seasonal calling activity beginning 1 June and ending 15 August in 2015 and 2016. However at the start of the 2015 field season, rain prevented us from deploying two ARUs until 2 June. Thus, to be consistent, we assessed seasonal calling activity between 2 June – 15 August in both 2015 and 2016.

Canada's newly designed National Nightjar Survey Protocol recommends surveying for nighthawks between 15 June – 15 July (Knight 2016). To assess whether the timing of the survey window aligns with peak calling activity in the North we explored the percent of total calls detected in biweekly time intervals throughout the summer.

As large fluctuations in photoperiod are a feature of northern latitudes, night length varied considerably between the shortest (21 June: 4 hrs 51 mins) and the longest (15 August: 8 hrs 18 mins) night during our study season. Because of this variation, a direct comparison between total number of calls across different summer nights is not appropriate. Using the number of hours in a night, we standardized the call data to ‘mean calls per hour’ and compared calling activity across the summer using this metric. We used the ggplot2 package (Wickham 2009) to generate a graph highlighting peak calling periods throughout the summer.

Calling activity relative to ambient light and temperature --- We explored how direct measures of ambient temperature (degrees celsius) and light (lux) influenced the probability of detecting a nighthawk call between 7 June and 8 August, 2015 and 2016. Data from early June (1 June – 6 June) and mid August (9 August – 15 August) were excluded to ensure our analysis targeted the time period which best captured the activity of resident breeding populations rather than the activity of potentially migrating individuals. Data were obtained from a single location (Snafu ARU; Table 3.1) as only this ARUs was accompanied by light and temperature logging equipment.

For every ARU recording night, we assigned a binary value to each recording hour based on the detection/absence (i.e., present = 1, absent = 0) of a nighthawk call during that hour, beginning one hour prior to sunset and ending one hour post sunrise (to reflect the ARU recording schedule). We calculated mean temperature (based on three readings per hour) and light (based on six readings per hour) values for each recording hour.

We hypothesized that nighthawk calling activity would be affected by both light and temperature. We predicted that nighthawks would call most at light levels between sunset and dark night (i.e., ambient light approximately 0 - 400 lux) and that calling would decrease with declining temperatures. To explore this relationship, we conducted a logistic regression (binomial generalized linear model, logit link function) where we included call as a binomial response variable and light, temperature, a light-temperature interaction term and light-period (to account for seasonality) as predictor variables. We evaluated model fit using a Hosmer-Lemeshow-goodness-of-fit test (Hosmer et al. 2013) in the ResourceSelection package (Lele et al. 2016). We used the effects package (Fox et al. 2017) to generate plots which explore the interaction between sun altitude and hour-after-sunset.

3.3 RESULTS

Daily calling activity --- Sun altitude influenced hourly calling activity throughout the whole summer (Table 3.2). Average calling activity was highest at sun altitudes of between -1 and -6 degrees relative to the horizon, with an average of 87% of calls being detected in this sun altitude range (Figure 3.2). This peak calling period reflects civil twilight conditions - the period between sunset/sunrise (sun altitude = 0 degrees) and when the sun is 6 degrees below the horizon. During evenings in early summer (7 June – 11 July), nighthawks were most active at sun altitudes between -1 and - 5 degrees, corresponding to approximately 0.5 – 3.0 hrs following sunset (Figure 3.3).

Table 3.2 Model output assessing the influence of sun altitude (degrees above/below the horizon) on nighthawk calling activity (hour^{-1}) between 7 June and 8 August in 2015 and 2016, based on data from Snafu, Grey Mtn and Fox Lake ARUs.

Model: tot calls ~ poly(sun altitude, 2) + location				$n = 2484$
Model Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Poly(Sun altitude, 2) _{1,2}	16.83	2.93	5.74	<0.001
Location	0.04	0.07	0.55	0.59

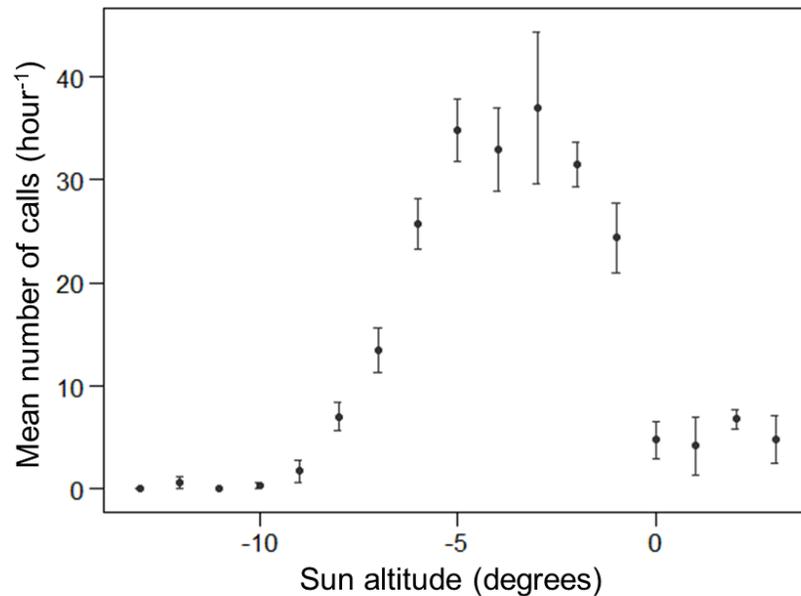


Figure 3.2 Mean number of nighthawk calls detected per hour (\pm standard error) as a function of sun altitude (the height of the sun above/below the horizon) between 7 June and 8 August of 2015 and 2016 at three ARU sites (Fox Lake, Snafu and Grey Mtn). Sunset and sunrise when sun altitude = 0 degrees. ARU's were programmed to begin recording one hour prior to sunset and cease one hour after sunrise.

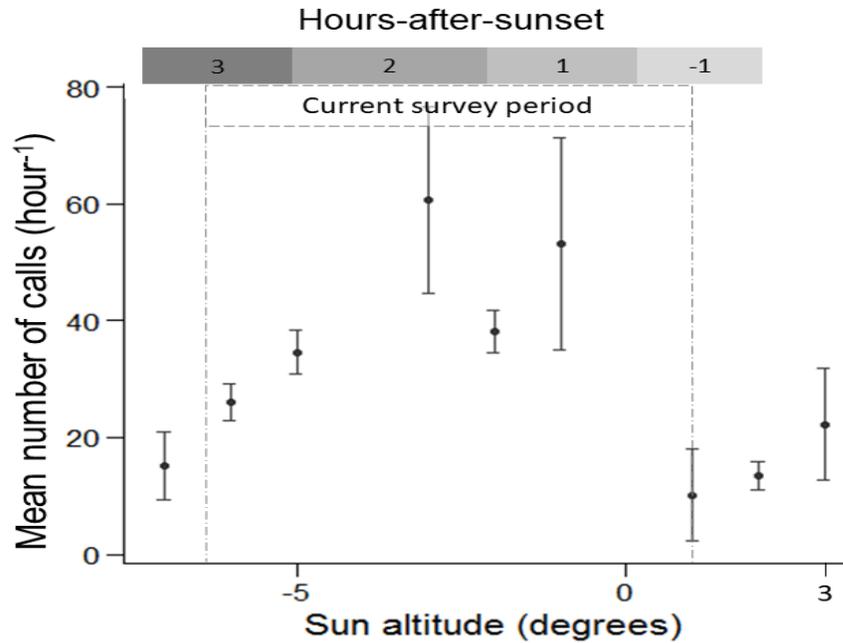


Figure 3.3 Evening nighthawk calling activity during early summer (7 June – 11 July) relative to sun altitude and hours-after-sunset. Data were collected in 2015 and 2016 at Snafu, Fox Lake and Grey Mtn ARUs. ARUs were programmed to begin recording one hour prior to sunset until one hour post sunrise. -1 represents one hour prior to sunset. No data were collected for sun altitude values of 0 and -4 degrees.

The interaction term between sun altitude and hour-after-sunset was significant in both early and late summer, indicating that nighthawk activity was affected by the combination of these variables (Table 3.3).

Table 3.3 Determinants of nighthawk calling activity during early (7 June – 11 July) and late (26 July – 8 August) light-periods in 2015 and 2016. Data were collected by three ARUs at Fox Lake, Snafu and Grey Mtn. Units were programmed to begin recording one hour before to sunset until one hour after sunrise. Each light-period was independently assessed using Model 1.

Model 1: tot calls ~ poly(sun altitude, 2) + hr-after-sunset + location + sun altitude:hr-after-sunset					
LightPeriod / (<i>n</i>)	Term	Coefficient	<i>S.E.</i>	<i>z</i> -value	<i>P</i> -value
Early (1373)	poly(Sun altitude, 2) ^{1,2}	17.20	5.63	3.06	<0.001
	Hour-after-sunset	-1.9	0.22	8.59	< 0.001
	Location	-0.21	0.08	-1.48	0.14
	Sun altitude:Hour-after-sunset	-0.17	0.02	-10.76	< 0.001
Late (580)	poly(Sun altitude, 2) ^{1,2}	39.87	8.48	4.70	<0.001
	Hour-after-sunset	0.43	0.20	2.17	0.03
	Location	-0.01	0.20	-0.03	0.97
	Sun altitude:Hour-after-sunset	-0.05	0.01	-3.11	0.002

In early summer, nighthawks called throughout the night, with sun altitude being the prominent predictor of activity (Figure 3.4). Birds were most likely to be active during the brighter part of civil twilight (sun altitude: -1 to -3 degrees), with activity declining at lower light levels (sun altitude < 5 degrees; Figure 3.4). When the sun was close to the horizon (sun altitude 0), birds were more likely to call after sunset than before sunrise (Figure 3.4).

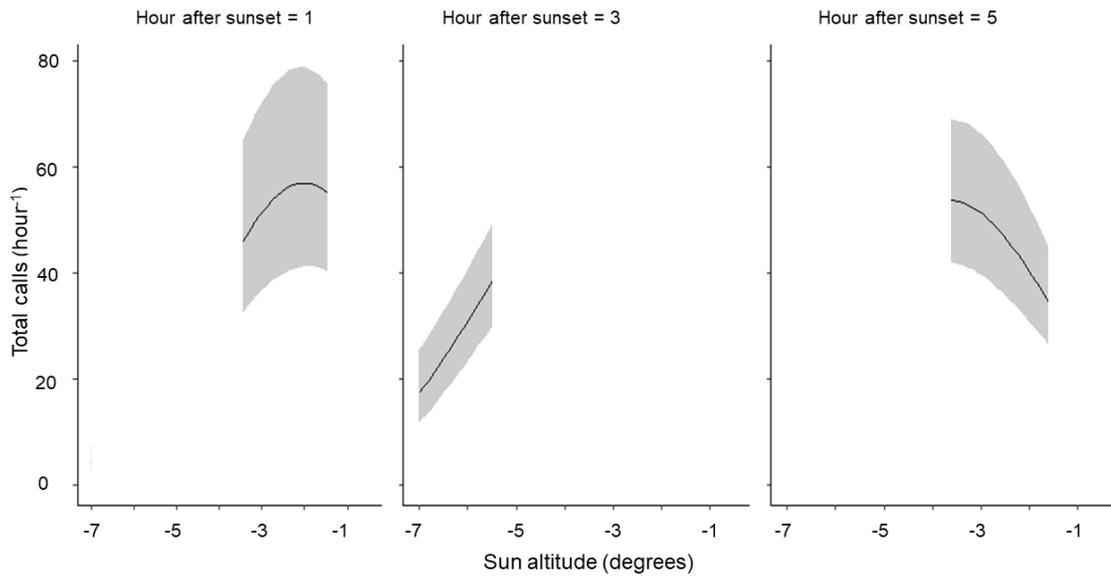


Figure 3.4 Interaction plots depicting call response to light (sun altitude) at different times of night ($\pm 95\%$ confidence intervals). Data were collected in early summer (7 June – 11 July) during 2015 and 2016 at three ARU sites (Fox Lake, Snafu and Grey Mtn). Civil twilight represents conditions when the sun is between 0 and 6 degrees below the horizon. Graphs are based on model predictions extracted from the ‘effects’ package (Fox et al. 2017).

While nighthawks called more actively in early summer than late summer, the overall calling patterns, relative to light conditions, remained similar between these light-periods (Figure 3.4; Figure 3.5). During late summer, nighthawks called during the brighter part of civil twilight (sun altitude: -2 to -3 degrees), regardless of time of night (Figure 3.5). Calling activity decreased considerably during nautical twilight (sun altitude: -7 to -12 degrees) and ceased entirely at the onset of astronomical twilight (sun altitude: -13 degrees; Figure 3.5). At the time of our study, the sun did not drop further

than 13 degrees below the horizon. Similarly to early summer, when the sun was close to the horizon (sun altitude 0), birds were more likely to call in the evening rather than in the morning (Figure 3.5). Relative to early summer (continuous activity), sun altitude appeared to have a greater impact on nighthawk activity later in the summer, as decreasing sun altitudes gave rise to darker conditions during which no nighthawks were detected.

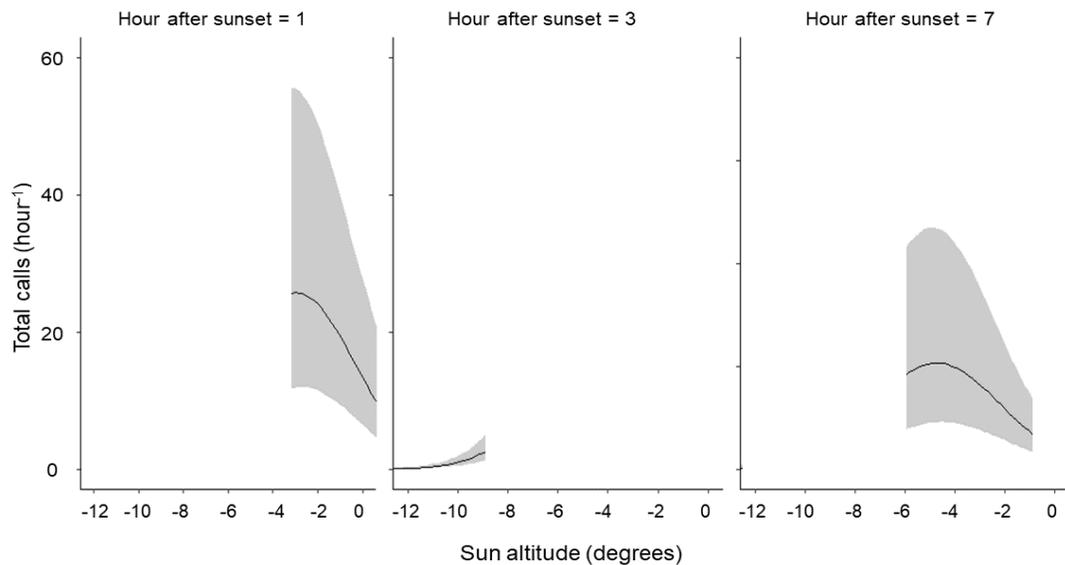


Figure 3.5 Interaction plots evaluating call response to light (sun altitude) at different times of night ($\pm 95\%$ confidence intervals). Data were collected in late summer (26 July – 8 August) during 2015 and 2016 at three ARU sites (Fox Lake, Snafu and Grey Mtn). Civil, nautical and astronomical twilights represent conditions when the sun is between 0 to 6 degrees, 7 to 12 degrees, 13 to 18 degrees below the horizon, respectively. No calls were detected when ‘hour after sunset = 5’, thus no graph is presented.

Seasonal calling activity --- Nighthawks were detected from 31 May – 13 August in 2015 and 3 June – 14 August in 2016. Between 2 June and 15 August in 2015 and 2016 (total recording nights, $n = 447$), the majority of nighthawk calls (96%) were detected in June and July, with only 4% of calls being detected in the first two weeks of August (Table 3.4). The 15 June – 15 July survey window suggested in the National Nightjar Survey Protocol (Knight 2016) captured just over half (57%) of the calling activity (Table 3.4). Nighthawk calling activity increased during the first week of June and remained elevated until approximately the first week of July (Figure 3.6).

Table 3.4 Percent of total nighthawk calls detected during two week intervals between 2 June – 15 August in 2015 and 2016. The percent of calls for each date range was calculated based on total calls throughout the summer. Data were collected at three ARU sites (Fox Lake, Snafu and Grey Mtn). The recording units were programmed to begin recording one hour prior to sunset and cease one hour after sunrise.

Date range (2015 & 2016)	Total calls detected	Percent of total calls
2 June – 15 June	10220	21%
16 June – 30 June	13942	30%
1 July – 15 July	13035	27%
16 July – 31 July	8773	18%
1 August – 15 August	1993	4%

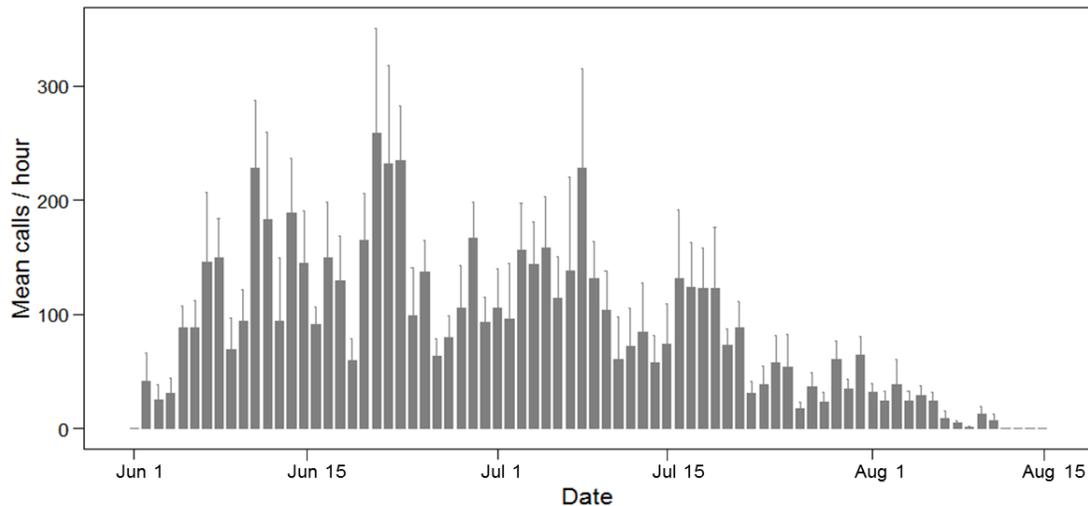


Figure 3.6 Mean number of nighthawk calls detected per hour (\pm standard error) between 2 June and 15 August in 2015 and 2016 at three ARU sites (Fox Lake, Snafu and Grey Mtn), thus each calendar night is represented by two years of data. Units were programmed to begin recording one hour before sunset until one hour after sunrise.

Calling activity relative to ambient light and temperature --- Nighthawks were detected at ambient temperatures between 3.5 – 21.1 degrees celsius and at light levels ranging from 0-3358 lux. The overall mean temperature and light values at our site were 11.0 ± 0.09 degrees and 418.3 ± 30.05 lux, respectively. The majority of call detections (76%; 262/345) occurred between 0-418 lux (min, mean respectively), with the mean temperature being 10.7 ± 0.10 degrees at the time of these calls. Additionally, 37% (127/345) of call detections occurred at zero lux (lowest light reading), with the mean temperature being 10.6 ± 0.25 degrees during these calls. A significant interaction between ambient light and ambient temperature indicated that the combination of both these variables influenced the probability of detecting a nighthawk call (hour^{-1}) (Table 3.5).

Table 3.5 Logistic regression model output exploring the effects of light and temperature on nighthawk calling activity between 7 June and 8 August in 2015 and 2016, at the Snafu ARU.

Model: call ~ temp + light + light:temp + light-period (n = 823 hours)				
Model Term	Estimate	S.E.	z-value	P-value
Temp	4.60x10 ⁻²	3.14x10 ⁻²	1.47	0.14
Light	-1.29x10 ⁻¹	4.28x10 ⁻⁴	-3.02	0.003
Light:Temp Interaction	9.01x10 ⁻⁵	3.40x10 ⁻⁵	2.65	0.008
Light-period	-7.14x10 ⁻¹	9.55x10 ⁻²	-7.48	<0.001

On colder nights nighthawks were more likely to call in low-light conditions, but on warmer nights they were more likely to call in brighter conditions (Figure 3.7). During bright conditions nighthawks were more likely to call at warmer temperatures (Figure 3.7 (b)). Overall, the highest probability of detecting a nighthawk call occurred under warm, bright conditions (Figure 3.7).

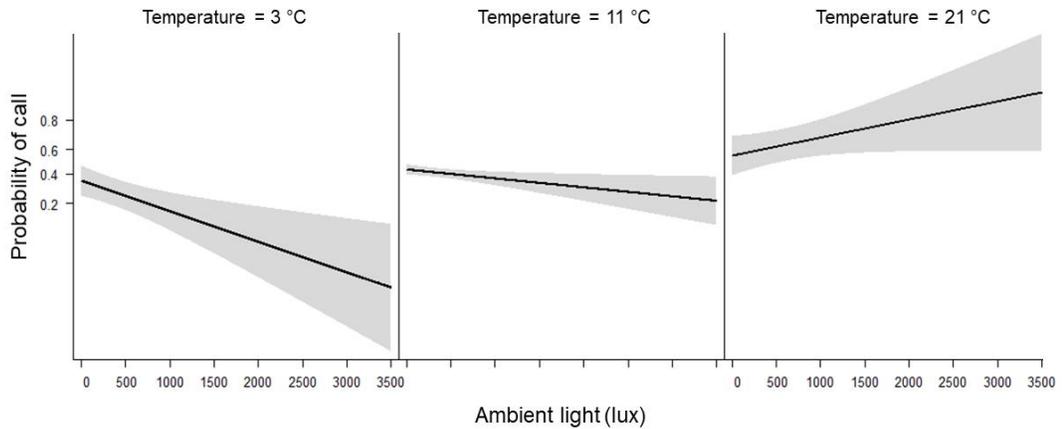


Figure 3.7 Interaction plot depicting nighthawk call response to light at different temperatures (min, mean, max) at the Snafu ARU between 7 June and 8 August in 2015 and 2016 (\pm 95% confidence intervals). Graphs are based on model predictions extracted from the ‘effects’ package (Fox et al. 2017).

3.4 DISCUSSION

Temporal variation in ambient light is an important predictor of biological activity patterns for organisms worldwide (Aschoff 1954). Given that the active period of crepuscular species is limited to just a few hours a day in most places (Mills 2008), we predicted that fluctuations in ambient light would have a pronounced effect on the activity patterns of crepuscular Common Nighthawks breeding in the northern boreal forest. We found that daily activity of nighthawks was influenced by a combination of time-of-night and ambient light conditions, with light conditions being the dominant predictor throughout the summer. Birds were most active for the duration of civil twilight (sun between 0 – 6 degrees below the horizon), particularly in the evening. Calling activity decreased during nautical twilight (sun 7 – 12 degrees below the horizon) and ceased at the onset of astronomical twilight (sun 13 degrees below the

horizon). As well, we found that on colder nights nighthawks were more active in low-light conditions, but on warmer nights, activity increased during brighter conditions. Seasonally, nighthawks called most between the first week of June and the first week of July. Considering the length of civil twilight remains fairly constant during this time period, we presume seasonal calling activity is dictated by a combination of ambient light and reproductive stage. Our results highlight the importance of considering temporal variation, as well as, life history when trying to understand and describe the activity rhythm of a species.

Daily calling activity --- As predicted, we found that sun altitude (indirect measure of ambient light) was a prominent predictor of nighthawk calling activity throughout the summer. We detected 87% of all calls when the sun was 1 - 6 degrees below the horizon. This suggests that 24 hr activity cycles of northern nighthawk populations are largely driven by the light conditions during civil twilight (sun 0-6 degrees below the horizon) and constrained by the onset of nautical twilight (sun 7-12 degrees below the horizon). The activity of more southern populations of nighthawks (i.e., southern British Columbia) is also thought to be constrained to civil and limited by the onset of nautical twilight (Aldridge and Brigham 1991). Our results indicate that despite the geographical separation, northern and southern populations respond to light conditions in similar ways. Given that nighthawks orient visually, we surmise that the ability to detect prey and obstacles is significantly reduced at low-light levels and thus illumination limits activity regardless of location.

During early summer evenings, when nighthawk surveys are conducted, nighthawks were most active approximately 0.5 – 3.0 hrs following sunset. This suggests that the current National Nightjar Survey Protocol (Knight 2016) which recommends a survey start time of 30 mins before sunset (survey duration: approximately 3 hrs) is appropriate for sampling northern nighthawk populations.

Overall, calling patterns in response to light conditions (sun altitude values) and time-of-night remained fairly constant between early (early light-period: 7 June – 11 July) and late summer (late light-period: 26 July – August 8), with nighthawk activity consistently reaching its peak during evening civil twilight periods. There is considerable seasonal variation in night-length over the course of the summer, and a greater range of light levels in late summer as nights grow longer and darker. Thus, nighthawks experienced darker conditions in late summer than during early summer. These seasonal (early vs late) discrepancies in light conditions likely account for the difference in activity we observed between early (continuously active) and late (decreased activity during dark conditions) summer.

Specifically, during early summer we determined that nighthawks altered their typical temporal pattern of calling only during the hours around sunset and sunrise (Poulin et al. 1996) to calling continuously throughout the night. During this time, the dark-night phase was replaced almost entirely by continuous civil twilight as the sun only dropped to 7 degrees below the horizon for one hour a night from 6 July – 11 July.

How animals adjust activity rhythms to changes in ambient light is not well understood. Responses appear to vary between species and among individuals (Steiger et al. 2013, Heurich et al. 2014, Agarwal et al. 2015, Nilsson et al. 2015). Depending on the

species, reproductive stage and sex, diurnal birds breeding during continuous Arctic daylight either maintain robust 24 hr activity cycles (pattern similar to 24 hr cycle), arrhythmic cycles (no pattern) or free-running activity cycles (pattern different from 24 hr cycle) (Steiger et al. 2013). For example, male Pectoral Sandpipers (*Calidris melanotos*) were arrhythmic all summer, whereas females exhibited arrhythmic activity until incubation commenced after which they exhibited entrained 24 hr cycle activity patterns (Steiger et al. 2013). It is also worth noting that large scale movement patterns of migrating passerines remained unchanged in terms of the timing of flight intensity peaks and the length of night-flights, despite continuous Arctic daylight (Nilsson et al. 2015).

While data on nocturnal species are relatively limited, Claretand and Anderson (1997) found that Boreal Owl (*Aegolius funereus*) calling activity peaked during extended periods of darkness at more northern latitudes. Additionally, true nocturnal nightjars are most active on brighter nights when the moon is full (Jetz et al. 2003, Ashdown and McKechnie 2008, Woods and Brigham 2008). Behavioral modifications to extended opportunities for activity by nocturnal and particularly crepuscular species may be more pronounced than for diurnal species, as their daily active period is limited. We propose that the crepuscular nature of Common Nighthawks, combined with the short breeding season at northern latitudes, best explains the continuous activity observed in early summer as individuals take advantage of increased foraging opportunities during extended periods of twilight.

In late summer, we also observed an influence of illumination on nighthawk activity. As nights grew darker, calling decreased considerably during nautical twilight

(sun between -7 and -12 degrees below the horizon) and appeared to stop entirely when the sun dropped further than 12 degrees below the horizon. We had expected that ambient light would be related to calling activity during late summer as shorter periods of civil twilight restrict the potential active hours of nighthawks compared to early summer. As discussed above, nighthawk's ability to navigate visually is thought to be constrained by light levels at the onset of nautical twilight (sun 7 degrees below the horizon). Our assessment of calling activity during late summer provides further support for this idea.

The interaction between sun altitude and time-of-night, suggests that at a given sun altitude (light condition), nighthawks tend to call more after sunset than before sunrise. Many diurnal songbirds participate in a phenomenon known as the "dawn chorus" (Catchpole and Slater 2008). The dawn chorus is a pronounced peak of bird song that takes place before sunrise (i.e., nautical and civil twilight) during the breeding season (Catchpole and Slater 2008, Bruni et al. 2014). The acoustic transmission hypothesis predicts that sound transmission is optimized under certain environmental conditions and that these conditions are related to both the surrounding environment (e.g., temperature, wind, background noise) and the sound source (e.g., frequency, complexity, height above receiver during communication attempt; Henwood and Fabrick 1979). Nighthawks may benefit from evening, rather than morning, communication attempts as acoustic interference from other songbirds (e.g., dawn chorus) will be greatly reduced during this time, thus allowing for increased call transmission (Henwood and Fabrick 1979).

In diurnal passerines, the dawn chorus plays an important role in mate choice and territory defense as song output (e.g., rate, duration, volume) is considered an honest signal of male quality (Zahavi 1975, Otter et al. 1997, Bruni et al. 2014). Having not fed overnight, energy reserves are typically most depleted at dawn for diurnal species (Catchpole and Slater 2008). Thus dawn singing, when temperatures are low, is considered to be energetically costly and a form of honest signalling. There is evidence to suggest that nocturnal species (Hardouin et al. 2008, Penteriani and Delgado 2009) have elevated song rates during the evening twilight period, thus effectively partaking in a dusk chorus. For these species, which do not forage during the day, dusk likely represents an energy-limited period. Thus, acoustic advertisement during evening twilight may be considered a reliable indicator of male quality for nocturnal as well as crepuscular species. While further research is needed to confirm this, the increased calling activity we detected during evening twilight suggests that nighthawks at northern latitudes may participate in a defined dusk chorus.

Aerial insect density, may also correspond with periods of increased nighthawk activity following sunset. The density of flying insects influences the activity of several nocturnal aerial insectivores including Freckled Nightjars (*Caprimulgus tristigma*; Ashdown and McKechnie 2008), Standard-winged Nightjars (*Macrodipteryx longipennis*; Jetz et al. 2003) and Australian Owlet-nightjars (*Aegotheles cristatus*; Doucette et al. 2012). Likewise, activity patterns of insectivorous bats, some of whom forage in open habitats similar to nighthawks, also respond to flying insect abundance (Mueller et al. 2012). Time of night is important for activity of many insect species, including Lepidopterans and Coleopterans (which nighthawks regularly consume; Poulin

et al. 1996), as peak flight times are limited to the hours around sunset (Csabai et al. 2012, Turner 2013). Thus, the availability of prey, influenced by time-of-night, is likely also an important determinant of nighthawk activity.

The primary limitation of using sun altitude as a proxy for ambient light is that site specific light variations due to weather variables (e.g., cloud cover, precipitation) are not accounted for. Our discussion must be interpreted in this context.

Seasonal calling activity --- We found that nighthawks called actively throughout the summer. This is an uncommon pattern amongst birds as song rates typically decrease after pairing (Catchpole and Slater 2008). We recorded high calling activity beginning the first week of June until approximately the first week of July. We suspect the extended twilight hours of early summer in the North enable nighthawks to remain active throughout much of the night and thus light availability is likely a contributor to the higher calling rates detected over this early summer period. However, calling began to decrease during the first week of July before civil twilight became significantly shorter (difference in civil twilight length 7 June – 7 July: 23 mins) suggesting that the activity patterns we observed are not reflective of just temporal changes in light availability.

Reproductive status is linked to vocal activity in many bird species (Pinxten and Eens 1998, Staicer et al. 2006, Amrhein et al. 2008). Generally, song rates reach a peak in early spring as males use song to defend territories and to attract mates (Slagsvold et al. 1994, Amrhein et al. 2008, Catchpole and Slater 2008). Male nighthawks establish breeding territories which they actively advertise to females upon arrival in the spring. Given that nest initiation (egg laying) in the Yukon is estimated to take place about the

second week of June, elevated calling rates during the first part of June may be partially attributed to males aggressively advertising for mates and defending territories against other males.

In contrast to other socially monogamous songbirds, where singing rate typically subsides following the establishment of breeding pairs (Kunc et al. 2007, Amrhein et al. 2008), we detected the highest percent of calls (30% - based on dividing the summer into two week intervals) from 16 June to 30 June, after pairs had likely formed. Changes in light conditions are unlikely to explain this behavior as twilight length varied only minimally between early and late June. Females spend the majority of this time incubating; therefore elevated detection of calls suggests that male calling rate increased after nesting commenced. High song rates following nest initiation may be beneficial in instances where males seek extra-pair copulations (Sexton et al. 2007). Nighthawks lay 2 eggs, 1-2 days apart and rarely have a second clutch (Poulin et al. 1996) leaving only a short window for extra-pair copulations between egg laying, while females are presumably most fertile (Barber and Robertson 2007, Bruni and Foote 2014). Sperm storage occurs when females are able to retain viable sperm, potentially from multiple mates, and then rely on sperm-competition (or other mechanisms) for ovum fertilization (Kleven et al. 2009). If female nighthawks are capable of sperm storage, which is common in birds (Briskie 1996, Barber and Robertson 2007, Kleven et al. 2009), then it is possible that increased calling during this early period may, in part, be explained by male competition for extra-pair copulations. Further, incubating female nighthawks rely strictly on camouflage for protection and thus are not able to maintain visual contact with males. Another potential explanation for the increased number of calls during incubation

may be that males are calling as a signal to convey his location (maintains pair bond) and to communicate to the incubating female that no predators are nearby. Support for the “all-clear” incubation song hypothesis has been reported for several species (Johnson and Kermott 1991, Wingelmaier et al. 2007), including in Song Sparrows which, like nighthawks, nest on the ground and may use vocalizations to maintain contact between partners (Foote and Barber 2009).

Despite little variation in twilight length (23 mins), nighthawk calling activity declined during the first week of July. Assuming that our estimates of Yukon breeding phenology are accurate, this corresponds approximately to the timing of hatching. A decrease in song output following hatching was also reported for Eastern Phoebe (*Sayornis phoebe*; Bruni and Foote 2014). These authors observed that song bouts were longer during pre-breeding and incubation stages than when feeding nestlings. Likewise, in Northern Mockingbirds (*Mimus polyglottos*) song activity was lowest during the nestling stage (Catchpole and Slater 2008). One explanation for why call detection may decrease during this stage is that the time and energy demands of feeding nestlings decreases the time available for vigilance and calling.

Activity relative to ambient light and temperature --- The effect of ambient temperature on nighthawk calling activity was contingent on ambient light conditions. During low-light conditions nighthawks called more when it was colder; during brighter conditions they were more likely to call at higher temperatures. We detected the highest percent of calls during light levels associated with times after sunset (0 to ~400 lux) rather than during brighter, warmer conditions as predicted by our model. Our ARU recording

schedule likely accounts for this finding. The ARU was scheduled to start recording one hour before sunset until one hour after sunrise thus collecting the majority of data during either twilight or night (a low-light window) without equal representation for brighter, daylight conditions ($> 10,000$ lux), which we documented only once. Based on the crepuscular nature of nighthawks (Poulin et al. 1996), and on our observations in the field, we surmise that had we recorded data over a 24 hour solar cycle (unbiased data), calls would have decreased under bright, day light conditions regardless of temperature.

Within the low-light window targeted by our study, nighthawks called more during warmer, brighter conditions. Higher activity on brighter nights is a well documented pattern for other North American (Woods and Brigham 2008, Cink et al. 2017) and African (Jetz et al. 2003, Ashdown and McKechnie 2008) nightjars. Foraging efficiency of nocturnal nightjars is elevated on brighter nights when insect prey is more visible (Csada and Brigham 1992, Jetz et al. 2003, Woods and Brigham 2008, Doucette et al. 2012, Cink et al. 2017). Furthermore, studies suggest that aerial insects increase in abundance during warmer (Jetz et al. 2003, Gruebler et al. 2008) and brighter (Gruebler et al. 2008) conditions. Therefore, we argue that capturing prey becomes easier on warmer, brighter evenings for visually orienting nighthawks and that this might explain the positive relationship we detected between these conditions and calling activity.

The activity times of southern populations are thought to be limited by both ambient light and temperature (Poulin et al. 1996, Ministry of Environment-Lands and Parks Resources Inventory Branch 1998) therefore the detection of more calls at colder temperatures, during low-light levels was unexpected. As discussed previously, the acoustic transmission hypothesis predicts that sound transmission is optimized under

certain environmental conditions and that these conditions are related to both the surrounding environment and the sound source (Henwood and Fabrick 1979). One potential explanation for increased calling during low-light and cool temperatures might be that the sound transmission of nighthawk calls is optimized under these conditions. Relative to southern conspecifics, northern populations are presumably adapted to cooler climates by traits which can include dense plumage (Koskenpato et al. 2016), large body sizes (Bergmann 1848) and shortened extremities (Allen 1877) to decrease heat loss. We argue that the benefits of potentially broadcasting calls over greater distances may outweigh the metabolic costs of sustained activity at lower temperatures (Maggini and Bairlein 2013) for nighthawks in our study area.

Nightjar activity is constrained by light and subtle differences in ambient light including presence/absence of the moon (i.e., change of 0.05 lux) and varying degrees of cloud cover can result in activity modification (Jetz et al. 2003, Ashdown and McKechnie 2008, Woods and Brigham 2008). Thus, the high percent of calls we detected at 0 lux must be interpreted with caution as light was recorded in increments of 10 lux. While the 10 lux scale generally depicts the overall relationship between light and nighthawk activity, the scale is too coarse to estimate the minimum light threshold at which nighthawks can remain active. Calls detected below five lux would have been documented as occurring at zero lux, giving the impression of continuous nighthawk activity in complete darkness (i.e. zero lux) rather than showing a decrease in activity as expected. Considering the sensitivity that nightjars exhibit toward ambient light levels, assessing light levels at a finer resolution are required to determine the threshold for nighthawk activity.

The use of ARUs for avian population monitoring is becoming increasingly popular as it allows a single researcher to gather large amounts of data during one field season (Colbert et al. 2015). One constraint of working with ARU data is the inability to distinguish whether recordings are of the same individual calling repeatedly or of multiple individuals calling once. However, acoustic data from ARUs do allow for the ability to generate an index of relative calling activity which can be used to understand activity patterns. Considering that ARUs have been successfully used to study birds (Sidie-Slettedahl et al. 2015), bats (Hecker and Brigham 1999), amphibians (Acevedo and Villanueva-Rivera 2006) and marine mammals (Sousa-Lima et al. 2013), we believe that these kinds of data represented an appropriate approach for addressing our research questions.

3.5 MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Our results have implications for monitoring nighthawks in the North. The newly developed National Nightjar Survey Protocol (Knight 2016) recommends surveying for nighthawks from 15 June to 15 July, with surveys beginning 30 mins before sunset and lasting for approximately 3 hrs. We found that slightly over half of all calls (57%) were detected during the proposed survey window and that during this time, evening calling was highest between 0.5 – 3.0 hrs after sunset. Based on these data, we conclude that this protocol is an appropriate survey tool and should be used without modification to survey for nighthawks at latitudes north of 60°.

Further attempts to explain nighthawk activity patterns should be directed towards understanding activity in relation to aerial insect abundance. A leading hypothesis for

nighthawk population declines (and indeed all aerial insectivores) is thought to be changes in insect communities along migratory routes as a result of insecticide use (Environment Canada and McKnight 2016). Understanding foraging behavior in the summer could not only help us better understand 24 hr activity cycles but could also help identify important insect prey groups to protect along nighthawk migratory routes.

Future research in the North should investigate the biological implications of the extended period of activity during early summer, particularly in the context of reproductive output and how it compares to that of southern populations. If nighthawks in the North have higher reproductive success than in the South, then these populations should be the focus of future conservation efforts.

3.6 LITERATURE CITED

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4.0 SUMMARY

4.1 GENERAL CONCLUSIONS

Understanding habitat associations is important for conservation efforts as species space use patterns, abundance and distributions are largely driven by the prevalence of suitable habitat conditions at any one time in a given geographical area (Watts 1991, Lombardi et al. 2003, Ye et al. 2013). Despite the northern boreal forest representing a significant portion of the breeding range of Common Nighthawks, populations in these areas remain virtually un-studied and thus poorly understood. Understanding patterns of space use and habitat associations of these birds across all environments is relevant and timely as in 2007, the species was listed as Threatened in Canada due to data from southern locations indicating steep declines in numbers (COSEWIC 2007). COSEWIC (Committee on the Status of Endangered Wildlife in Canada) is currently re-assessing the status of the Common Nighthawk. New insights into the life history of these birds will allow for more informed decisions about the conservation status of this species in Canada. Thus, in an effort to gain a better understanding of space use patterns, I evaluated habitat associations of Common Nighthawks in the northern boreal forest from both a spatial and temporal perspective. My study is among the first to explore activity patterns and habitat associations of nighthawks in the boreal forest using survey methods specifically targeting this species.

From a spatial perspective, my objective was to evaluate habitat associations of breeding nighthawk populations in the northern boreal forest by assessing abundance relative to forest age (landscape scale) and vegetation characteristics (territory scale).

From a temporal perspective, my goal was to inform the timing of future sampling efforts by investigating how seasonal fluctuations in ambient light and temperature impact the daily and seasonal activity patterns of breeding nighthawk populations throughout the summer.

In chapter 2, I focus on describing the abundance of, non-breeding and breeding, nighthawks in the northern boreal forest relative to spatial habitat attributes at multiple scales. At the landscape scale, I found that forest age was a predictor of relative nighthawk abundance, with the highest number of detections occurring in forests less than 20 years old. At the territory scale, nighthawks were negatively associated with increasing tree canopy cover and low shrub cover, for all forest ages. I found that wing-booming males (which are indicative of breeding habitat) exhibited the same abundance trends relative to vegetation variables as calling nighthawks overall, suggesting that both breeding and non-breeding activities are concentrated in proximity to open habitats. I argue that the reason nighthawks select more open, recently burned habitats may be explained by increased foraging and nesting opportunities as well as the likely decrease in small mammal predators typically associated with open areas. I conclude that breeding populations of nighthawks are associated with early successional, post-fire habitat in the northern boreal forest because they are readily able to exploit and take advantage of the unique combination of resources that this habitat provides. Further, my results suggested that moon phase and temperature both impact the daily activity of nighthawks across the study area. More nighthawks were detected on point counts conducted at colder temperatures and on brighter nights. We found that nighthawks are common in the northern boreal forest. We detected birds on 19 out of 20 survey routes and recorded

consistently high relative abundances in forests under 20 years of age (>1.5 individuals per point count). Further research is needed to confirm that populations in these areas are not declining; however our findings are highly encouraging in light of the Common Nighthawks 'Threatened' conservation status (COSEWIC 2007). Given the overall association of nighthawks with early post-fire habitats, I recommended that, in consideration with other factors (e.g., social, economic), land managers should allow naturally triggered fires to burn, as natural fire regimes are likely crucial to maintaining a habitat matrix with ample open habitat for breeding Common Nighthawks.

In Chapter 3, I evaluated the activity patterns of nighthawks in the northern boreal forest in the context of changing photoperiod (light availability) and temperature. I concluded that temporal variation in ambient light and temperature are predictors of calling activity. Over the evening-night time window, during low-light conditions birds tended to call more at low temperatures, however during brighter conditions they were more likely to call at higher temperatures. Daily activity rhythms of northern nighthawks appear to be regulated by a combination of light conditions and time-of-night, although overall ambient light appeared to be the primary predictor of activity. Calling activity was highest during the evening civil twilight period and ceased when the sun dropped further than 12 degrees below the horizon. Additional factors related to time-of-night (e.g., temporal prey distribution, dawn chorus) may also play a role in dictating nighthawk calling patterns. Seasonally, peak calling activity occurred between the first week of June and the first week of July. I speculated that seasonal activity by nighthawks at northern latitudes is governed by a combination of civil twilight length and reproductive stage but that further research on breeding phenology is necessary to draw

more firm conclusions. These relationships highlight the importance of temperature and light availability on the temporal space use patterns of Common Nighthawks in the North. Based on my overall findings, I recommended that the National Nightjar Survey Protocol (Knight 2016) be used, without modification, to survey for nighthawks at northern latitudes as the survey period put forward in this protocol captures the times of peak calling and therefore is suitable for accurate population monitoring.

The importance of relating distributions and space use patterns of species to spatial habitat attributes is well documented and considered an integral component of understanding what habitats species are associated with (Wiens 1989, Block and Brennan 1993, Price et al. 2013). My results are in agreement with these previous studies, as my data indicate that nighthawks respond to spatial habitat attributes (e.g., vegetation structure) at both the landscape and territory scale. Additionally, my research substantiates the suggestion that temporal variability in an environment is important when examining a species pattern of space use (Block and Brennan 1993, Price et al. 2013, Steiger et al. 2013, Digby et al. 2014). Thus, when possible, I recommend that temporal variables be included in studies examining habitat associations.

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