Migratory behaviour of Eastern Whip-poor-wills (*Antrostomus vociferus*): quantifying return rates and the effects of artificial light on flight paths

By

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Abstract

Migration poses significant challenges for organisms, especially those traveling long distances. It is hypothesized that despite these challenges, migration evolved as a method of resource maximization and competition reduction. Along with morphological adaptations, species often develop life history traits in complement with their migratory habits. Urbanization and artificial light have further complicated migration patterns for many species. This thesis was aimed at addressing gaps in our understanding of the life history of the Eastern Whip-poor-will (*Antrostomus vociferus*) in relation to their migratory behaviour and to determine the impact of artificial light on their migratory routes. I captured whip-poor-wills at their breeding locations in southern Manitoba and north-western Ontario and used direct-tracking technologies (archival GPS units; radio telemetry tags) to collect data on timing, routes, and return rates. I used the resulting migration tracks and Bayesian generalized linear models to test for an effect of artificial light levels on route tortuosity along fall migratory pathways. I found that whip-poor-wills took more indirect flight paths on nights when a direct path would result in exposure to more intense artificial light, suggesting they sacrifice efficiency for light avoidance. Next, I used 6 years of capture data, a displacement experiment, and automated radio-telemetry to quantify recapture rates and site-fidelity at breeding territories. I found evidence for high survival rates and site fidelity: annual recapture rates ranged from 50 – 80% and average recapture of birds on the same territory in subsequent years was 75%, 75% of birds returned after displacement, and 90% of radio-tagged birds survived to be detected by receiver towers along the spring migratory routes in the year following tagging birds. Since whip-poor-wills have a longer than average life span and lower annual clutch sizes for a small migratory land bird, my results showing high site fidelity and return rates align with predictions based upon these traits. My results demonstrating sensitivity to artificial light and high site fidelity could be incorporated into conservation and management planning for this threatened species.

Table of Contents

List of Tables

List of Figures

Acknowledgements

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I would also like to thank the Nature Conservancy for allowing us to access properties where whip-poor-wills were trapped for this study. Thank you to Diane and Keith Hill who allowed me to stay on their beautiful property in Kenora, Ontario while completing this work. I would also like to thank the Ontario Ministry of Natural Resources office in Kenora for all the assistance they provided to this project.

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Chapter 1: General Introduction

While there are many hypotheses as to the evolution of migration in birds, the most accepted theories include the push of escape from competition at tropical latitudes and the pull of a flush of seasonal resources that occurs in spring in temperate locations (Cox 1968, 1985; Levey and Stiles 1992, Alerstam et al. 2003, Newton 2008a, Winger et al. 2019). Migration and avian flight in general are very energetically taxing and migration has been shown to cause higher levels of mortality than other parts of the annual cycle of avian species (Alerstam and Lindstrom 1990, Sillett and Holmes 2002, Klaassen et al. 2014). With the increasing urbanization of human populations, migration has become an even more dangerous prospect (Bairlein 2016). Not only do humans create physical obstacles that can disrupt flight paths and cause direct impact and fatalities (Bairlein, 2016; Loss et al., 2014, 2015), we create artificial light sources that can disrupt many physiological processes and can alter migration paths by drawing birds towards them (Verheijen 1958, Gauthreux and Belser 2006, Sanders et al. 2020).

Bird mortality and species decline have been garnering attention in recent years as it has been shown that close to 3 billion birds have been lost in North America alone since the 1970s (Rosenberg et al. 2019). While certain genera that have received special conservation attention such as raptors and waterfowl have shown increases in this time frame, other groups have seen steep declines in population levels (Anon 2019; Rosenberg et al. 2019). One such group is aerial insectivores, which have seen a 69% decrease in numbers across Canada alone and a 73% decrease in across North America (Anon 2019; Rosenberg et al. 2019). This decrease, as with most, is likely driven by multiple factors but has been inferred to be primarily due to insect prey declines and habitat loss (Nebel et al. 2010, Spiller and Dettmers 2019). Insect prey declines also have many influencing factors but are mainly related to agricultural pesticide use and habitat destruction (Wagner 2019).

The Eastern Whip-poor-will (*Antrostomus vociferus*, hereafter referred to as 'whip-poor-will') is an aerial insectivore whose populations have been steadily declining across its entire breeding range (Pardieck et al. 2020, Cink et al. 2020). Whip-poor-wills are a neotropical migrant and seasonally alternate between breeding sites in southern Canada and the northern United States and overwintering sites in Central America (English et al. 2017a, Korpach et al. 2019, Tonra et al. 2019, Cink et al. 2020). Populations from Southern Ontario, for example, migrate up to 4500 km during fall migration to their overwintering sites in Costa Rica (English et al. 2017a, Korpach et al. 2019).

The habitat requirements of whip-poor-wills include a mix of moderate canopy cover as well as a low density of the understory for nesting, and open areas for foraging (Tozer et al. 2014, Akresh and King 2016, English et al. 2017b, Spiller and King 2021, Thompson et al. 2022). Whip-poor-wills have been positively associated with areas of forestry activity and burned stands, which has caused many to view them as disturbance specialists (Wilson and Watts 2008, Akresh and King 2016, Farrell et al. 2017, Spiller and King 2021). Recent work by Korpach et al. (manuscript in prep.) has identified a variable home range size that varies between around 7 to 136 hectares with weak associations to habitat characteristics such as density of conspecifics, nearby wetlands, and the density of forest edge habitat.

The declines in populations of whip-poor-wills caused the species to be listed as threatened by the Committee for the Status of Endangered Wildlife in Canada (COSEWIC) in 2009 and in the Species at Risk Act in 2011 (COSEWIC 2009, Environment and Climate Change Canada 2018) though in 2022 the species was downlisted to special concern status. Whip-poor-wills are also still listed on the IUCN Red List as near threatened (BirdLife International 2021). Across multiple provinces and states, whip-poor-wills are listed as either threatened or special concern including most eastern provinces (including Manitoba), and northern states such as Vermont, and New York(NYS Department of Environmental Conservation 2014, Vermont Center for Ecostudies 2020, Environment and Energy Ontario 2023, Government of Nova Scotia 2023, Natural Resources and Northern Development Manitoba 2023, NB

Canada Natural Resources 2023) . The whip-poor-will is crepuscular or nocturnal in habit (Mills 1986, Cink et al. 2020). Due to their nocturnal habit and camouflage this species is considered cryptic and has been poorly studied until recently (Slover and Katzner 2016, English et al. 2018, Cink et al. 2020).

The poorly studied nature of whip-poor-wills leaves any improvement to their conservation status in question as there is no way to know whether populations are recovering without proper background information and monitoring. For example, in the recovery strategy for whip-poor-wills, 3 of the 4 items in the feasibility summary are listed as "Unknown" (Environment and Climate Change Canada 2018). These items are related to the amount of habitat available, the threats faced by whip-poor-wills, and the existence of techniques that can aid in recovery of the species. Any areas where data and information gaps can be filled will therefore have an outsized impact in assisting with conservation and management plans for this species. Identifying baseline population levels and rates of return as well as areas of concern and potential improvement can assist in policy and management decisions for the future of this species.

My thesis was aimed at providing evidence towards a better understanding of the life history and behaviour of the Eastern Whip-poor-will. My main thesis objectives are to expand on existing studies that examine migratory decisions in the face of anthropogenic disturbance (Chp 2) and to demonstrate the propensity of individuals to navigate back to territories they have previously occupied (Chp 3). I also provide a concluding chapter (4) that summarizes the main results of both data chapters and considers them collectively to identify unresolved questions and make recommendations for further research.

Chapter 2: The impact of artificial light on the nocturnal migratory behaviour of the Eastern Whip-poor-will

Abstract

Artificial light at night (ALAN) has been identified as a driver of behavioural change in many avian migratory species, influencing timing, pathways, and stopover habitat use. Nocturnal birds may be most sensitive to ALAN during their migrations owing to their adaptations for moving and foraging in darkness. We predicted that the flight paths of Eastern Whip-poor-will (*Antrostomus vociferous*) would be influenced by ALAN encountered during their fall migrations. We installed archival GPS tracking tags on whip-poor-wills at their breeding grounds in Manitoba and Ontario. We programmed the tags to collect points every 2 hours for the duration of each bird's fall migration to overwintering sites in Central America. We retrieved 18 tags with useable data and measured flight path tortuosity (straightness) in relation to artificial light levels encountered over full routes and on nightly flights between stopover locations. We found that the tortuosity of nightly flight paths increased when birds would have encountered more light on (simulated) direct paths, suggesting birds took more indirect routes to avoid artificial light. At the full track scale, there was no effect of artificial light levels on the tortuosity of flight paths, indicating a scale-dependent effect of artificial light on migratory paths. Further research should investigate how additional environmental factors such as habitat, wind, or physical structures may also contribute to flight path selection in whip-poor-wills and other nocturnal migrants.

Introduction/Background

As human populations have expanded and urbanized, light pollution has followed suit (Cinzano et al. 2001). The term ecological light pollution has been coined to describe light pollution that not only disturbs the view of the night sky but has wide-ranging effects on wildlife and ecosystems (Longcore and Rich 2004). Artificial light at night has been identified as a driver of behavioural change in many species (Bolshakov et al. 2013, Ouyang et al. 2017, McLaren et al. 2018, Smith et al. 2020, Sanders et al. 2020, Bani Assadi and Fraser 2021). It has been shown in many cases to impact physiological processes in avian species (Ouyang et al. 2017, Sanders et al. 2020, Aulsebrook et al. 2021).

Light can often have a trapping effect, where birds and other animals are drawn towards it (Verheijen 1958, 1981; Gauthreux and Belser 2006, Bolshakov et al. 2013, Van Doren et al. 2017). This is especially dangerous for nocturnally migrating avian species and has been well documented as having caused mass fatalities and may increase the energy expenditure required for migration if birds are drawn from their original course (Verheijen 1981, 1985; Gauthreux and Belser 2006, Van Doren et al. 2017). Mclaren et al. 2018 showed that artificial light alters stopover densities and locations and suggested that birds may spend longer searching for suitable stopover habitat with increased artificial light, thus expending more energy (Mclaren et al. 2018). Migrating passerines also altered their flight paths to be more curvilinear in response to coastal vertical light beams (Bolshakov et al. 2013).

Birds that are primarily nocturnal in nature have specialized eye structures that allow them to hunt and forage more effectively at night (Rojas et al. 1999, Beckwith-Cohen et al. 2015, Potier et al. 2020). Eyes that must primarily see at night have much higher sensitivity to light than those evolved to see during the day (Warrant 1999). Indeed, Nicol and Arnott (1974) report that the eyes of nightjars are highly sensitive due to elongated rods and a tapeta lucida which allow for increased reflection and absorption of light at the retina (Zynar and Ali 1975). Owing to these differences, nocturnal birds may have a different response to artificial light at night than diurnal species. Since light pollution can alter habitat use in avian species (Ouyang et al. 2017, McLaren et al. 2018), it can also effectively change the habitat itself. Sierro and Erhardt (2019) found that the European Nightjar (*Caprimulgus europaeus*) abandoned breeding sites with higher illumination from artificial sources. This observation suggests that artificial light harmfully alters breeding habitat for nocturnal species of this kind and can prevent breeding altogether if it is extreme enough (Sierro and Erhardt 2019).

Many variables factor into decisions made by birds while they are migrating (Alerstam and Lindstrom 1990). Since migration requires a great amount of energy (Butler and Woakes 1990), these variables typically relate to energy efficiency and include trade-offs depending on the condition and size of the bird, and the time of year (Alerstam and Lindstrom 1990, Nilsson et al. 2013, La Sorte et al. 2014). Korpach et al. (2019) showed that a nocturnal species, the Eastern Whip-poor-will (*Antrostomus vociferus*), does not migrate during the day, suggesting that they may need to avoid daylight during migration due to the sensitivity of their visual system that is adapted to darkness. There is also evidence that whip-poor-wills select for dark sky connectivity while on their migratory routes as well as dark, rural stopover areas (Korpach et al. 2022b). Given the at-risk status of whip-poor-wills and the existing evidence for alteration of their migratory routes due to artificial light, it is pertinent to further determine its effects on this species.

Tortuosity refers the amount of bendiness or entropy in a pathway, or rather the lack of straightness (Benhamou 2004). Many measures of tortuosity exist with differing amounts of mathematical complexity needed to calculate them (Batschelet 1981, Katz and George 1985, Benhamou 2004, Almeida et al. 2010, Shepard et al. 2013). Measures of tortuosity are important in movement analysis because the straighter a path is, the more efficient it should be (Benhamou 2004).

We examined the migratory paths of whip-poor-wills on multiple scales to determine whether there was an effect of artificial light on the straightness of the birds' paths and at what scale this might be occurring. We believed that artificial light would influence the tortuosity of flight paths of Eastern Whip-poor-wills and predicted that as the amount of artificial light occurring in the most efficient straight-line pathway of the birds increased, the straightness of those paths would decrease. We also predicted that this would occur on both a nightly scale (stopover to stopover) as well as across the entire migration route of whip-poor-wills.

Methods

Field

We captured whip-poor-wills (n = 47) at their breeding territories in southern Manitoba, north-western Ontario, and southern Ontario (Figure 2.1) during the breeding seasons of 2018-2020. Only adult male birds were selected for the experimental procedure due to their increased reactivity to song playback and territoriality as compared to females. Birds were captured using mist nets and a song playback lure. Birds were fitted with archival GPS tags (NanoFix Mini; 2g, PathTrack Ltd., Otley, UK) using 0.75mm Teflon cord leg-loop harnesses (Rappole and Tipton 1991). Birds were recovered using the same methods in the following breeding season, and tags were removed for data harvesting and analysis.

Flight Path Quantification

Data was extracted from the GPS units using Pathtrack Host software (Pathtrack Ltd. 2018). To examine the tortuosity of the flight paths in as much detail as possible, we used only tracks that contained points taken at a high intensity interval (every 2h). This resulted in a total of 18 fall migration paths; 17 full and 1 partial, where some of the data were corrupted. The paths we collected from the GPS tags were verified, stopovers were identified, and missed point fixes were removed using GIS (Geographic Information System) software (ArcGIS Pro 2.6.3). We made centroids from each collection of stopover fixes so that only migratory flights would be included in our analysis. Short foraging flights at stopovers would inherently be more tortuous and bias results. Since whip-poor-wills fly around rather than over the Gulf of Mexico (Korpach et al. 2019), any points taken below 30°N latitude were excluded from the trajectories to eliminate potential bias owing to this large obstacle that birds must avoid (i.e. increasing tortuosity values as birds fly around this barrier). We then processed the paths into flight trajectories using the *trajr* package (version 1.4.0) in R statistical software (version 4.2.2) (McLean and Volponi 2018). The result was 18 flight trajectories (Figure 2.2).

From these trajectories, we quantified the flight path tortuosity in the form of a straightness index, which is defined as the straight-line distance between the start and end points divided by the distance traveled (Batschelet 1981, Benhamou 2004). This measure of tortuosity results in a ratio increasing from 0 to 1 as the birds fly in a straighter line. Distance was measured between each 2 hour point and summed between the stopover intervals as well as the full track. We chose this measure of tortuosity based on the simplicity of measurement as well as the applicability to our study and our measure of artificial light intensity. To evaluate the scale at which flight decisions are made in this species, we calculated both the straightness of the entire trajectory as well as nightly segments between stopovers. Any straightness values equal to 1 were removed as they indicated missed fixes between stopovers.

Impact of Light Pollution on Flight Paths

We obtained light intensity data from the National Oceanographic and Atmospheric Association's Earth Observations Group (Elvidge et al. 2017). The data consist of an annual composite of nighttime images from the Visible Infrared Imaging Radiometer Suite Day/Night Band. This data is set at a pixel resolution of 750m and corrected for stray and ephemeral light, outliers, and clouds. The radiance values are measured in nanoWatts/cm/sr and multiplied by 1E9 to ensure a usable scale for testing and software compatibility.

We created linear buffers of 20 and 40 kilometres on each side of each flight trajectory to examine the level of light birds are exposed to. These buffer sizes were chosen based on analyses done by Korpach et al. (2022), where birds were found to select for dark skies at the 20 to 40 km scale. Light data was overlain with the buffers (Figure 2.3) and mean light intensity values within the buffer constraints were extracted using the *terra* (version 1.7-29) R package (Hijmans et al. 2023). Hypothetical straight-line flight paths were created between stopovers and subjected to the same procedure to obtain the mean light intensity that birds would have encountered on the most efficient pathway from stopover to stopover. Light values were averaged on a segmental scale consisting of the values encountered on nightly flights from stopover to stopover as well as on the scale of the full track from the northernmost point to the final point prior to 30N latitude, as was calculated for the tortuosity measure.

We created a light ratio from the mean straight-line light values divided by the mean used (actual) light values to show the relative amount of light that birds are assumed to be avoiding by choosing a path that is not completely straight (Figure 2.4). This value also directly relates to the tortuosity measure we selected, as both variables are measures of the straight pathway relative to the used pathway.

Statistical Analysis

We used a generalized linear mixed model (GLMM) to analyse data on the nightly segment scale. We used the straightness index as a dependent variable and the light ratio as a fixed explanatory variable, individual ID was used as a random effect variable to account for the multiple measures at this scale. The slope of the random effect was allowed to vary so that birds would be considered independently of each other. Other random effects were considered such as year, and population grouping but were ultimately ruled out given their lack of effect on the results.

We used a generalized linear model (GLM) to analyse data on the full track scale. Again, the straightness index was used as the dependent variable and the light ratio was the explanatory variable. There were no random effects to consider in this analysis as there was only one mean value of the variables for each bird. To test for the potential of a non-linear relationship, polynomial models were considered for both scales as well.

The models were run using Bayesian inference in the brms (version 2.19.0) R package (Bürkner 2021). Bayesian inference was chosen due to the small sample size of the study (n = 18) and the robustness of this style of analysis to small sample sizes (Kruschke et al. 2012). Within the Bayesian framework, weakly informative normal priors were chosen for both tested scales (Normal (0,1)) to minimize the chance of Type I errors (Lemoine 2019). Multiple priors including uninformative and more conservative estimates were used within models to ensure that these did not affect the model output, and only small changes were seen, if any. A beta error distribution was selected because both the explanatory and response variables are positive and proportions; posterior checks showed a good fit of the model. All testing was done with mean light ratio values for both 20km and 40km wide buffers. The explanatory variable was considered to have a strong effect when the 95% credible interval did not cross 0. To further validate these results, we calculated the probability of direction for the light ratio variable (Makowski et al. 2019).

Results

The average straightness value for all individual birds during nightly flight segments was 0.972 (range 0.715 to 0.999). Average straightness values for individual birds ranged from 0.934 to 0.989 at this segmented scale. On the full track scale, the mean straightness value for all birds was 0.836 (0.719 to 0.974). Ranges of artificial light values can be seen in Table 1.

Whip-poor-wills showed no strong response to increasing light ratio (straight-line light intensity vs encountered light intensity) at the scale of the full migratory pathway (Figure 2.5) whether examining the buffer size of 20km [0.02, 95% CI -0.20, 0.24] or 40 km [-0.25, 95% CI -1.76, 1.35]. At the scale of nightly flights (stopover to stopover) there was an effect of the light ratio on the straightness of flight paths (Figure 2.6). Whip-poor-wills showed a decrease in the straightness of their migratory flights as the light intensity of direct, straight-line pathways increased relative to the pathways they chose [-0.40, 95% CI -0.58, -0.18]. This effect was only seen when analysing the light values generated with a 20km buffer surrounding the flight routes. A probability of direction of >99% was found, indicating a strong likelihood of detection of a true effect. This model was also tested for spatial autocorrelation using Moran's I and no significant pattern was found (all p values > 0.45). When analysing values obtained using a 40km buffer, one outlier impacted the overall trend of the data (Figure 2.7), but removing it continued to show no strong effect [-0.41, 95% CI -0.83, 0.10]. Upon testing for a non-linear effect using polynomial terms within the models, no strong effects were found at any scale.

Discussion

The process of migration can demand significant energy input, particularly for long distance migrants (Gwinner 1990). Given the high mortality rate birds experience during migration (Sillett and Holmes 2002, Klaassen et al. 2014) factors that make migration more difficult or less efficient should be considered when examining conservation concerns for species-at-risk. Dark sky can be considered as a resource for nocturnally migrating avian species, and there is evidence that whip-poor-wills use dark connected skies preferentially on migration (Korpach et al. 2022). Whereas Korpach et al. (2022) showed the preference for dark connected skies, we quantified this preference by measuring the amount whip-poor-wills alter their migratory pathway in the presence of intense artificial light. This work has also provided evidence that the relative intensity of light is important between the pathways rather than just the connectivity itself.

We showed that whip-poor-wills seem to exhibit a scale-dependent avoidance of artificial light at night along their migratory routes. There was no effect of avoidance of artificial light at the overall migratory scale, but an effect was detected on the scale of nightly migratory flight bouts. This difference suggests that whip-poor-wills are making decisions regarding their flight paths on a night-by-night basis and based primarily on the environment or conditions they are experiencing during their flights. It is also then implied that these birds are sacrificing efficiency on their migratory flights to avoid artificial light.

The general range of light values for the migratory pathways that we quantified were not highly differentiated between the chosen routes and more efficient routes at either scale (Table 2.1, Figure 2.8). As would be expected, there is a highly correlated relationship between the light intensity present on each pathway. In this study, we examined the largest and smallest scales available to test for an effect. At the largest scale, this effect may be masked by the averaging of an environmental variable (light) over such a broad area. At the smallest scale, we may not be effectively including the entire scope of the environment that the bird is basing decisions on. It may be that whip-poor-wills are choosing their migration routes on a scale more akin to several nights of flying and likely factoring in more variables to their decisions on where to fly. This work can be furthered by examining whip-poor-will migration at more geographic scales.

Future studies could work to quantify the energetics of flight in this species and determine the true impact of the loss of efficiency we have found and whether there are carry-over effects on timing and fitness. Whip-poor-wills exhibit site-fidelity on their wintering grounds (Bakermans et al. 2022). Carry-over effects of wintering habitat quality have been shown to impact other migratory species in the following breeding season (Billie and Peach 1992, Sherry and Holmes 1996, Norris et al. 2004). If whip-poor-wills are being made less efficient depending on the amount of artificial light they are encountering on migration, this inefficiency could lead to a later arrival time at their over-wintering territory. This may lead to an individual's territory being usurped by another bird and subsequently the delayed bird may have to accept a lower quality territory, which could have longer term consequences on their fitness.

There are areas of North America where light is seemingly inescapable as human development is extremely prevalent, such as the northeastern United States (Cinzano et al. 2001, Olsen et al. 2014). In these areas birds may be using other strategies to mitigate the effects of artificial light, such as faster speeds through the more direct routes or a shift in altitude. There are also environmental factors besides artificial light that have not been considered but may make a measurable difference in the route chosen by whip-poor-wills. Korpach et al. (2022) suggested that whip-poor-wills are also selecting for "non-impervious" land cover, indicating that they might be avoiding cities themselves alongside artificial light. Within that overall preference, they may also be selecting based on distinct types of non-impervious land cover. Given that whip-poor-wills are forest and edge dwelling birds, they may also be selecting for a migratory pathway that allows access to their preferred resources for roosting and foraging.

In addition to artificial light, several other factors not examined in our study that may contribute to flight path selection in migratory landbirds. Birds on migration can be positively affected by winds depending on the direction and velocity of the winds they are encountering, and the speed of a bird's flight can vary significantly in association with wind (Alerstam 1979, Gagnon et al. 2011, Safi et al. 2013). There are several compensations that birds can make to optimize their flight patterns in the face of influential winds, such as altering speed, compensating for drift, or adjusting their altitudes (Alerstam 1979, McLaren et al. 2012, Safi et al. 2013, Norevik et al. 2021). It is possible that any of these adjustments are being implemented by whip-poor-wills, but we were unable to test for them with our current sample size and general lack of knowledge regarding the flight altitude of whip-poor-wills and how it may vary over migration. It is possible that there might be stronger effects of light when accounting for compensation or altitude shifts due to the effects of wind. These elements will have to be considered in further analysis to fully elucidate the driving forces behind the decisions that whip-poor-wills make while completing their migratory flights.

Avian migration decisions are made based on many variables and can involve trade-offs of different degrees to accomplish the overall goal of arriving at a destination (Alerstram and Lindstrom 1990). These results show that whip-poor-wills may be making some of these trade-offs to avoid exposure to bright artificial light. Given the complexity of population declines, it is necessary to identify any areas of potential added stress in species-at-risk so that conservation plans can be thorough and effective. Adding to the growing body of evidence showing that artificial light at night can impact species in different ways is important in the consideration of future policy and management decisions.

Tables

Table 2.1. Values of artificial light at night averaged using the terra package in R (Hijmans et al. 2023) from beneath either 20 or 40km buffers surrounding the migratory pathways of Eastern Whip-poor-wills. Light observed by the NOAA's Earth Observations Group VIIRS Day/Night Band 2016 annual composite (Elvidge et al. 2017). Data with clouds removed, corrected for ephemeral light, stray light, and outliers. Shown in units of nanoWatts/cm/sr and multiplied by 1E9.

Pathway Type	Scale	20km Buffer min	20km Buffer max	Light Ratio min (20km)	Light Ratio Max (20km)	40km Buffer min	40km Buffer max	Light Ratio min (40km)	Light Ratio Max (40km)
Straight/Hypothetical	Nightly-segmented	0.029	10.021	0.116	5.092	0.030	7.763	0.289	16.035
Tortuous/Actual	Nightly-segmented	0.032	10.137			0.029	7.813		
Straight/Hypothetical	Full Track	0.214	2.713	0.605	1.620	0.285	2.437	0.794	1.285
Tortuous/Actual	Full Track	0.272	2.809			0.299	2.520		

Figures

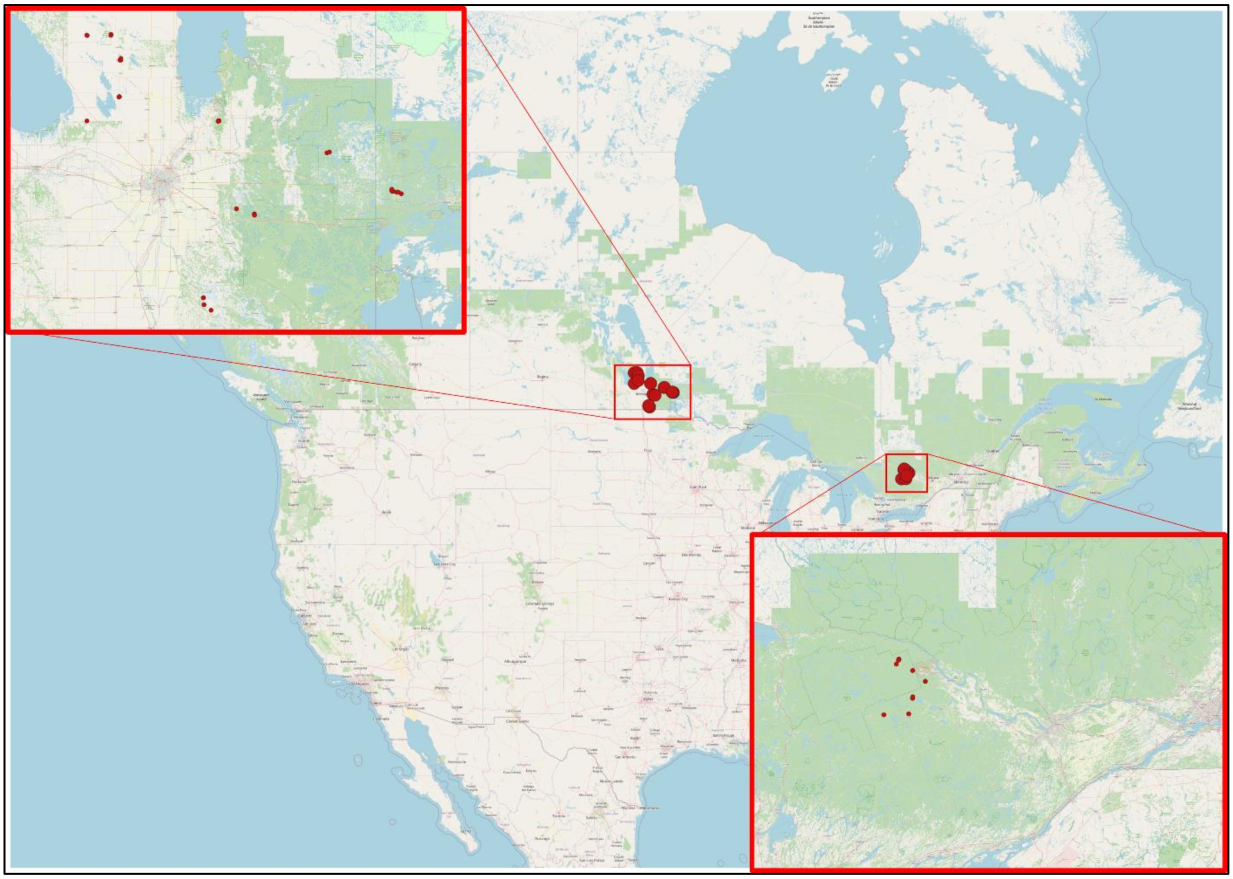

Figure 2.1. Site locations for Eastern Whip-poor-will captured in Manitoba and Ontario during the breeding seasons of 2018 – 2020 and fitted with archival GPS tags. Inset showing the distribution of the birds in the northern and southern populations. n = 47

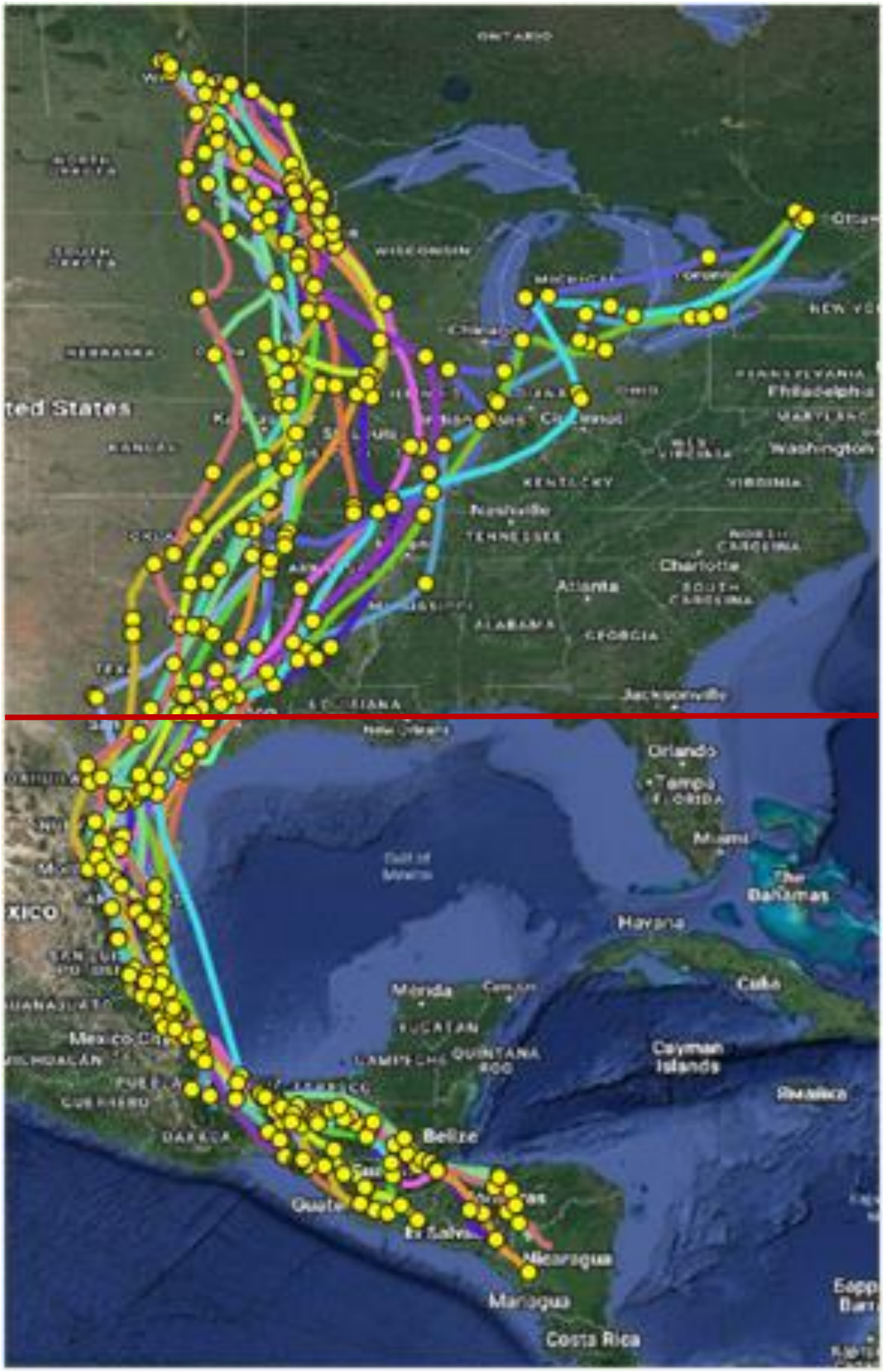

Figure 2.2. Fall migratory routes of Eastern Whip-poor-wills (*Antrostomus vociferus*) with individuals shown in varying colours and stopovers shown as yellow circles. Red line indicating the cut off point at 30N latitude for analysis due to the Gulf of Mexico. Data collected from 2018 – 2020 using Pathtrack Nanofix Mini archival GPS tags set to collect one point every two hours. n = 18.

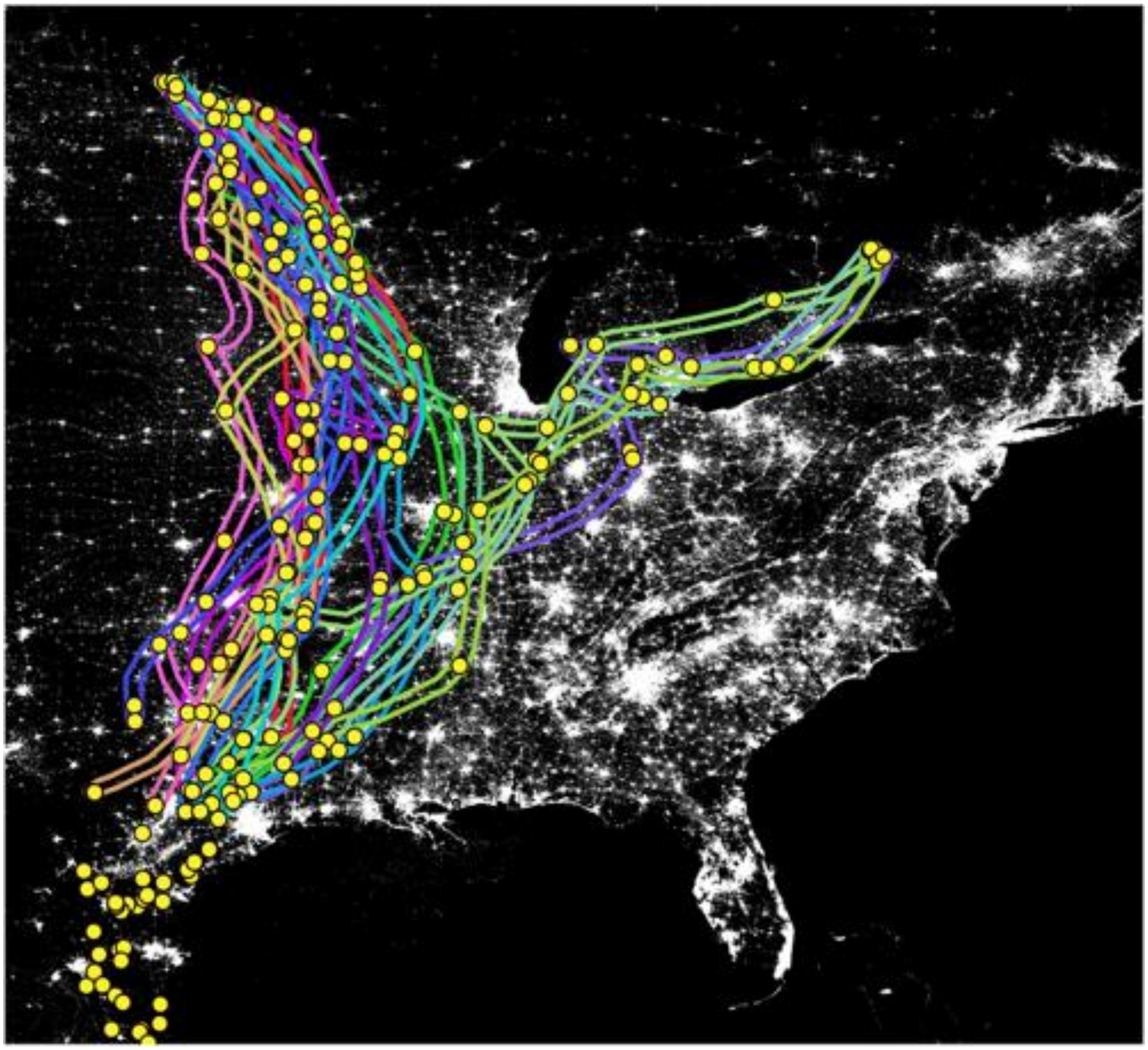

Figure 2.3. Buffers of 20km created surrounding the fall migratory pathways of Eastern Whip-poor-wills (*Antrostomus vociferus)* overlain with satellite data of artificial light collected by the NOAA's Earth Observation Group. Individual birds shown in varying colours and stopovers shown as yellow circles. Buffers limited to 30N latitude to account for the Gulf of Mexico. Data collected from 2018 – 2020 using Pathtrack Nanofix Mini archival GPS tags set to collect one point every two hours. n = 18.

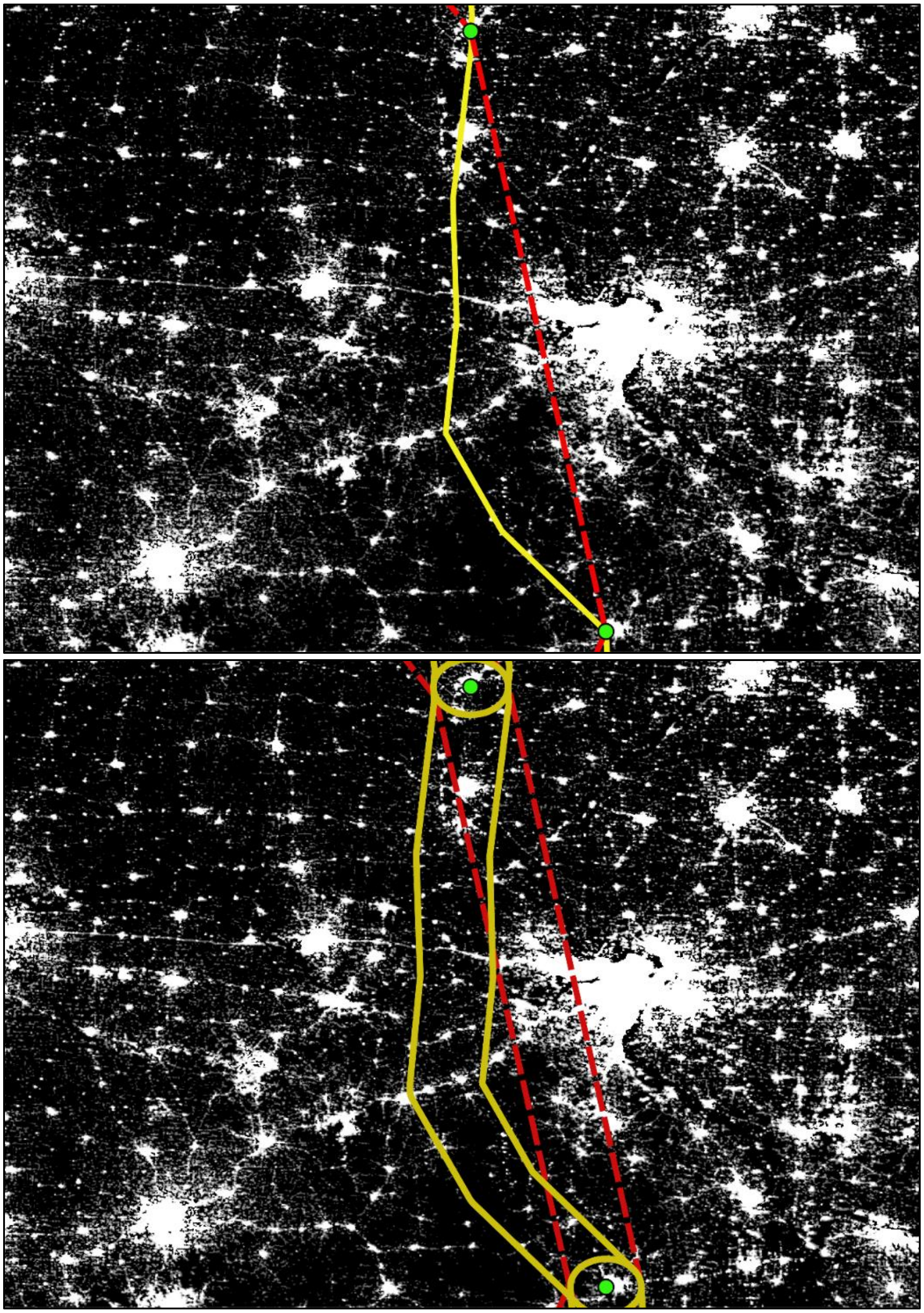

Figure 2.4. The hypothetical straight-line pathway (red dashed line) and true flight path (yellow solid line) between nightly stopovers (green dots). Top: Trajectory line without buffers. Bottom: Buffers that light values were extracted from. Light values were compared via a ratio of straight to curved paths.

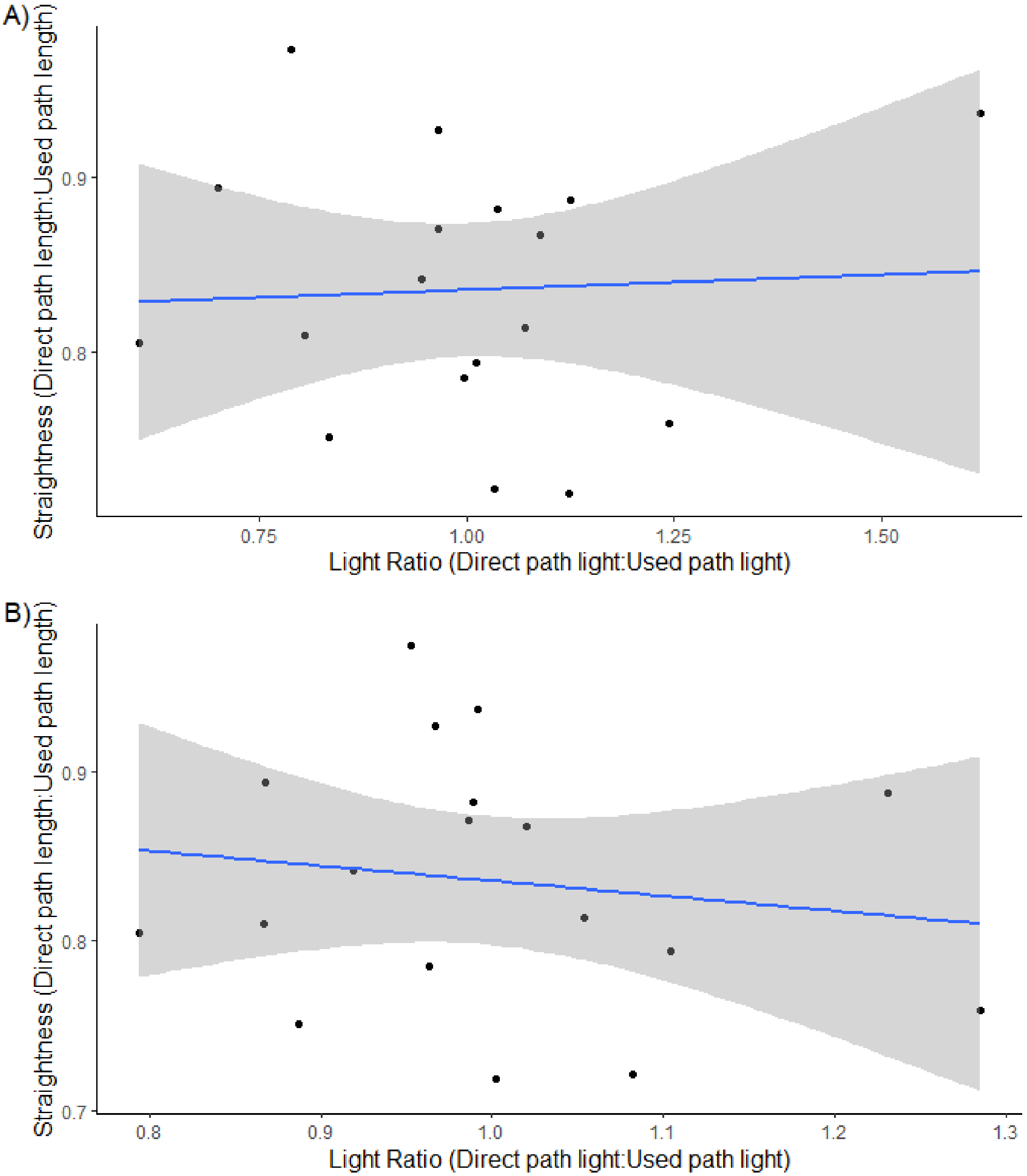

Figure 2.5. The relationship between the ratio of light intensity that Eastern Whip-poor-wills could be avoiding and the straightness of migratory flight paths on an overall migration route scale. Light ratio calculated as the average light intensity under the hypothetical most efficient, straight-line route divided by the average light under the encountered by birds on their actual flight paths. Light values averaged under either a 20km (A) or 40km (B) buffer around the paths. Straightness measured as the distance from start to finish in a straight line divided by the distance of the actual flight paths. No effect found. n = 18 individuals

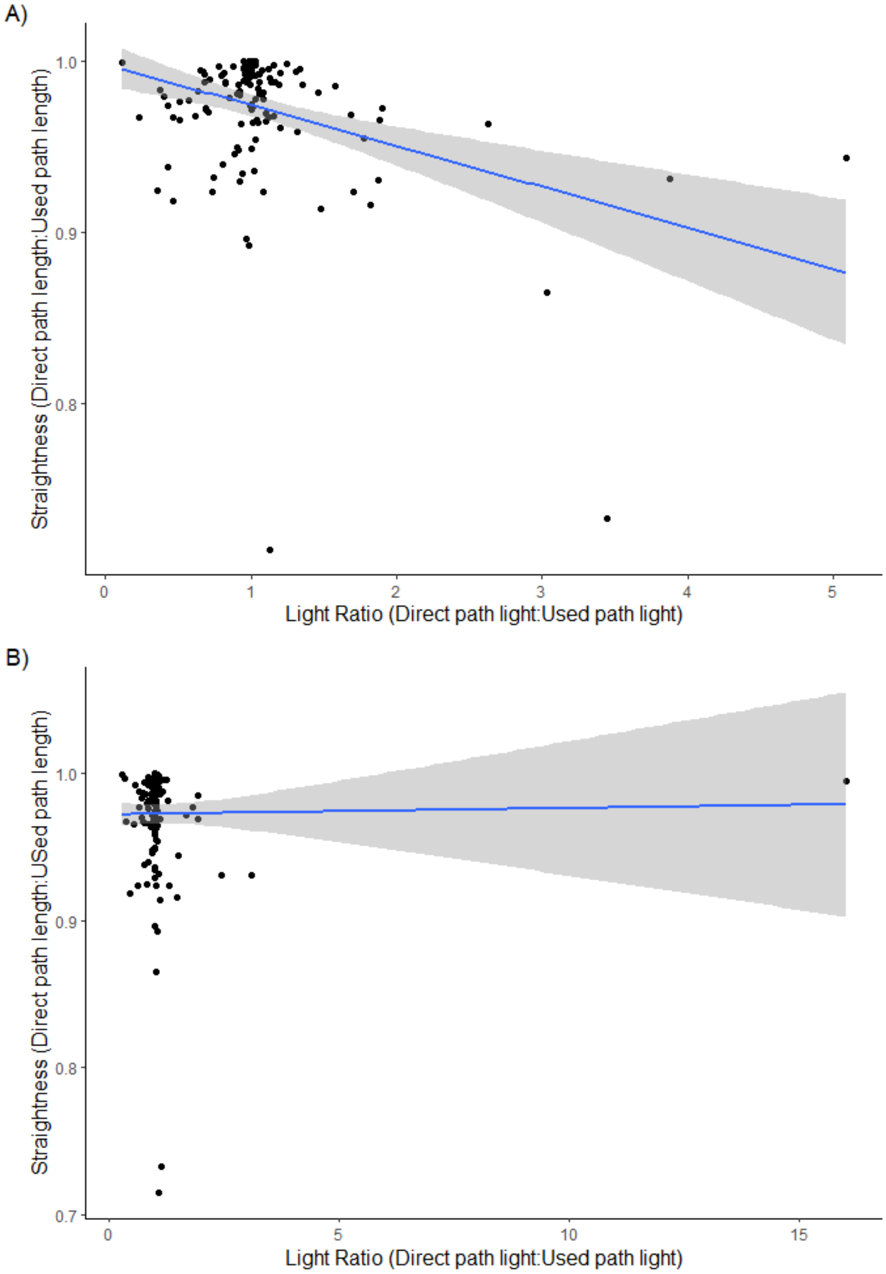

Figure 2.6. The relationship between the ratio of light intensity that Eastern Whip-poor-wills could be avoiding and the straightness of migratory flight paths on the scale of nightly flight bouts at a 20 km scale. Light ratio calculated as the average light intensity under a 20km (A) or 40km (B) buffer on the hypothetical most efficient, straight-line route divided by the average light under a 20km or 40km buffer encountered by birds on their actual flight paths. Straightness measured as the distance from start to finish in a straight line divided by the distance of the actual flight paths. Analysis indicates that flight paths are less straight at higher relative intensity of light on the straight flight paths. n = 18 individuals.

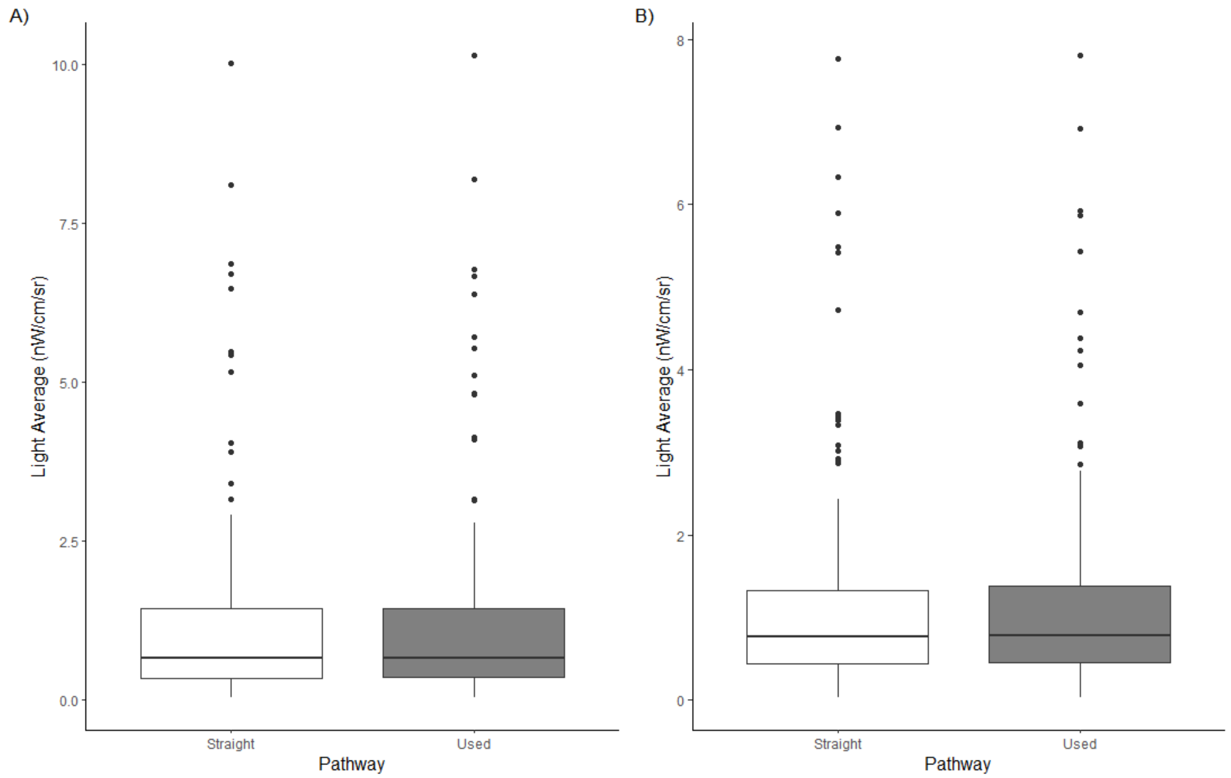

Figure 2.7. Light values on hypothetical straight-line paths (white) and used tortuous paths (grey) of Eastern Whip-poor-wills (*Antrostomus vociferus*) averaged from underneath either a 20km (A) or 40km (B) buffer surrounding the migratory paths of individual birds.

Chapter 3- Site Fidelity and Homing in a Nightjar, the Eastern Whip-poor-will

Abstract

Long-lived species tend to have smaller clutch sizes and exhibit high site fidelity across years; both can be resource allocation strategies that allow for an increase in lifetime fitness. The Eastern Whip-poor-will (*Antrostomus vociferus)* is one such species but has thus far been only anecdotally known to return to the same breeding territory as in years prior. The aim of this study was to compile research from 6 years of capture and 3 different tagging experiments to quantify and estimate the rates of recapture and site fidelity of this species. The first method was to consider capture and recapture rates across 5 years of tracking birds using archival GPS tags that require recapturing to extract data (n = 101). The second was an experiment where birds were displaced ~140km from their breeding territory and recaptured after they had returned (n = 8). The third used automated radio telemetry over fall and spring migration and detection on breeding territories in the following year (n = 10). Using the first method, we found an average annual recapture rate of 60% (range 50-80%). Overall, 75% of birds that returned were found on the same territory as in the year prior. In the displacement experiment, 75% of birds that were displaced returned to their original territory. Receiver stations across the spring and fall migration range in North America detected 90% of tracked birds on their spring migration, indicating survival between the breeding season and spring migration in the next year. Subsequently, 67% of those birds were detected using handheld receivers or captured on their former breeding territories using song lures. Our results suggest a high site fidelity and annual survival, which is consistent with longer-lived species of land birds with small clutch sizes such as whip-poor-will. Knowledge about the survival and site-fidelity of this species can aid in management decisions and aid in further conservation efforts.

Introduction/Background

Life history traits and strategies vary widely and culminate in an overall profile of adapted attributes that are expected to increase the overall fitness of a species. In birds, classic interpretations of these traits include clutch size, age of sexual maturity, and number of clutches per year (Stearns 1976). More generally, life history features can be any aspect affecting the reproduction, growth, or survival of an individual. There tend to be trade-offs between certain of these traits, dictated by the energy and resources that they require and environmental conditions (Cody 1966). These trade-offs are described in overall categories of ‘fast’ and ‘slow’ or r and K selected traits and are on a continuum (Macarthur and Wilson 1967, Pianka 1972, Martin 1981). For instance, birds that are long-lived tend to have smaller clutch sizes, as clutch size is negatively correlated with survival (Haukioja and Hakala 1979, Reznick 1985, Zammuto 1986, Saether 1987, Bennett and Harvey 1988, Martin 1995). Different combinations of feeding and nesting strategies, as well as environmental factors, can result in marked interspecific variation in life histories and survival (Martin 1995). An example of this is seen in the work of Martin (1995), who showed that among aerial insectivores, those with cavity nests exhibited greater reproduction but lower survival than those with uncovered nests.

It is widely hypothesized that migration to more northern latitudes evolved to take advantage of the resource flush and decreased competition available in temperate zones as well as increased photoperiod to aid in the acquisition of these increased resources (Cox 1968, 1985; Levey and Stiles 1992, Alerstam et al. 2003). These factors make reproduction more favourable and therefore migratory behaviours of species can be considered as a life history trait (Ricklefs 1980, Alerstam et al. 2003). Site-fidelity may be at play in determining migratory behaviours as well (Winger et al. 2019). Site-fidelity is the affinity that an individual might have for a territory or site that it has previously occupied or bred in (Switzer, 1993; Winger et al., 2019). This affinity when related to breeding sites is likely due to habitat quality and stability, as well as previous reproductive successes on that territory and potential costs of switching to an unknown territory (Switzer 1993, Vergara et al. 2006, Illera and Díaz 2008). Birds who exhibit high site-fidelity often experience increased breeding success (Greenwood and Harvey 1982, Payne and Payne 1993, Pärt 1995, Kokko 1999, Hoover 2003, Vergara et al. 2006). Increased breeding success may be because a known location with suitable habitat is faster and easier to find as opposed to seeking out a new location, wasting less energy and conferring the benefit of arriving earlier, which is also tied to increased reproductive success (Perrins 1970, Price et al. 1988, Kokko 1999, Blums et al. 2003, Winger et al. 2019). The benefit of site-fidelity to current year breeding success may be less important in long-lived species since they may be implementing a longer-term strategy for reproduction (Ward and Weatherhead 2005, Öst et al. 2011). Despite this possibility, many long-lived species still exhibit high levels of site-fidelity (Olsen and Larsson 1997, Bried and Jouventin 2002, Krüger et al. 2015, Mäntylä et al. 2020).

Eastern Whip-poor-wills (*Antrostomus vociferus*) are long-distance migrants, and it has long been recognized that they maintain site-fidelity (English et al. 2017a, Korpach et al. 2022a). The tendency towards high site-fidelity in this species may correlate to their need for large individual territories, with diverse habitat requirements (Korpach et al. manuscript in prep). Like many other nightjar species (Ingels et al. 1984, 2017; Jackson 1985, Schaaf et al. 2015), whip-poor-wills have very low clutch sizes and only lay 2 eggs per year (Peck and James 1983, Mills 1986, Akresh and King 2016, Cink et al. 2020). While they have been shown to lay up to 2 clutches per year this is less common in northern latitudes (Mills 1986, Cink et al. 2020). These traits go along with reports of very long lives for a migratory songbird, including banded individuals of the species living up to 15 years (Cink et al. 2020). As a comparison to other small land bird species, other insectivores have been shown to have an average life span of only 3.1 years and the average life span of most songbirds has been estimated to be less than 2 years (Welty 1975, Peach et al. 2001). My goal in this study is to provide a quantification of the rate of recapture and site-fidelity of this poorly studied species. We will take advantage of several experiments using data collected over the course of 6 years (2017 – 2022) that track space use and migratory behaviour and have included mark-recapture, automated radio telemetry, and a displacement and homing experiment to address this goal.

Methods

Capture and Banding

This work was completed using a synthesis of datasets from the years of 2017 to 2022. All birds in this study were captured using the same general methodology. Male whip-poor-wills were captured using mist nets and song lures during the breeding seasons (n = 192). Study sites were located across southern Manitoba, north-western Ontario, and southern Ontario (Figure 3.1). Captured birds were fitted with federal identification leg bands. Recaptures were attempted in following years using the same methods. At the time of capture, location data (latitude and longitude) as well as morphological measurements were taken on all individuals.

Site Fidelity and Overall Return Rates

For this analysis, I used breeding location data collected between 2017 and 2020. Only birds banded and outfitted with an archival GPS tag were targeted for recapture, resulting in a total of 101 capture points. These data were then input into a geographical information system (GIS) software (QGIS 3.32.0) and visually analyzed for overlap of capture points of individuals using the identification numbers on their bands. If a different bird was captured within the territory in a subsequent year, a note was made of its identification number. If the original bird that had been usurped was captured in that year as well, the distance from the original capture site was measured using within application measurement tools and rounded to the nearest metre.

The proportion of birds with the same identification number recaptured each year and the proportion of those birds that were recaptured within the same territory as in the previous year(s) were calculated. A more formal survival analysis could not be done on the entire data set because effort or number of site visits for recapture attempts were not quantified and therefore could not be accounted for. Base functions in R statistical software (R4.3.0) were used to calculate the number of birds returning, the number of new birds in each year, and the number of birds recaptured on their original vs a new territory. Birds were considered to be on the same territory as in the year prior if they were within 500m of their original capture site and no other bird was found closer to the original capture site. This estimate is conservative given the mean home range size of 53.8 hectares, equivalent to a diameter of 825m, found in recent unpublished work by Korpach et al. (manuscript in prep).

Displacement

Birds used in the displacement experiment were captured in 2022 near Spruce Siding and Stuartburn, Manitoba (n = 8; Figure 3.2). Birds were placed in a padded box and displaced to locations ~140km away. Birds from the Spruce Siding capture site (n = 5) were taken to Little Mountain Park, birds from the Stuartburn site (n = 3) were taken to a location just west of Miami, MB (Figure 3.2). All birds were fitted with archival GPS tags (NanoFix Mini; 2g, PathTrack Ltd., Otley, UK) using 0.75mm Teflon cord leg-loop harnesses (Rappole and Tipton 1991) for another experiment. We returned in the following weeks to recapture all birds. The return paths of birds relocated to Little Mountain Park traversed urban areas with artificial light and the birds relocated to Miami flew over rural, dark areas.

Radio Tracking

Whippoorwills captured in 2022 near Kenora, Ontario (n = 10; Figure 3.3) were used for this analysis. Following capture and banding, we fitted birds with Motus Wildlife Tracking System nanotag (NTQB2-3-2-M, 0.65g, Birds Canada 2022). We returned in June of 2023 to detect whether birds had returned to their territories using a handheld receiver and capturing any birds located on territories where the receiver could not detect any tags, but birds were heard singing. Tag detections were also monitored through the fall and spring using the network of Motus detection towers located throughout North America (Birds Canada 2022).

Results

Return Rates and Site Fidelity

In 2018, 8 out of the 10 birds captured and tagged in 2017 were recaptured (80%), 6 of those birds were re-tagged, 28 new birds were captured and tagged with archival GPS units. In 2019, 20 of 34 birds that were GPS tagged were recaptured (59%), 11 of those were re-tagged, 50 new birds were captured and tagged. In 2020, 33 of 61 birds were recaptured (54%), 17 were re-tagged and 11 new birds were captured and tagged. In 2021, 14 of 28 tagged birds were recaptured (50%). Of the recaptured and retagged birds in 2018 (6), 5 were recaptured in 2019 and 2 in 2020. Of the birds initially captured in 2018 and retagged in 2019 (11), 7 were captured again in 2020 and 3 in 2021. Therefore, at least 5 birds were captured repeatedly across 4 years of study.

All 8 of the recaptured birds in 2018 were captured on the same territory as in the prior year. In 2019, 13 of the 20 recaptured birds were captured on the same territory. In 2020, 25 of 33 birds were captured on the same territory as in the year prior. Finally, in 2021, 11 of the 14 recaptured birds were on the same territory as in the year prior. This means that of all 75 birds recaptured across all years of the study, 57 (75%) were recaptured on the same territory at least once. The farthest that any bird was found away from its original territory was 6486m, but many were recaptured within meters of the original net site from year to year. The average distance away from an original capture site for a bird to be found was 168m. This number is skewed by the bird found farthest away from his original site. When removing that data point, the average falls to 78m. The median distance that recaptures occurred at was 22m from the original capture site.

Displacement

Of the 8 birds that we displaced, 6 returned to their original territories. All 3 birds from Stuartburn returned and 3 of 5 from Spruce Siding returned, a return rate of 75%. The birds that we were not able to find and recapture were an adult bird (after second-year) who was displaced on the first night of the trials (May 16th) and a younger (second-year) bird. Both territories had other birds defending them that we were able to capture and identify as another adult and another second-year bird.

Radio Tracking

In fall of 2022, 8 out of 10 birds (80%) that were Motus tagged were detected flying south to their wintering ground by at least 1 detection tower (Figure 3.4). In spring of 2023 those 8 birds were again detected flying north, and an additional bird was detected, making the total 9 out of 10 (90%) (Figure 3.5). In June of 2023 we returned to the breeding territories the birds were previously captured on, 6 of 10 (60%) birds were found in the same territory that they occupied previously. Of the 4 territories that the original occupants were not found on, 3 were occupied by new (unbanded) adult males. All the birds that were nearby while we surveyed were detected by the handheld Motus receiver, including one up to 2km away. The 4 birds that were not located on their territories were not detected by the receiver, including while surveying up to 600m in any direction from the original capture site. The birds that had been present on territories that were nearby forestry operations were still present on those territories and were captured to ensure there was no fault in the Motus detections.

Discussion

Eastern Whip-poor-will are a long-lived species with clutch sizes of only 2 eggs per nest (Mills 1986, Cink et al. 2020), which would suggest that they should exhibit other ‘slow’ life history traits such as high levels of site-fidelity, and that annual recapture rates should be high. This study can help to quantify what has thus far only been anecdotal knowledge regarding the year-after-year recapture and site fidelity. Our data showed that not only do male Whip-poor-wills exhibit high levels of site fidelity and survival between breeding seasons, but also that they will return to their territories after being experimentally displaced, including when they are faced with a bright and likely stressful obstacle such as a city. Survival was likely higher than exhibited through the return rates themselves due to individuals being displaced from their habitats, not able to be recaptured, or both.

Migration can be one of the most dangerous and energetically taxing periods in the annual cycle of a bird (Alerstam and Lindstrom 1990, Sillett and Holmes 2002, Klaassen et al. 2014). Post migratory return rates of birds year-to-year can be variable between species and even between years within the same species (Askenmo 1979, Newton 2008b). Since reproduction is another phase with large energetic demands, high reproductive output is traded-off with adult survival (Haukioja and Hakala 1979, Reznick 1985, Zammuto 1986, Saether 1987, Bennett and Harvey 1988, Martin 1995) and longer-lived birds have lower clutch sizes and more fixed reproductive investment (Ricklefs 1987; Saether 1987; Erikstad et al. welty 1998; Mccleery et al. 2008), which is consistent with our findings. Our survival findings are consistent among other nightjar species, such as the Red-necked Nightjar and European Nightjars, which were found to have a 0.74 (males, Forero et al. 2001) and 0.70 (Silvano and Boano 2012) average annual survival probability, respectively. In contrast, annual survival rates of 50 species of passerines were 0.49 in a study by Peach et al. (2001). Given that our study only looked at birds that were fitted with tags, there is a possibility that our return rates were skewed by these attachments although in a meta-analysis on tracking technology in birds, it was shown that small tags do not influence return rates (Brlík et al. 2019).

Whip-poor-wills do not seem to reap certain of the benefits that have been hypothesized to have influenced the evolution of migration; since they are nocturnal, they do not enjoy increased photoperiod for resource acquisition (Cox 1985). They also do not seem to reap the same reproductive benefits as other species that migrate to temperate areas given that their clutch sizes are typically only 2 eggs, whereas clutch sizes of most birds at northern latitudes are greater than their non-migrating counterparts (Moreau 1944, Lack 1947, Cody 1966, Ricklefs 1980). It might be that whip-poor-wills are benefitting by increasing adult survivorship rather than increasing yearly fecundity, thus potentially benefitting their lifetime reproductive output and fitness (Ricklefs 1977, Haukioja and Hakala 1979, Murphy 2007). Though no average life expectancy estimate exists for whip-poor-wills, they have been shown to live to 13 or 15 years old in some cases (Cink et al. 2020) and in our study, a bird that was originally captured and banded in 2011 was tracked starting in 2017 and recaptured in 2018 and 2019. That would make this bird at least 9 years old at the time of its final capture. In another species of nightjar, both females and males were banded and recaptured in multiple cases for up to 10 years (Silvano and Boano 2012) and in Common Nighthawks (a closely related North American species), birds live to least 4 years and have been shown to live up to 9 (Dexter 1961, Brigham et al. 2020). This is in contrast to species of passerines that have been estimated to have an average life expectancy under 2 years (Welty 1975, Peach et al. 2001).

Site-fidelity has been inferred anecdotally in this species (English et al. 2017a, Cink et al. 2020, Korpach et al. 2022a) but has only been studied more formally in related species (Dexter 1952, Jackson 1985, Doucette 2010). Whip-poor-wills within our study returned to their previous breeding territories multiple times over years during typical migratory behaviour. To add to this, most of the birds that we experimentally displaced were able to navigate their way back from an unfamiliar location to be trapped in the same territory and in many cases the same net site. It is unlikely that the birds would have had any prior knowledge of the areas that they were released in because they were released 140km north-west of their territories, whereas these birds likely approach from the south when returning from their wintering habitats (Korpach et al. 2022a). While birds commonly have intrinsic navigation cues that they use on migration, for a bird to navigate back from an unknown direction and area requires a true compass and navigation that has been shown in other species (Willemoes et al. 2015). Compass navigation is consistent with other homing studies in avian species (Southern 1959, Sargent 1962, Nastase 1982) but to our knowledge, has not been shown previously in other nightjars.

Survival analyses can be important to understand more about the life history traits of a species and population trends over time (Lebreton et al. 1992). These types of studies become especially important for declining yet poorly studied species like whip-poor-will, where population sizes have been estimated to have fallen by nearly 70% over 50 years (COSEWIC 2009). In the future, a dedicated study of recapture, site fidelity, and survival probabilities could be completed in this species. A study of this sort could be stronger at estimating survival and occupancy if multiple site visits or surveys are used per season (repeat sampling) and effort is recorded, though methods have been developed statistically to deal with single surveys in detection probabilities (Lele et al. 2012). In at least 2 cases within our study, birds were captured and tagged in one year, missed in the year immediately following tagging, and then recaptured 2 years after their initial capture. This shows that the probability of recapturing birds is not always perfect even if they did survive and return to the territories they occupied previously. While we could likely use this data to estimate a more accurate probability of survival, the ability to control for effort would be preferable. It would also be useful for population monitoring and estimates to include birds other than adult males, since it has been shown that survival estimates can differ between sexes in nightjars (Forero et al. 2001).

Figures

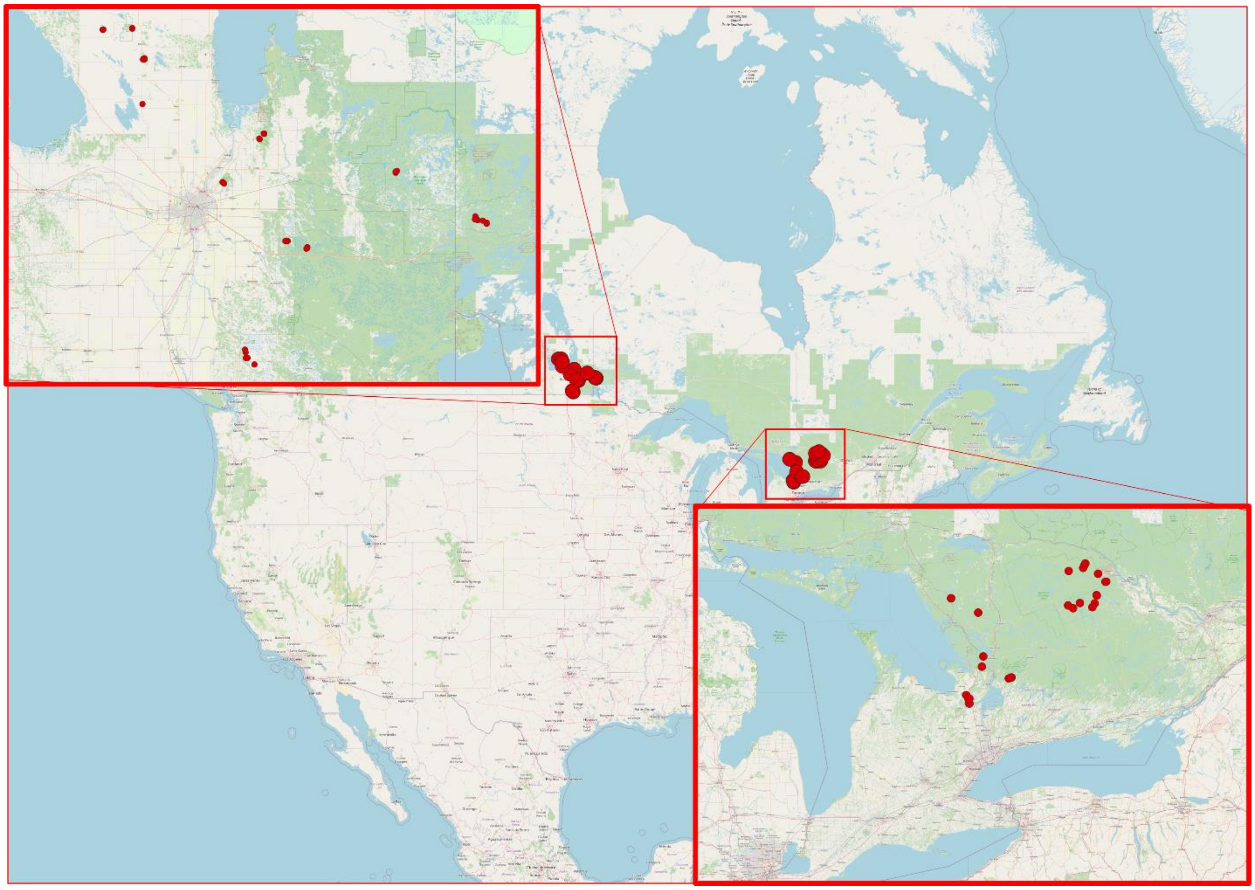

Figure 3.1. Study sites of Eastern Whip-poor-wills captured during the breeding seasons of 2017 – 2022 in southern Manitoba, and north-western and southern Ontario. n = 192

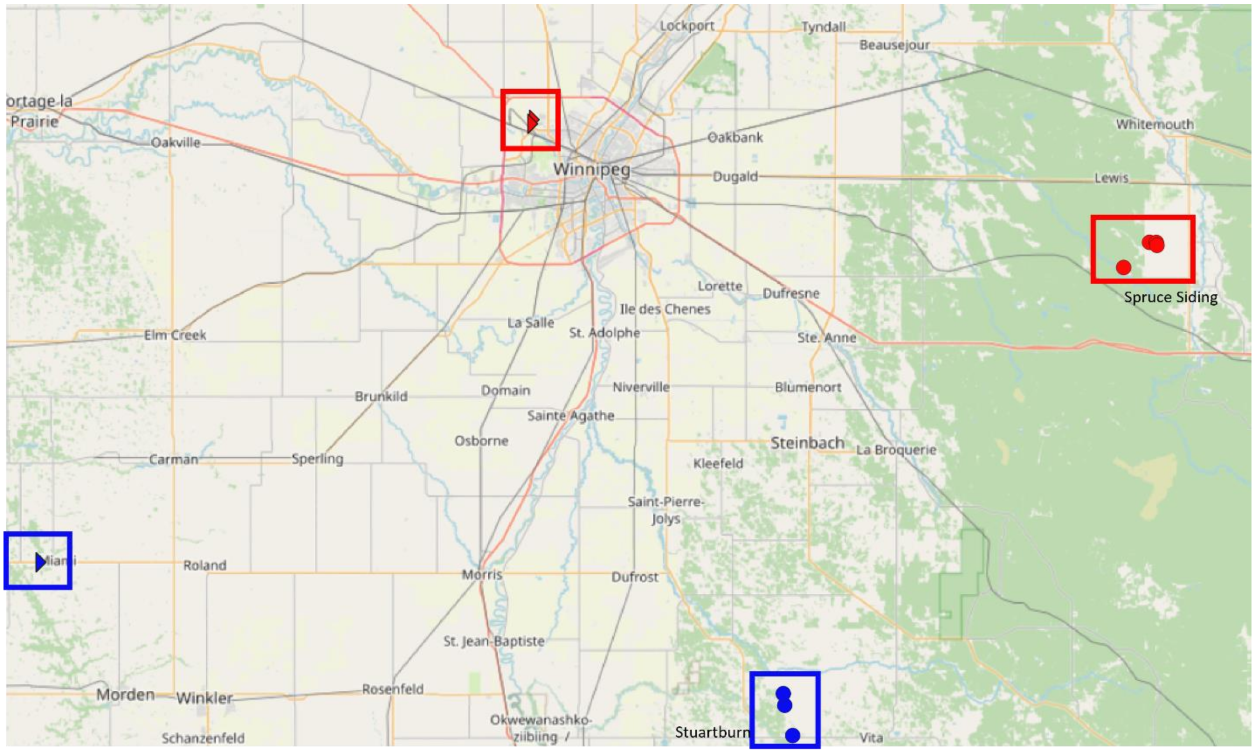

Figure 3.2. Capture (circles) and release sites (triangles) of Eastern Whip-poor-wills displaced from their breeding territories to sites ~140km away either with (red) artificial light as an obstacle, or without (blue). n = 8

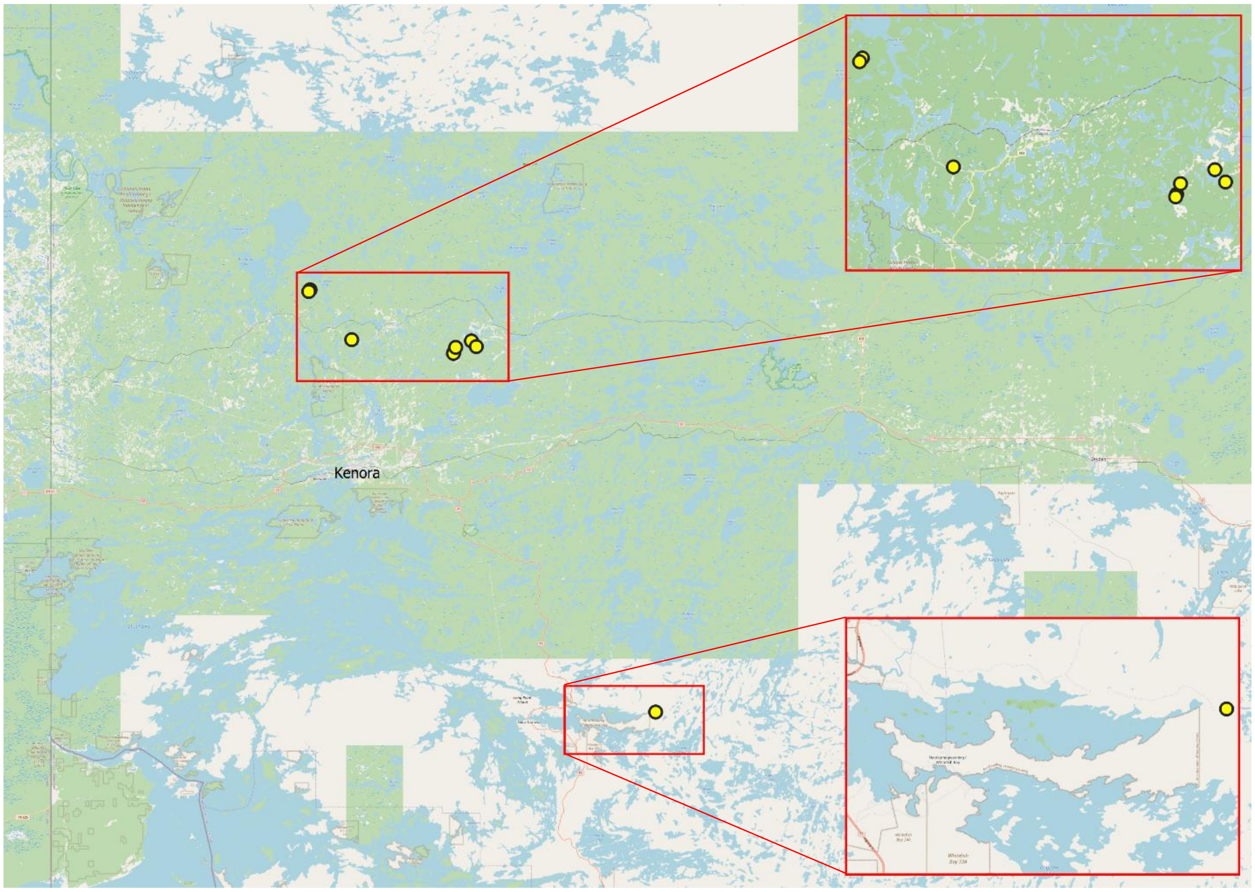

Figure 3.3. Capture sites of Eastern Whip-poor-wills subject to radio tracking (Motus Wildlife Systems)

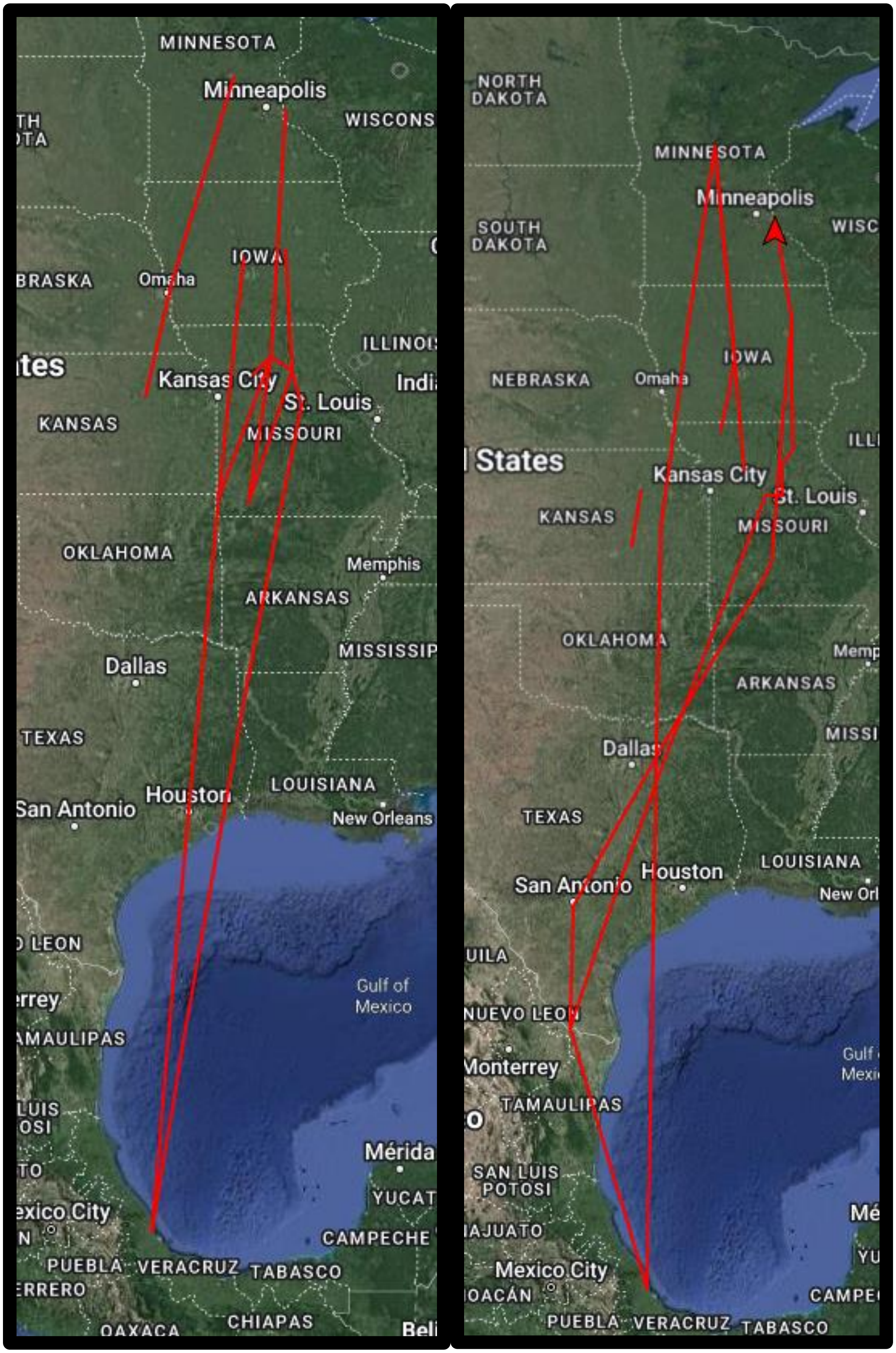

Figure 3.4. Estimated fall (left) and spring (right) migration (Sept – Oct, 2022 & Apr – May, 2023) tracks of birds captured in June and July of 2022 near Kenora, Ontario. Points are individual detections at radio towers, lines are hypothetical straight paths between points. n = 8 (left) and n=9 (right)

Chapter 4 – Overall Conclusions

I found that migrating whip-poor-wills take more winding, less direct flight paths in response to more intense artificial light. This effect was found at the scale of nightly flights from stopover to stopover along fall migration routes. Interestingly, the effect was not found on the overall scale of migration routes. This indicates that whip-poor-wills are making their migratory decisions based on environmental conditions or other factors they are experiencing while in flight. Other scales, such as multi-night or latitudinal gradients will have to be investigated to examine these effects further.

In the future, studies could examine the flight energetics of this species to be able to quantify the efficiency loss that we have shown in this study. With further studies, we could also determine the potential carry-over effects of the avoidance of light. If migration takes longer due to a loss of efficiency en route, then birds might not be able to get to and defend their preferred territory. Since whip-poor-wills exhibit site-fidelity at their wintering grounds (Bakermans et al. 2022), and site-fidelity is often linked to habitat quality (Haas 1998, Illera and Díaz 2008, Blackburn and Cresswell 2016), delays on migration may allow another male to arrive first and usurp the territory. This could lead to carry-over effects in the following spring migration and breeding season (Billie and Peach 1992, Sherry and Holmes 1996, Norris et al. 2004). In consideration of this, future work could also examine arrival timing, whether there are any compensations in timing for birds with routes that are more impacted by intense artificial light, and subsequent impacts on fitness measures over the full annual cycle in whip-poor-wills.

This effect will also have to be examined in relation to more environmental and landscape level factors that could be responsible for some of the tortuosity I have observed, or interacting with artificial light to produce the effect we are seeing. These are variables such as wind strength and direction, and land cover type. In this study I have collaborated with a PhD student who is currently examining the potential alternative responses of whip-poor-wills to artificial light such as speed and altitude changes in flight.

In chapter 3, I found that recapture rates of whip-poor-wills ranged from 50% to 80% and that 75% of returning birds were found inhabiting the same territory as in the year prior. Further, 75% of birds that were displaced from their breeding territories prior to nesting were found and re-captured on those same breeding territories and likely had returned within a timeframe of only two days. This experiment demonstrates the site-fidelity of whip-poor-wills, but also shows an ability for true navigation in this species, which has recently been found in other species through similar experiments (Willemoes et al. 2015). I also found that 90% of birds with radio tracking tags were detected on their way north in spring, indicating that they had survived at least until the last point they were detected at. By combining these results, we can see that this species has a very high survival rate and site-fidelity to the point that they were able to navigate back from unknown areas very quickly.

Whip-poor-wills are long distance migrants that do not seem to derive the same benefits of migration by way of increased annual fecundity that other species do, due to their consistent clutch size of only 2 eggs (Peck and James 1983, Mills 1986, Akresh and King 2016, Cink et al. 2020). They have been shown, as with some other nightjar species (Dexter 1961, Silvano and Boano 2012), to live for a relatively long time as compared to migratory songbirds, though no formal description has been made for whip-poor-wills. For example, whip-poor-wills have been recorded as surviving up to 13 and 15 years (Cink et al. 2020) and in our study a bird that had been captured in 2011 was also captured in 2019, making him at least 9 years old. In contrast, most migratory songbirds are estimated to live an average of 2 years and other aerial insectivores have been shown to have an average life expectancy of close to 3 years (Welty 1975, Billie and Peach 1992, Peach et al. 2001). The additional resources that they might be gaining from completing long distance migrations could be going towards adult survival rather than annual fecundity and adding to the lifetime fitness of the species.

While these data were collected over a long period of time and there was concerted recapture effort implemented to retrieve birds and GPS tags, the level of effort was not explicitly recorded. Future studies of these birds should include some estimate recapture effort as a measured variable to provide additional information that can be tested using statistical methods that use mark-recapture and repeat sampling to estimate true survival probability without capture or detection (Lebreton et al. 1992, Lele et al. 2012).

In summary, we found that the migration of this long lived, long-distance migratory species is likely being disrupted by anthropogenic disturbance and that despite this, whip-poor-wills are still finding their way back to their breeding territories at high rates of return every spring. Likely owing to their large and complex habitat requirements as well as the increased reproductive success that tends to come with known breeding sites, whip-poor-wills show high levels of site-fidelity. Avoidance of light could be causing delays in migration that have the potential to impact the fitness of whip-poor-wills via carry-over effects. Since birds from southern Ontario are exposed to more light on their migratory paths (Korpach et al. 2022b) these effects could be more pronounced within that population. A more detailed breakdown of recapture and survival across populations would be useful to monitor these potential impacts over time. Whip-poor-wills have only recently become the subject of more research and attention, and more work will have to be done to fully elucidate the behaviours and natural history of the species.

Despite the recent federal downlisting of whip-poor-wills from threatened to species of concern, populations are not yet recognized as stable and they are still listed as threatened in most of the provinces that they occupy. Conservation and restoration of species includes risk assessments and requires studies and information on areas of potential hazards as well as information on population demographics. In this thesis I have provided necessary information about survival and site-fidelity of whip-poor-wills across years of tagging, and quantified a behavioural response to disturbance that could have further impacts on fitness. This information can assist with management plans and policies, particularly in areas where the impacts of human activity are greatest.

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