HABITAT USE AND HOME RANGE CHARACTERISTICS OF COMMON NIGHTHAWKS (CHORDEILES MINOR) IN MIXED-GRASS PRAIRIE

A Thesis

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Janet Wai-Man Ng, candidate for the degree of Master of Science in Biology, has presented a thesis titled, **Habitat Use and Home Range Characteristics of Common Nighthawks *(Chordeiles minor)* in Mixed-Grass Prairie,** in an oral examination held on November 12, 2009. 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

I examined common nighthawk (*Chordeiles minor*) space use in grassland regions of Saskatchewan. Common nighthawks range over large parts of North America, but few studies have attempted to characterize habitat use and home range. More information about nighthawk space use will provide greater insight into pattern and mechanisms of habitat use and recommendations for habitat management for this declining species.

In 2001, surveys for nighthawks were conducted throughout southwestern Saskatchewan, where the landscape is composed of both native grassland and cropland, with varying degrees of human disturbance and development. Surveyors recorded 153 nighthawks during 699 point surveys on 45 transects. I used a geographic information system (GIS) and an information theoretic approach to assess habitat and environmental variables associated with the presence of nighthawks at local (400-m buffer around point counts) and landscape (800-m buffer and 1600-m buffer around transects) scales. High proportions of grassland cover, particularly in combination with low productivity of aboveground vegetation, and proximity to water were associated with nighthawk presence. Temperature and light levels were also positively associated with detecting nighthawks.

In 2005-2006, I characterized the nature of nighthawk home ranges by radio-tracking individuals captured near the Rafferty Reservoir (49°14'N, 103°08'W). Minimum convex polygons (95%) showed average home range size and standard deviation to be 86 ± 99 ha (n = 6). I also recorded multiple activity centers within some home ranges, which generally corresponded to different types of activity or different time blocks. Home ranges spatially overlapped to varying degrees, which was unexpected in

this typically aggressive territorial species. My data also suggest that nighthawks caught in mist nets are more likely to possess established home ranges compared to birds caught on gravel roads using the spotlight method. These individuals were generally wide ranging and did not exhibit predictable movement patterns.

A substantial proportion of the Common Nighthawk population breeds in Canadian prairies and information regarding habitat associations and home ranges is important to provide recommendations for nighthawk management and conservation.

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DEDICATION

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1.0 GENERAL INTRODUCTION

Describing and understanding how animals use space is a fundamental objective of ecological research. Patterns in space use vary geographically and through time, and also between individuals and species. By studying spatial and temporal patterns of space use, ecologists can better understand proximate factors behind patterns of habitat use and the consequences of variation on population and species levels (Clark and Shutler 1999, Boyce et al. 2002).

One potential factor influencing space use is the scale at which it is considered (Wiens 1989). Spatial scale is often incorporated into current ecological studies because scale has differing influences on ecological and physical interactions (Levins 1992). Since these patterns and processes occur at different scales, the effect on biological patterns, like space use, will vary with scale (Anderson et al. 2005).

Intrinsically linked to space use is the concept of habitat, a collective term for the resources and conditions an individual or species needs to survive or reproduce (Hilden 1965, Odum 1971, Block and Brennan 1993, Garshelis 2000). The study of habitat use is an important part of ecological research because habitat quality is intrinsically tied with fitness, and ultimately population dynamics (Boyce and McDonald 1999).

Patterns of habitat use can be hierarchically defined using spatial order, ranging from the geographic range of a species to site-specific components (Johnson 1980). Landscape scale habitat studies examine broad patterns of habitat use and may be crucial for wide ranging animals like large mammals or birds (Kristan 2006). However, even wide ranging animals typically demonstrate smaller scale selection of space to use, which can vary from home ranges, and foraging areas, to nesting sites. Multi-scale analysis is needed to address the hierarchical nature of habitat use (Fletcher and Koford 2002, Whittingham et al. 2005).

Little is known about both landscape and local scale space use by Common Nighthawks (*Chordeiles minor*, hereafter referred to as nighthawks). This far ranging species typically occupies defended territories (Armstrong 1965, Poulin et al. 1996), but there are some data suggesting that nighthawks forage at sites that are distant from these defended spaces (Brigham 1990, Firman et al. 1990). Furthermore, nighthawks occur across a variety of ecoregions in North America. Multi-scale research into nighthawk space use is timely and relevant because the species was recently assessed as Threatened in Canada, with habitat cited as a potentially limiting factor for populations (COSEWIC 2007). Previous research on this species has been limited to the southern interior of British Columbia and forested areas in Saskatchewan (Firman et al. 1993, Fisher et al. 2004, Fletcher et al. 2004). Mine is the first study to focus on space use by these birds in a grassland system, which represents an area where a large proportion of nighthawks breed in Canada (COSEWIC 2007).

My objectives were to examine patterns of habitat use by nighthawks in areas with intact native grassland and to investigate the effect of environmental variables on the detection of nighthawks during population surveys. I also documented nighthawk home range characteristics and spatial-temporal movement patterns in a patchy landscape consisting of native grassland, planted grassland and cropland.

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2.0 HABITAT ASSOCIATIONS OF COMMON NIGHTHAWKS (*CHORDEILES MINOR*) IN SOUTHWESTERN SASKATCHEWAN: A LANDSCAPE SCALE PERSPECTIVE

2.1 Introduction

The concept of habitat is more than simply a reference to the place where an organism lives (Odum 1971), it is the sum of distinctive resources and conditions that individuals need to survive and reproduce (Block and Brennan 1993). For all organisms, these resources typically include food, cover, and water, while other, more specific factors typically differ between species (Leopold 1933). While general habitat requirements can be species-specific, components are chosen by individuals to meet their own specific requirements for reproductive success and survival (Hilden 1965).

Many species' habitat associations are scale dependent (Michaels and Cully 1998, Saab 1999, Cushman and McGarigal 2002, Kristan 2006) and are related to fitness consequences (Chalfoun and Martin 2007). Therefore, habitat studies need to include spatial scale to assess the possibility of scale-dependent habitat associations (Johnson 1980, Hutto 1985). From these habitat associations, inferences about ecological patterns and processes, which can also be scale specific (Wiens 1989), may reveal the mechanisms and cues used for habitat selection.

Habitat selection may be at least partly determined by how an individual is first able to evaluate habitat suitability (Hutto 1985, Koford and Fletcher 2002). For example, a flying bird migrating into an area may select habitat using a top-down approach because they first perceive a landscape from the sky, while a ground bird (e.g., galliform) would evaluate habitat using a bottom-up approach because their perspective is from the ground and they likely evaluate habitat from within a patch. From an aerial perspective, birds should be able to evaluate large-scale habitat characteristics such as habitat type, patch size, degree of fragmentation, and other general features of the environment (Orians and Wittenberger 1991). Some migrants may use this approach to select habitat when they first arrive from their wintering grounds because general habitat types and features typically determine the types of microhabitats within a patch. Based on this assumption, it seems prudent to begin habitat evaluation of migrants from a landscape perspective before investigating the finer scale habitat features used by these individuals.

Common Nighthawks are Neotropical migrants and thus are likely to use a top-down approach to assess coarse habitat characteristics in a variety of landscapes before assessing finer characteristics within habitat patches. Following Hutto's paradigm (Hutto 1985) and the assumption that fitness is related to scale dependent habitat selection (Rettie and McLoughlin 1999, Rettie and Messier 2000, Chalfoun and Martin 2007), I studied nighthawk habitat associations at a landscape level. I included multiple spatial scales because understanding the scales at which nighthawks' respond to habitat composition will allow us to better understand the mechanisms by which birds select their habitat.

Habitat requirements of nighthawks are largely unknown, despite the widespread distribution of this species over most of North America (Poulin et al. 1996). In prairie ecosystems, nighthawks are believed to prefer natural or semi-natural (i.e. tame pastures) grasslands over cultivated lands (Poulin et al. 1996), but there are no published data specifically addressing nighthawk habitat use in the Great Plains. Previous studies have focused on small scale roost-site level selection in a grassland/forest ecoregion (Fisher et al. 2004) or have lacked the sample size to conduct robust habitat analysis (Rottenberry and Wiens 1980, Debinski and Brussard 1994, Saab 1999). Mine is the first landscape-scale habitat study focused on nighthawks and is relevant and timely because understanding nighthawk habitat associations will enhance our ability to address issues surrounding their conservation and management.

Interest in nighthawk habitat conservation is increasing because recent data indicate that the population is declining (Jones and Bock 2002, Sauer et al. 2005). Breeding Bird Survey data indicate an annual decline of 3.9% over the past 30 years, which has increased to 9.5% during the last decade (Committee on the Status of Endangered Wildlife in Canada; COSEWIC 2007). In response to this declining population trend, COSEWIC assessed this species as 'Threatened' in Canada. Factors contributing to nighthawk declines are unknown and probably multi-factorial, but habitat loss is perceived to be a major factor contributing to the decline (COSEWIC 2007).

Habitat in the Great Plains is a potentially limiting factor for nighthawk populations because extensive anthropogenic change has altered the natural landscape, creating a mosaic of cropland, planted grassland, and native grassland fragments (Samson and Knopf 1994). Even the structure and function of remaining grassland fragments are different from those of historical grasslands because humans manage many of the ecological processes, like fire and grazing, on most remaining patches of planted and native grassland (Samson and Knopf 1994).

It is difficult to precisely determine the effect of grassland loss on nighthawk populations because these birds occur in a variety of habitats, ranging from urban neighbourhoods to boreal forests to open plains (Poulin et al. 1996). Their widespread distribution may be due to their ability to exploit different habitats, including cropland. Superficially, cropland might be expected to provide suitable habitat for nighthawks because fields represent open space which should be suitable for foraging. Conversely, cropland may not provide other habitat components, like areas to nest. Thus, a landscape composed of entirely cropland is unlikely to represent a functional landscape which would enable nighthawks to meet their survival and reproduction needs. Wildlife managers are currently unable to quantitatively evaluate the usefulness of cropland for nighthawks because so little is known about their general habitat requirements.

The objective of my study was to assess large-scale habitat associations of nighthawks in southwestern Saskatchewan. I examined both local and landscape responses to landscape composition and features. Understanding avian habitat use at different spatial scales is important for inferring mechanisms behind patterns (Wiens 1989, Clark and Shutler 1999), particularly in understanding how a facultative grassland bird like the nighthawk responds to landscape factors.

2.2 Methods

In 2001, the Saskatchewan Watershed Authority (SWA) conducted a survey for Common Poorwills (*Phalaenoptilus nuttallii,* hereafter poorwills) in southwestern Saskatchewan (MacDonald et al. 2003). Members of the surveying team detected low numbers of poorwills, but commonly recorded nighthawks. I used the data on nighthawk detections from the SWA poorwill survey to evaluate large-scale habitat associations by nighthawks.

2.2.1 Study Area

The study area encompassed the southwestern corner of Saskatchewan, Canada (Figure 2.1) near the northernmost edge of the mixed grassland ecoregion within the Great Plains. This area is about 7,000,000 hectares and has the greatest remaining area of native grassland in the province (Hammermeister 2001). Natural or semi-natural grasslands compose approximately 63% of the study area with the remainder being mostly cropland. Southwestern Saskatchewan provides an ideal area to examine large-scale habitat use by nighthawks due to the gradient of highly contiguous grassland in the west that becomes highly fragmented as cropland density increases towards the east. This area is considered semi-arid, with an annual average of 348 mm of precipitation and daily mean temperature of 15.7°C during the summer months (May-August: Val Marie, Environment Canada).

2.2.2 Common Nighthawk Detection

From a Geographic Information System (GIS) map, 90 townships in the southwest corner of Saskatchewan were randomly chosen to be surveyed. Townships had to include at least 75% grassland (defined as native grassland, seeded pasture, and woody vegetation less than 2 m in height) based on Saskatchewan's Southern Digital Landcover classification. Townships were chosen according to grassland composition because poorwills are generally not associated with cultivated areas (Woods et al. 2005); anecdotal evidence suggests that nighthawks share the same aversion. Surveys were generally conducted from gravel or dirt roads, thus townships that did not contain either were not included in surveys.

Surveys were conducted as road-based transects, where a random point within each selected township was used to establish a starting point. Road surveys began as near as possible to the random point and traveled in a random direction relative to the direction of the road. The initial starting direction was continued as far as possible and if a 'T' intersection was encountered, the direction taken was chosen randomly. In remote areas, random starting points and direction were disregarded due to a limited availability of roads. Most transects were road-based, but three additional walking transects were included because some areas with potential habitat did not have road access.

Surveys were conducted between 23 May and 11 July 2001. The timing coincided with when poorwills call most intensely in late spring and early summer (Kalcounis et al. 1992, Woods et al. 2005). The breeding season for nighthawks largely overlaps with poorwills, making the timing of the survey also ideal for nighthawks. Surveys began 30 minutes after sunset and continued for 1.5 hours because poorwills and nighthawks are both most active during crepuscular periods. Road-based point surveys were conducted every 800 m, where observers exited the vehicle to conduct a point count. Observers remained at each survey point for three minutes. The first minute was spent listening without playback, followed by playbacks of four or five poorwill calls, followed by another listening period. This procedure was repeated several times until the end of the three minute period. The abundance of poorwills and nighthawks, weather

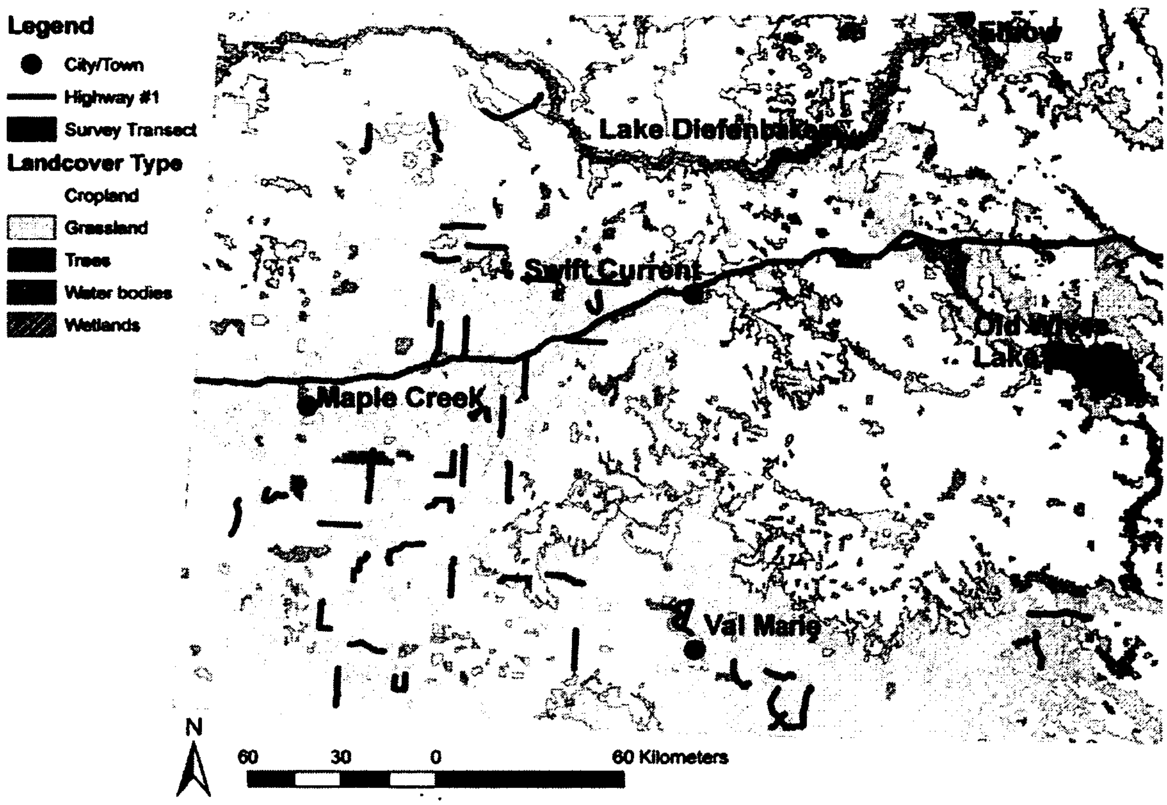

Figure 2.1. Southwestern Saskatchewan study area and survey transects (black lines). Surveys were only conducted in rural municipalities which had more than 75% grassland landcover.

condition, location, moon phase, and relative insect activity were recorded at each point. Transects consisted of 13 to 20 point surveys. The majority (79%) of transects had 16 point surveys. Each transect was surveyed once to maximize the total area surveyed and to increase sample size. Surveys were not conducted during bad weather (i.e. rain and/or strong winds) and those surveys conducted when the wind speed was > 29 $kmhr^{-1}$ were not included in the analysis.

2.2.3 Scale-dependent Design

My purpose was to evaluate habitat associations of common nighthawks at the local and landscape scale, corresponding to Johnson's (1980) second and third order resource selection. I used a scale-dependent design by deriving each variable at two scales. At the local scale, each survey location was buffered with a 400-m radius and the 50 ha within this buffer was evaluated. At the landscape level, each transect was buffered with an 800-m and 1600-m radius, thus the area evaluated for each transect was an average of 2504 ha and 4838 ha, respectively (Figure 2.2).

2.2.4 Landscape Variables

Landscape variables for each transect buffer were derived from a GIS database assembled for the study area. Transects in the Cypress Hills were excluded from the analyses because the area is composed of more trees and has greater elevations than the other transects, thus potentially acting as an outlier. All GIS analyses were undertaken using Arc Info 9 (Environmental Systems Research Institute, Redlands, CA).

My main source of habitat data was a vector layer of the Generalized Landcover for the Canadian Prairies provided by the Prairie Farm Rehabilitation Administration (PFRA 2003). These data were initially collected as LANSAT 7 imagery between 1993 and 1995 at a 30 m resolution and then converted from raster into seamless vector coverage of the agricultural extent of western Canada. This generalized format may actually be more accurate than the original imagery (PFRA 2003). I used the Generalized Landcover layer and Hawth's Tools (Beyer 2006) to calculate the percentage of grassland cover (%GRASS) and distance to nearest water (DWATER) at each scale (Table 2.1). Water sources included rivers, lakes, and wetlands. Distance to nearest water was evaluated from the centre of each point count and averaged among each point count within each transect (DWATER).

As a surrogate for vegetation height and aboveground productivity, I used a normalized difference vegetation index (NDVI) to assess the concentrations of green vegetation in each point count and transect. My digital NDVI layer was provided by the National Aeronautics and Space Administration's (NASA) MODIS (Moderate Resolution Imaging Spectroradiometer) database (NASA 2006).

2.2.5 Environmental Variables

I also included the environmental conditions during surveys in my model selection procedure because these potentially influence detection of nighthawks. Cloud cover (CLOUD) was recorded as percent cover. Moonlight was characterized using two variables, percent moon face illuminated (%MOON) and number of minutes after moonrise (MOON_RISE). The second moonlight variable reflects the cyclical

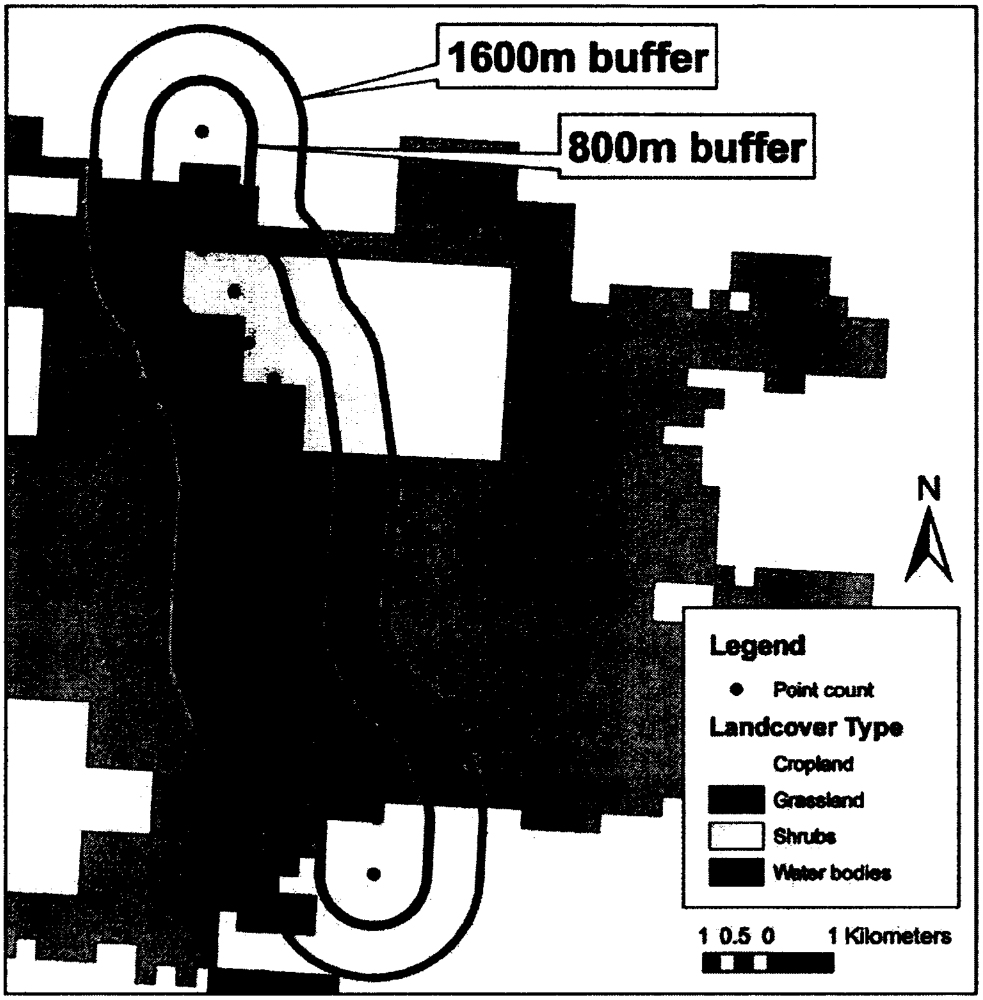

Figure 2.2. Schematic diagram of a survey transect and associated landcover. Transects were surrounded by 800 m and 1600 m buffers and used as replicate units of landscapes to examine habitat associations of Common Nighthawks in grassland ecosystems.

Table 2.1. Explanatory variables of landscape characteristics and environmental conditions used in my analyses of Common Nighthawk habitat association in southwestern Saskatchewan, Canada, 2001. Each variable was generated for replicates of 800 m and 1600 m buffered transects, and 400 m point counts.

Variable	Description
%GRASS	Percent composition of grassland habitat
DWATER	Average distance to nearest water
NDVI	Aboveground vegetation productivity
CLOUD	Percent of cloud cover
%MOON	Percent of moon face illuminated
MOON_RISE	Number of minutes after moonrise
TEMP	Temperature during survey

nature of the lunar cycle by incorporating moonrise times and subsequently, takes into account whether the moon was waxing (i.e. increasing moon face) or waning (i.e. decreasing moon face). The number of minutes after moonrise was calculated by subtracting the time each point count was conducted from the time of moonrise. I used zero in the analysis when moonrise and moonset occurred before the surveys began (i.e. no moon during surveys). Temperature (TEMP) was recorded during each point count and the average for each transect used in the analysis.

2.2.6 Statistical Modeling

Percentage data were arcsine transformed to normalize their distributions (Zar 1999) and I eliminated correlated ($r \geq 0.7$) variables by choosing the variable with the lowest p-value based on univariate tests of characteristics of presence and absence locations. I modeled each spatial scale separately to avoid the pseudoreplication that would result from analyzing the several concentric buffers generated for landscape variables at each location. Landscape variables were modeled separately from environmental variables.

I used an information theoretic approach to select the most parsimonious models of nighthawk habitat use (Burnham and Anderson 2002). This method employs Akaike's Information Criterion (AIC) to compare the fit of a suite of *a priori* candidate models. I modeled seven sets of habitat models, six sets of environmental models, and null models for each spatial scale (See Appendix A). I used logistic regression to generate log likelihood for each model (SYSTAT 2004) and calculated AIC values for the suite of models using:

$$AIC = -2\ (\text{log-likelihood}) + 2K$$

where K is the number of parameters.

The model with the lowest AIC value is considered to be the best model of those examined. For transect models, I corrected AIC values for small sample sizes.

$$AICc = AIC + (2(K)(K+1))/(n - K - 1)$$

I ranked each model by comparing the AIC value of the best model with the remaining models using:

$$\Delta AIC = AIC_i - AIC_{min}$$

I calculated Akaike weights, w_i, relative to compared models using:

$$w_i = e^{(-\Delta AIC/2)} / \sum e^{(-\Delta AIC/2)}$$

The sum of w_i's from candidate models is equal to 1 and each of these ratios is the probability that model *i* is the best model considered.

Confidence sets of models were fitted to each data set by finding the smallest subset of candidate models which for the w_i sum to 0.95. This set of models represents with 95% confidence, the set that contains the best fitting model relative to the true model. I also calculated the probability of each variable being in the best fitting model. This functions as a variable selection method that considers all models by their weighted plausibility.

Slopes and standard errors for each variable included in my top models were reported as weighted averages (Burnham and Anderson 2002).

I evaluated model goodness of fit using area under the curve (AUC) of receiver operating characteristic (ROC) plots (Boyce et al. 2002). I scored AUC's according to Hosmer and Lemeshow's general rule where AUC = 0.5 has poor discriminative power (random chance) and 1.0 is a perfect model (Hosmer and Lemeshow 2000).

2.3 Results

In 2001, Saskatchewan Watershed Authority staff conducted 699 point counts on 45 transects in southwestern Saskatchewan detecting a total of 153 nighthawks in the process. Of the 45 transects, I included data from 39 in my analysis. Three transects were eliminated because they were conducted in forested landscapes (Cypress Hills) and three were eliminated due to the occurrence of high winds during surveys. The final dataset included 148 nighthawks detected at 99 points along 23 transects.

The parameters I measured were not strongly correlated and correlation coefficients ranged from 0.00 (environmental and landscape variables) to 0.38 (distance to nearest water and vegetation productivity). I therefore included all parameters in the analysis. Only two 3-way interaction terms (%MOON*MOON_RISE*TEMP) and (%MOON*MOON_RISE*CLOUD) were not included in the final global models after my initial exploratory analyses.

2.3.1 Model Selection

Transect Model – 800 m Buffers

Both habitat and environmental variables were important predictors of the presence of nighthawks on transects with 800-m buffers. The best model was a moderately good fit to describe variation in nighthawk occurrence ($R^2 = 0.28$). Using 95% confidence sets of model weights, I constructed five plausible models of nighthawk habitat use. The landscape models that had the highest AIC weights all included the parameter reflecting grassland landcover.

In summary, using an 800 m buffer around transects, nighthawks were associated with areas containing a high proportion of grassland habitat and that were closer to water (Table 2.2, 2.3, 2.10).

Table 2.2. The best two of eight landscape models based on transects buffered by 800 m in southwestern Saskatchewan, 2001. Rankings are based on AIC values.

Models[a]	K	AICc	Δ AIC	w_i	AUC
%Grass + Dwater	3	44.16	0	0.43	0.82
%Grass + Dwater + %Grass*Dwater	4	45.11	0.95	0.27	0.84
Null	1	54.91	10.75	0.00	

[a] See Table 1 for variable descriptions. Null refers to the model containing no habitat variables.

Table 2.3. Means (± SE) for variables within an 800 m buffered transect. $n_{present} = 23$, $n_{absent} = 16$.

Variable	Present	Absent
% Grassland	78 ± 18	50 ± 8
Distance to nearest water (km)	12.6 ± 1.6	18.8 ± 10.4
Vegetation Productivity (NDVI)	0.42 ± 0.01	0.45 ± 0.02
% Cloud cover	37.9 ± 7.1	22.8 ± 8.4
% Moon face	42.8 ± 6.7	38.9 ± 9.7
Temperature	15.7 ± 1.1	11.4 ± 0.7

Transect Model – 1600 m Buffers

Competing models in my 1600-m transect landscape model were the same as the 800 m transect models. The top model was a moderately good fit for the variation in nighthawk occurrence ($R^2 = 0.31$). I found five plausible candidate models using 95% confidence sets and these models all included grassland cover.

In summary, at the largest landscape scale I assessed, nighthawks are more likely to be detected in areas with a high proportion of grassland and close to water (Table 2.4).

For transects, temperature was the only competing model in the environmental models ($R^2 = 0.19$). Nighthawks were more likely to be detected on warmer nights (Table 2.5, 2.6, 2.10).

Point Count Model – 400 m Buffer

At a local level, both habitat and environmental variables were important predictors of nighthawk occurrence. The top landscape model was my global model and it moderately fit the variation in nighthawk presence and absence ($R^2 = 0.11$).

I found three plausible candidate models based on the 95% confidence sets, which all included proportion of grassland and distance to nearest water.

The variables in my best fitting model consisted of proportion of grassland, distance to nearest water, and average aboveground primary productivity (Table 2.7).

Locally, my analysis shows that nighthawks were more likely to be detected in areas with a high proportion of grassland and close proximity to water.

The probability of nighthawk detection increased with increased light and warmer temperatures (Table 2.8, 2.9, 2.10).

2.4 Discussion

Nighthawks were more likely to occur in areas with high proportions of grassland in the landscape regardless of the scale considered (Figure 2.3). The variable "proportion of grassland" was consistently included in all of the top competing models at all three spatial scales. This is consistent with other multi-scale studies of grassland birds that found grassland habitats are used more frequently than cropland (Ribic and Sample 2001). Grassland habitat clearly provides one or more components critical for nighthawks to survive and reproduce. Nighthawks in the prairies generally nest on rock, bare ground, gravel, or in areas of short grass (Poulin et al. 1996). These microhabitats are more likely to be found in native grassland compared to cropland where vegetation cover is more homogenous and more densely covered in taller vegetation during the growing season which coincides with the birds nesting period.

In addition to nesting habitat, foraging nighthawks may also exploit the higher insect diversity in relatively natural landscapes compared to monoculture landscapes, such as cropland (Billeter et al. 2008). Nighthawk's prey, flying insects, are probably

Table 2.4. The best two of eight combined habitat models based on transects buffered by 1600 m in southwestern Saskatchewan, 2001. Rankings are based on AIC values.

Models[a]	K	AICc	Δ AIC	Weight	AUC
%Grass + Dwater	3	42.58	0	0.44	0.84
%Grass + Dwater + %Grass*Dwater	4	43.54	0.96	0.27	0.84
Null	1	54.91	12.33	0.00	

[a] See Table 1 for variable descriptions. Null refers to the model containing no habitat or environmental variables.

Table 2.5. The best of six models combined environmental models based on transects in southwestern Saskatchewan, 2001. Rankings were based on AIC values.

Models[a]	K	AICc	Δ AIC	w_i	AUC
Temp	2	46.01	0	0.64	0.76
Null	1	60.70	14.68	0.00	

[a] See Table 1 for variable descriptions. Null refers to the model containing no environmental variables.

Table 2.6. Means (± SE) for variables within a 1600 m buffered transect. $n_{present} = 23$, $n_{absent} = 16$.

Variable	Present	Absent
% Grassland	67 ± 12.7	46 ± 4.7
Distance to nearest water (km)	12.6 ± 1.6	18.8 ± 10.4
Vegetation Productivity (NDVI)	0.42 ± 0.01	0.45 ± 0.02
% Cloud cover	37.9 ± 7.1	22.8 ± 8.4
% Moon face	42.8 ± 6.7	38.9 ± 9.7
Temperature	15.7 ± 1.1	11.4 ± 0.7

Table 2.7. The best two of eight combined habitat models based on point counts buffered by 400 m in southwestern Saskatchewan, 2001. Rankings are based on AIC values.

Models[a]	K	AIC	Δ AIC	W_i	AUC
%Grass + NDVI + %Grass*NDVI + Dwater + %Grass*Dwater	6	401.07	0.00	0.49	0.74
%Grass + Dwater + %Grass*Dwater	4	401.77	0.70	0.35	0.74
Null	1	534.70	133.63	0.00	

Table 2.8. The best of six models combined environmental models based on point counts in southwestern Saskatchewan, 2001. Rankings were based on AIC values.

Models[a]	K	AIC	Δ AIC	W_i	AUC
%Moon + MoonRise + %Moon*MoonRise + Temp + Cloud	6	456.6	0	0.99	0.69
Null	1	534.7	78.01	0.00	

[a] See Table 1 for variable descriptions. Null refers to the model containing no environmental variables.

Table 2.9. Means (± SE) for variables within a 400 m buffered point count. $n_{present} = 99$, $n_{absent} = 488$.

Variable	Present	Absent
% Grassland	87 ± 3	63 ± 2
Distance to nearest water (km)	11.2 ± 0.9	16.1 ± 1.4
Vegetation Productivity (NDVI)	0.41 ± 0.03	0.43 ± 0.0
% Cloud cover*	24.9 ± 3.1	32.6 ± 1.7
Temperature (°C)	16.1 ± 0.5	13.2 ± 0.7
% Moon face	42.8 ± 3.2	38.9 ± 5.6

Table 2.10. Model averaging of variable estimates included in top models.

Model	AIC[a]	*wi*	ß	SE
Point count				
Landscape Models				
%Grass	503.49	0.00	-1.96	3.79
%Grass*NDVI	492.06	0.00	10.14	7.66
Dwater	429.31	0.00	0.00	0.00
%Grass*Dwater	401.77	0.35	0.00	0.00
Environmental Models				
Temperature	500.78	0.00	0.14	0.03
Transect (800 m buffer)				
Landscape Models				
%Grass	48.06	0.06	0.39	12.75
Dwater	51.72	0.01	0.00	0.00
%Grass*Dwater	45.11	0.27	0.00	0.00
Transect (1600 m buffer)				
Environmental Models				
%Grass	46.48	0.05	-0.16	27.08
Dwater	51.72	0.00	0.00	0.00
%Grass*Dwater	43.54	0.27	0.00	0.00
Transect				
Environmental Models				
Temperature	46.01	0.64	0.30	0.12
Cloud			0.10	0.13
%Moon*MoonRise	59.39	0.00	0.00	0.00

[a] AIC values for transect data is corrected for small sample sizes.

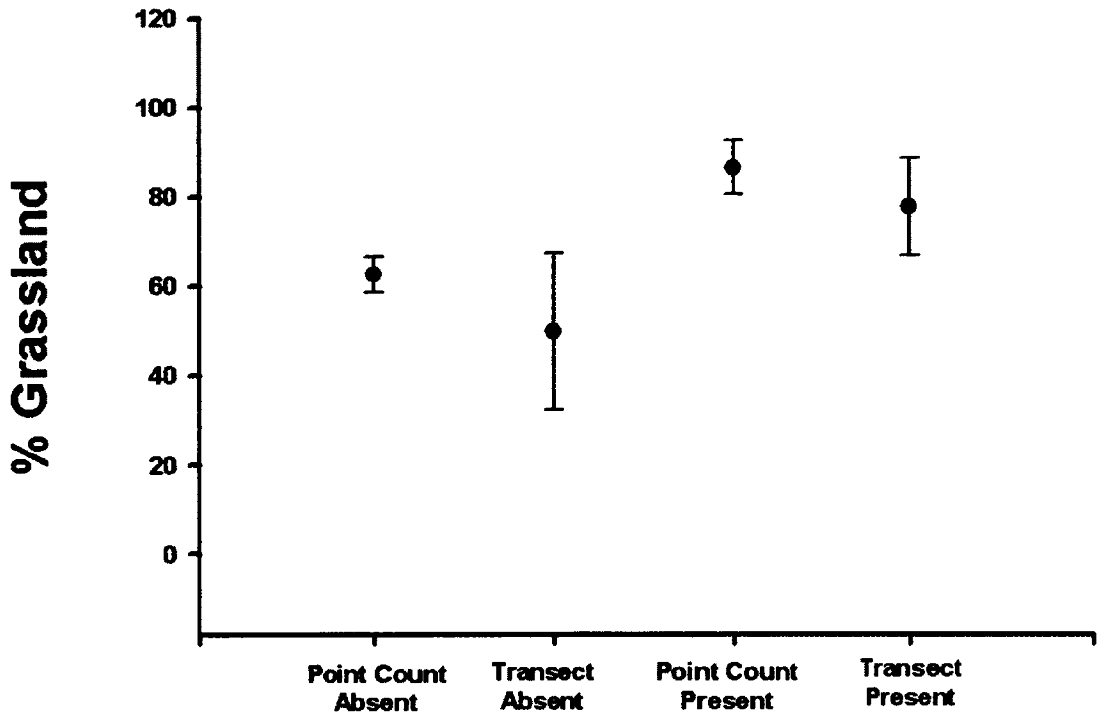

Figure 2.3. Mean percentage of grassland (±95% CI) around point counts (400-m buffer) and transects (1600-m buffer). At both scales, the proportion of grassland habitat was higher where nighthawks were present.

also less abundant over croplands that are routinely sprayed with pesticides compared to grasslands and around water sources.

Nighthawks were detected more frequently closer to water at both the point count and transect scales. Proximity to water was more consistently important at the point count scale, but this difference may have resulted from averaging the distances across point counts for each transect and thereby using a relative index (i.e. average) in the transect analysis rather than a precise measurement (per point count). Despite being one of several parameters included in competing models, distance to nearest water still ranked high among the competing models for data averaged from transects. Furthermore, transects where nighthawks were detected were on average 30% closer to water compared to transects on which nighthawks were not detected. While nighthawks have been observed drinking from standing water sources, it is unknown whether they actually require standing water for drinking. More commonly, these birds are observed hawking prey over water sources, where flying insects, like Chironomids and Trichopterans, are abundant (Brigham 1990, Firman et al. 1990). Water sources may provide a relatively predictable and reliable source of food for nighthawks and therefore close proximity may be advantageous to minimize the time and energy spent foraging. Previous studies of nighthawk habitat selection did not consider proximity to water as a potential variable (Rotenberry and Wiens 1980, Saab 1999, Fisher et al. 2004).

Examining probability curves based on model averaged slopes, the interaction between grassland landcover and proximity to water did not perform better than a simple additive model. However, this interaction was included in the top models of both transect models. Nighthawks may require both components for their life history, grassland for habitat and water for foraging and potentially drinking. A similar species, the Whip-poor-will (*Caprimulgus vociferous)*, selects for habitat patches close to foraging grounds (Wilson and Watts 2008), suggesting a similar resource complementation argument for nighthawks. Future studies should include analysis of more detailed spatial information about water bodies, that includes smaller sources like wetlands and ephemeral water bodies.

Aboveground primary productivity was consistently included in all competing transect models. Average aboveground primary productivity was lower where nighthawks were detected and this pattern is consistent with observations that nighthawks are more common in areas with low vegetation height and bare rocky ground. Areas with high primary productivity likely have tall and dense vegetation, which are structural characteristics that make areas not suitable for nest sites or roosts. While my assumption that low aboveground primary productivity is an indicator for low vegetation height likely holds true in most cases, actual measures of groundcover parameters such as average vegetation height and bare ground cover would be meaningful parameters to include in future studies. Previous studies did not include aboveground primary productivity in their analysis (Rotenberry and Wiens 1980, Saab 1999), but my results suggest that these variables warrant further exploration.

Temperature was important in all three models. Ambient temperatures were generally higher on nights when nighthawks were detected. Other nightjars also increase foraging activity when ambient temperatures are higher (Jetz et al. 2003), likely because insects are more active (Jetz et al. 2003) and therefore easier to exploit. Nighthawks also likely spend less energy thermoregulating on warm nights and may be more actively displaying. Temperature may affect detectability and future studies should consider its effect on estimates of abundance.

The percentage of moon face that was illuminated combined with time of moon rise were both positively correlated with nighthawk detection and included in competing models for both point counts and 800 m buffered transects. The % moon face illuminated only differed by an average of 4% between surveys where nighthawks were detected. For these reasons, moonlight probably has some, albeit a small direct influence on nighthawk activity. Nightjars are typically visual predators and therefore activity is constrained by low light levels. However, while most other nightjars are less active during periods with low light (Brauner 1952, Holyoak 2001, Jetz et al. 2003, Woods and Brigham 2008), nighthawks are not active during periods of true night, regardless of moonlight levels (Aldridge and Brigham 1991, Brigham and Fenton 1991, Brigham and Barclay 1992). Furthermore, insects are more abundant at dusk than at night (Jetz et al. 2003), and therefore nighthawks likely have higher foraging efficiency at dusk when insects were more active when they are able to see prey best. During surveys in bright moonlight conditions, it is possible that birds were taking advantage of the slightly brighter conditions to forage when insects are more detectable.

2.4.1 Model Performance

Using ROC curves, competing transect models for landscape variables scored a mean 0.83 AUC, which is considered excellent discrimination (Hosmer and Lemeshow 2000). In comparison, the environmental model also scored slightly lower, but still with what is considered acceptable discrimination (0.76 AUC). The competing point count models scored on average 0.74, which is considered acceptable (Hosmer and Lemeshow 2000), but the environmental model showed less discrimination (0.69 AUC).

2.4.2 Limitations

The data I used were collected using a survey protocol specifically designed to detect Common Poorwills. Thus poorwill calls were used for playback surveys and the surveys were conducted beginning at late dusk and into the night when poorwills are most active (Holyoak 2001, Woods et al. 2005). Using playbacks of nighthawk calls should increase nighthawk detectability. While an appreciable number of nighthawks were detected during the surveys, the actual abundance of nighthawks was almost assuredly underestimated, which limited my analysis to presence/absence data rather than abundance.

While the competing point count models were good predictors for nighthawk presence, the landscape (transect) models were even better. I interpret this to suggest that the habitat parameters I modeled were more highly associated at a landscape level. The uneven sample sizes between presence and absence data for point counts ($n_{present} = 99$, $n_{absent} = 488$) may have contributed to the lower predictive performance at the local spatial level (Capen et al. 1986, McMaster and Davis 2001). Samples sizes between point counts where nighthawks were present and absent were considerably uneven, where absences outnumbered presence by approximately 4 times. In addition, both of the top competing models at the point count level had a high number of parameters and one was the global model. These models are valuable for understanding local nighthawk responses to landscape features, but the lack of specificity needs to be considered when formulating conservation management strategies.

While the results of my study are region-specific (i.e., northern mixed grassland), some of the variables I found to be important need to be assessed in other systems. For example, water bodies may also be important as foraging areas for other nighthawk populations (e.g., arid or boreal systems). Observations from other studies often cite records of several nighthawks foraging over wetlands and bogs in boreal systems and over water sources like rivers in arid systems (i.e., the Okanagan Valley in British Columbia; Brigham 1990, Firman et al. 1993, Brigham and Barclay 1995). While other habitat features may differ according to ecotype, exploiting abundant insects above water bodies is a likely a common foraging strategy of nighthawks.

2.4.3 Management Implications

My results indicate that nighthawks are more likely to be found in areas with a high proportion of grassland, particularly grassland where aboveground primary productivity is low. This association with natural or semi-natural grassland is a potential factor in prairie nighthawk population declines given that other studies have shown that birds associated with grassland have declined significantly in the past century (Herkert 1995, Jones and Bock 2002). Furthermore, Jones and Bock (2002) hypothesized that increased levels of cultivation coupled with reduced livestock grazing have reduced the amount of available nighthawk habitat from historical levels. Conservation plans should incorporate grassland acquisition and protection, particularly in areas with high proportions of grassland in large patches (Herkert et al. 2003) because these characteristics are associated with higher reproductive success for many grassland bird species (Koper and Schmiegelow 2006). To provide habitat, grassland conservation should be incorporated into management and recovery strategies (Coppedge et al. 2001).

I found that habitat associations differed between spatial scales which likely have important implications for understanding nighthawk habitat requirements. In particular, knowledge of landscape scale requirements is needed to inform grassland bird management (Gergin et al. 2000, Ribic and Sample 2001, Fletcher and Koford 2002, Herkert 2003, Koper and Schmiegelow 2006). The composition (Saab 1999, Ribic and Sample 2001), size (Gergin et al. 2000, Herket et al. 2003, Koper and Schmiegelow 2006) and structure of surrounding landscapes (McMaster et al. 2005) can influence avian productivity; hence grassland bird conservation should include landscape level management (Cunningham and Johnson 2006).

2.4.4 Future Directions

Being crepuscular, nighthawks are difficult to detect during typical avian surveys (e.g. Breeding Bird Surveys) which are normally conducted in the early morning. Several previous studies have attempted to characterize nighthawk habitat in multi-species surveys, however, the limited sample sizes that resulted did not allow for robust statistical analyses (Rottenberry and Wiens 1980, Debinski and Brussard 1994, Saab 1999). Although my surveys were conducted in the evening, only poorwill playbacks were used and therefore the survey likely did not maximize detection efficiency for nighthawks. Nighthawk surveys should be conducted in the evenings using playbacks of nighthawk territorial calls and booming displays to increase effectiveness, but also to increase sample size to enable more rigorous analysis. Analysis using abundance data would provide considerable additional information.

Data about diet and foraging ecology are needed to reveal limiting factors on nighthawk populations. For example, I found that nighthawks were more likely to occur in close proximity to water sources. However, with only anecdotal observations of nighthawks foraging over water and without more detailed investigation, it is unknown why nighthawks are associated with water bodies, what specific kinds of water sources are important, or details about the level of dependence on standing water.

While I examined habitat features, I did not include demographic data like survival and productivity. While I found that nighthawks were associated with native grassland in close proximity to water, my data do not allow me to link these associations with habitat quality and individual fitness. Some studies assume fitness consequences (Hilden 1965, Radford and Bennett 2007), but without the demographic link from the study area and during the study's time period, this assumption is equivocal (reviewed by Garshelis 2000). Habitat use is not synonymous with habitat preference and is not necessarily indicative of high habitat quality (Pulliam 1988, Boyce et al. 2003, Kristan et al. 2007). Some habitats can be ecological traps, where animals select areas that retain high quality habitat cues, but which negatively affect fitness (Shochat et al. 2005, Robertson and Hutto 2006). The steep population decline and conservation status of nighthawks as a threatened species in Canada highlights the need for more information about this species' demography.

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APPENDIX A: Models

Landscape Models

Grass

Dwater

Grass + Dwater

Grass + Dwater + Grass*Dwater

Grass + NDVI + Grass*NDVI + Dwater

Grass + NDVI + Grass*NDVI

Grass + NDVI + Grass*NDVI + Dwater + Grass*Dwater

Null

Environmental Models

%Moon + MoonRise + %Moon*MoonRise

%Moon + MoonRise + %Moon*MoonRise + Temp

%Moon + MoonRise + %Moon*MoonRise + Cloud

Temp

Temp + Cloud

%Moon + MoonRise + %Moon*MoonRise + Temp + Cloud

Null

3.0 SPATIAL-TEMPORAL VARIATION IN THE HOME RANGE OF COMMON NIGHTHAWKS (*CHORDEILES MINOR*)

3.1 Introduction

The concept of home range is central to understanding a species' habitat requirements and population dynamics because resources within an individual's home range should fulfill its needs for both survival and reproduction (Nice 1941, Burt 1943, Anderson et al. 2005). Because home range size is typically linked to individual fitness and population dynamics (Both and Visser 2000, Maguire 2006), it is important to understand home range parameters such as boundaries and how an animal uses it's home range, as well as factors which generate variation in these parameters (Borger et al. 2006).

In the breeding season, the home range for individuals of many species' include territories. These two spatial concepts differ in that territories are defended from conspecifics (Begon et al. 2006). Boundaries and spatial use of territories and home ranges differ among species and individuals, and variation depends on a variety of potential factors, including body size (Reiss 1988, Mazerolle and Hobson 2004), hormone levels (Chandler et al. 1994), habitat and resources (Elchuck and Wiebe 2003), season (Anderson et al. 2005, Grund et al. 2008), and level of intraspecific competition (Maher and Lott 1995, Zabala et al. 2007). Home ranges and territories can be classified into types of territories, where behaviour and activity determine categories (Nice 1941).

During the breeding season, Common Nighthawks (*Chordeiles minor,* hereafter referred to as nighthawks) are considered a strongly territorial species (Armstrong 1965, Caccamise 1974, Wedgwood 1973). Male nighthawks have been reported to aggressively defend territories from competing males and are often seen displaying to females in their territories (Poulin et al. 1996). Nighthawk territories are conspicuously demarcated at dusk and dawn when males repeatedly call and display. Displays consist of fast swooping dives punctuated by a loud "boom" or "buzz" at the bottom of the dive (Poulin et al. 1996). When not displaying or defending territories, male nighthawks typically roost in the territory during both the day and night (Poulin et al. 1996). While roosting, nighthawks are difficult to detect because they possess both cryptic plumage and employ behavioural camouflage (Rust 1947). Nighthawks are conventionally thought to occupy a territory that fulfilled mating, nesting, foraging, and roosting requirements (Type A, Nice 1941).

Previous studies assumed that nighthawks roosted within their territories, and only used data on the spatial distribution of displays (mostly at dusk) to delineate space use (Armstrong 1965). Armstrong (1965) reported that average home range size of nighthawks was 10.4 ha in urban areas, while Wedgwood (1973) found that home range size was 28 ha in rural areas. Both of these estimates were based on the assumption that nighthawks fulfilled all their basic requirements (e.g., foraging) within the confines of the defended territory.

The assumption that all breeding season activity occurs within the defended territory has never been directly evaluated. Nighthawks have been observed to concentrate foraging activities in specific locations with high food abundance, like water bodies (Brigham 1990, Aldridge and Brigham 1991, Brigham and Fenton 1991, Brigham and Barclay 1995), suggesting that individuals sometimes leave spatially explicit territories to exploit food sources. Particularly in grassland ecosystems, nighthawks may forage over riparian areas which usually support rich concentrations of flying insects. Furthermore, nighthawks are capable of flying long distances to exploit resources. Some strong flyers of similar size have larger home ranges (i.e. Burrowing Owl (*Athene cunicularia*) (33.5 ha; Sissons et al. 2001), Steller's Jay (*Cyanocitta stelleri*) (80 ha; Marzluff et al. 2004), and Merlin (*Falco columbarius*) (630 ha; Sodhi 1991)). A closely related species, the Lesser Nighthawk (*Chordeiles acutipennis*), does not generally defend territories, but ranges widely to find food and water (Caccamise 1974).

Information about space use in the context of home ranges and territoriality is especially crucial given that nighthawk populations are declining (COSEWIC 2007). Breeding Bird Survey data in Canada indicate that there has been a population reduction of 50% since 1968 (Downes et al. 2005). The decline in prairie nighthawk populations has been primarily attributed to human-induced habitat loss (Jones and Bock 2002, COSEWIC 2007). Thus, characterizing space use by nighthawks is important to understand the suite of habitat requirements needed by this species, given that grassland landscapes are fragmented (increasing the distance needed to travel to acquire resources) and are likely of lower quality than they were historically.

My objectives were to use data collected by tracking radio-tagged individuals to characterize nighthawk home ranges in a grassland ecosystem by measuring space use and home range size. This information should be useful to wildlife managers to better understand nighthawk habitat requirements that are relevant for population and landscape level management.

3.2 Methods

3.2.1 Study Area

I collected data on movements by nighthawks carrying radio-transmitters from May to August in 2005 and 2006. My research was conducted in the vicinity of the Rafferty Reservoir (49°14'N, 103°08'W), which is formed by a dam blocking the Souris River in south eastern Saskatchewan, Canada. Located in a semi-arid area (average temp 3.7°C, mean annual precipitation 433.3 mm), the reservoir is surrounded by a strip ranging in width from 1 – 3 km of mixed native prairie used primarily for grazing by domestic animals. The landscape around the strip of native prairie is dominated by cropland (e.g. flax, canola, and mustard) and tame pasture (e.g. alfalfa).

While mostly composed of native prairie, the landscape immediately surrounding the reservoir also includes several different kinds of human altered habitats. Located on the east side of the reservoir, Mainprize Regional Park consists of 260 ha of recreational area. The park includes two small subdivisions of homes (33 houses), a campground, a golf course, and a marina. In addition to the recreational area of the park, there is also considerable oil and gas development in the region (2600 ha) that includes a dense network of gravel roads, two compressor stations, and at least 37 well sites where oil and natural gas are extracted.

3.2.2 Movement and Home Range

All work was completed in accordance with protocol cleared by the University of Regina Animal Care Committee (Appendix B).

I captured nighthawks using two methods. In the evenings, I used playbacks of territorial calls and a decoy to lure territorial male nighthawks into mist nets. Mist nets were set up under displaying nighthawks, in open grassy areas. At night, I used a spotlight and hand net to catch nighthawks that roosted on gravel roads. I attached 3 g radio transmitters (Holohil Systems Ltd., Carp, ON) to all adult males (65 – 98 grams) I captured. Transmitters were attached using thin elastic cord slipped over the wings in a backpack-style harness (Brigham 1992). All birds were released at the point of capture within 20 minutes of being captured.

I stratified the 24 hour day into four different time blocks to reflect different activity periods for nighthawks. Daytime (1000-1900) and true night (2300-0400) are typically periods when roosting occurs and birds are not active (Poulin et al. 1996). During the period around dawn (0400 – 1000) and dusk (1900-2300), nighthawks are typically most active, foraging and or displaying (Poulin et al. 1996). I attempted to track each individual bird during one active period and one roosting period, in non-adjacent time blocks each. By separating the day into time blocks based on different types of anticipated behaviour, I generated an unbiased sample of daily activity by nighthawks.

Tracking birds in different time blocks also reduced the problem of spatial and temporal autocorrelation. Individuals were located during different times of the day, thereby allowing time for the individual to not only change location, but for individuals to move to any point in their home range (Andersen and Rongstad 1989, Leary et al. 1998). For statistical analysis, each spatial location can therefore be treated as an independent sample (Erickson et al. 2001). I further minimized spatial autocorrelation by tracking birds during two non-adjacent time blocks.

I plotted the number of re-locations against the estimated home range area to generate area-location curves to determine the minimum number of nighthawk spatial locations needed to reliably estimate home range area (Harris et al. 1990). Based on the asymptote of these curves from four nighthawk home ranges, I determined that 50 observations is a robust sample size to reliably estimate home range. This value is consistent with recommendations from other studies (Seaman et al. 1999). However, to maximize the number of individuals included in my analysis, I also included home ranges that were mapped using a minimum requirement of 30 observations (Seaman et al. 1999).

I defined home range as the area with 95% probability of an individual's occurrence, within a specified time period (i.e., breeding season; Kernohan et al. 2001). To map nighthawk home ranges into 95% minimum convex polygons (MCP; Mohr 1947), I used the Home Range Extension (Rodgers et al. 2007) in ArcGIS. Within this extension, I used the 'Added Area' method to calculate 95% MCP because it removes outliers that add the most home range area until 95% of the observations remain. Other methods are calculated using a subset of points with a mean or median coordinate, which estimates home range area based on an assumed centre which may or may not be realistic. My visual interpretation of each mapped MCP confirmed that this method removed outlier observations.

I only produced home range estimates for male nighthawks for which I had data from all four time blocks and at least 29 spatial locations. Of the six individuals included in my analysis, one home range was estimated based on 29 spatial locations and the asymptote of the area-location curve for this individual suggested that 29 was a sufficient number of observations to estimate home range size.

I performed fixed kernel analysis on two home ranges to illustrate spatial structure that was common among other home ranges. I used Hawths Tools' Fixed Kernel Density Estimator (Beyer 2006) using the reference bandwidth calculated by Home Range Extension in ArcGIS. Because my sample size of spatial locations for most birds were relatively low to accurately produce fixed kernels, reference bandwidth sometimes oversmoothed the polygon, which was evident because the maps overestimated home range area and lacked spatial detail. In those cases, I used a default bandwidth of 100. I visually inspected the home range contours to determine if each bandwidth produced a realistic home range estimate that did not overestimate home range size or create artificially detailed contours.

For my analysis, I included five home ranges that were calculated despite having a limited number (zero locations) of observations from the true night period. These were important to include because they are representative of the magnitude in size differences between previous studies and my data. I did not include these home range estimates in my summary statistics of home range size knowing that the outcomes are underestimates. My purpose in using them was to illustrate spatio-temporal variation in structure and size variability.

3.3 Results

I affixed radio-transmitters to 19 adult male nighthawks during the two summers of my study. One tagged bird could not be re-located likely because it either flew out of receiver range, the transmitter malfunctioned, or the bird was caught by a predator. Data from five birds did not meet the minimum required sample size for observations ($n < 29$) because the radio signal was lost. Two birds died from unknown causes, and five individuals are missing spatial data during the true night sampling period because they roosted in an area outside of receiver range and were never found despite extensive searching. My values for mean home range size are based on the data for six male nighthawks that I located during all four behavioural periods and for whom I met the minimum recommended sample size (Table 3.1).

Of the 19 male nighthawks to whom I affixed radio-transmitters, I caught 15 using targeted mist netting and four were caught in hand nets by spotlighting. Over the entire study area on both sides of the reservoir, I set up mist nets wherever I observed nighthawks displaying. In comparison, I only spotlighted for nighthawks on the gravel roads on the west side of the reservoir because this area had the highest concentration of both birds and roads. Of the 15 nighthawks caught in mist nets, I collected usable spatial data from ten individuals. One individual was never located again, and four exhibited long-range movements until they left the study area (i.e., number of relocations <10). Of the four nighthawks caught using spotlighting while roosting on gravel roads, only one yielded usable data to calculate a home range estimate. The remaining three birds were

Table 3.1 Size of nighthawk home ranges based on 95% minimum convex polygons (MCP), the number of spatially explicit observations used to calculate area (n = 5), and the number of tracking days per bird.

Home Range	95% MCP (ha)	n	Number of days tracked
1*	7.45	21	16
2	144.95	88	58
3	52.81	81	55
4	45.18	58	34
9*	1094	22	16
17	3.74	29	16
19*	7.48	56	43
20	259.23	35	19
24	11.89	47	37
25*	17.33	22	25
27*	16.62	58	17

* Missing night observations, thus incomplete estimate of home range size

extremely wide ranging until they finally could not be relocated (i.e., number of relocations <10).

Average home range size (95% MCP) was 86 ± 99 ha (range: 3.7 – 259 ha; n = 6; Fig. 3.1). I recorded multiple activity centres within some home ranges and these core areas generally corresponded to different types of activity which occurred during different time blocks. For example, one individual night-roosted in a spatially concentrated area, different from its crepuscular defended territory and its day roosting area (Fig. 2.2). Fixed kernel estimates best demonstrate this distinct spatial structure in two home ranges, where the birds flew 2.7 km and 4.3 km respectively between roosting and display areas (Fig. 3.3).

None of the spatial locations I used to calculate home ranges included foraging observations. This was largely because the nighthawks either flew out of receiver range to forage or, when birds could be tracked, foraging bouts were generally too brief (~15 – 30 minutes at dusk and dawn) for me to locate and record spatially the foraging locations. Furthermore, most nighthawks that carried transmitters appeared to forage over the reservoir, making it impossible to track them accurately because they ranged over the length (7 km) and width (0.5 km) of the water body.

Some home ranges spatially overlapped to varying degrees (Fig. 3.4). In 2005, all five nighthawks that carried radio transmitters had overlapping home ranges. While trapping location and trapping effort was similar in 2006, only two of the six radio-tracked birds in 2006 had overlapping home ranges. I suspect that the true extent of home range overlap is higher than the telemetry data suggest, because I observed unidentified males roosting inside a radio-tagged bird's territory and home range.

Furthermore, as many as five males were commonly observed roosting simultaneously within 25 m of each other along the horizontal portion of a split-rail fence in the study area. The frequencies of these types of observations are habitat dependent because birds are more easily detected when they roosted on raised structures compared to the ground where their plumage provided excellent camouflage.

3.4 Discussion

While there was considerable variation in my estimates of home range size, the average value (86 ± 99 ha) based on telemetry data was three times larger than previous estimates for nighthawks in rural areas (28 ha) (Wedgwood 1973). Given that nighthawks are strong flyers, accustomed to making long migratory flights, and are aerial insectivores (Poulin et al. 1996), it is not surprising that the home range size of this species is large. Previous estimates were made based only on observations of displaying birds (Armstrong 1965, Wedgewood 1973). My data indicate that nighthawks will range outside of defended display areas. For comparison, I averaged the territory size (i.e. based only on displays and interaction behaviour) for five birds and found the average 95% MCP to be only 2.1 ha.

Nighthawks' specialized foraging tactics often result in high concentrations of birds foraging over water bodies where insect abundance is high (Brigham 1990, Aldridge and Brigham 1991, Brigham and Fenton 1991, Brigham and Barclay 1995). Assuming that birds flying over the reservoir in my study area at dusk and dawn were foraging, I found that eight tagged birds consistently foraged over the reservoir. These eight birds defended upland territories to which they commuted at dusk and dawn, resulting in

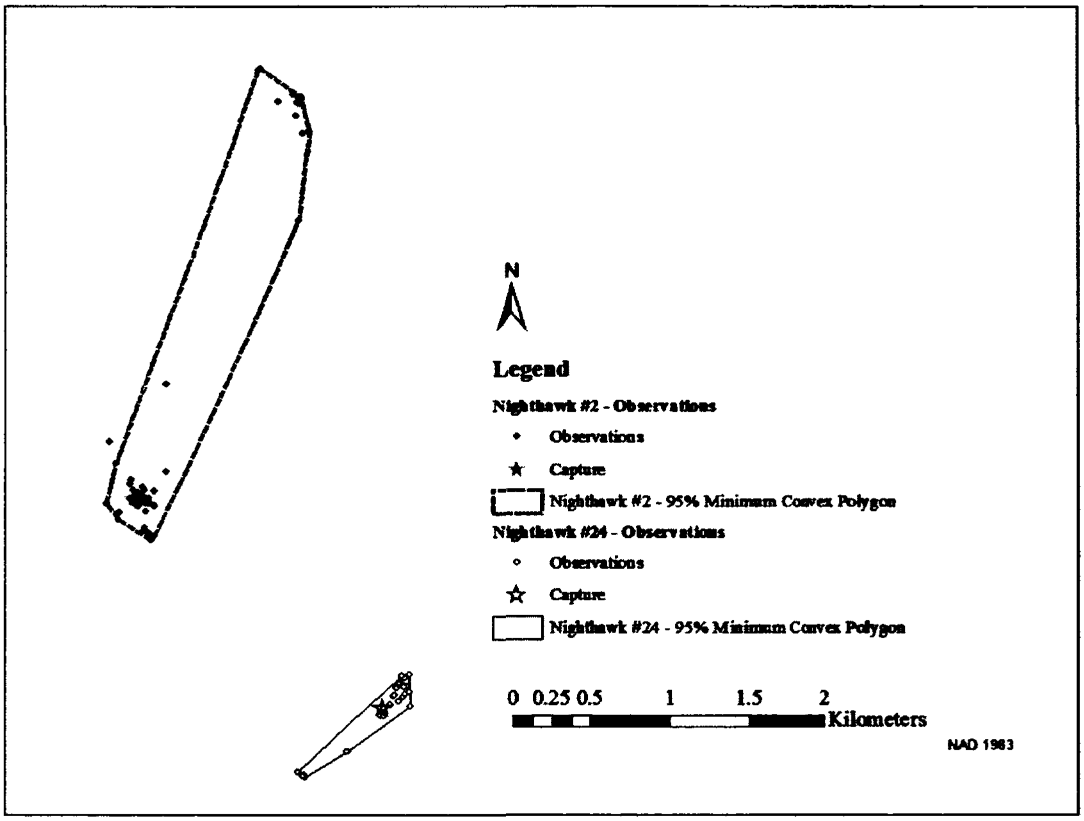
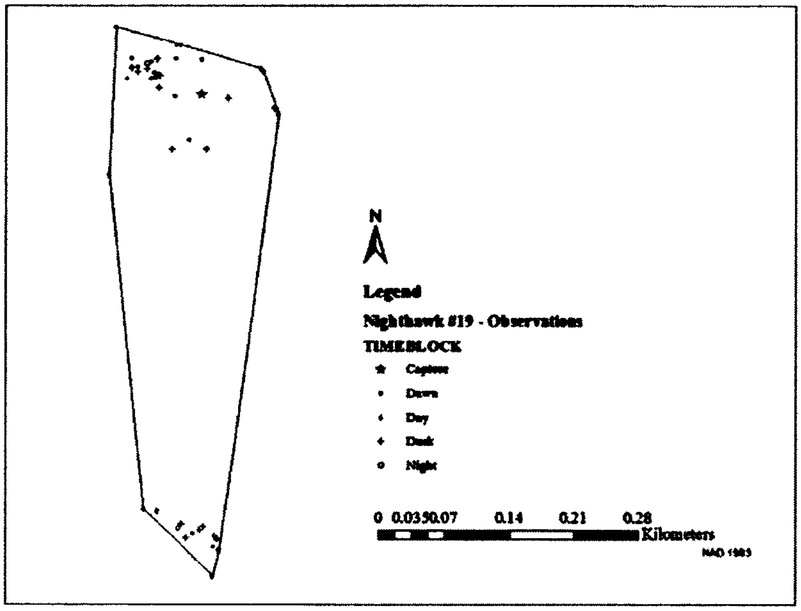
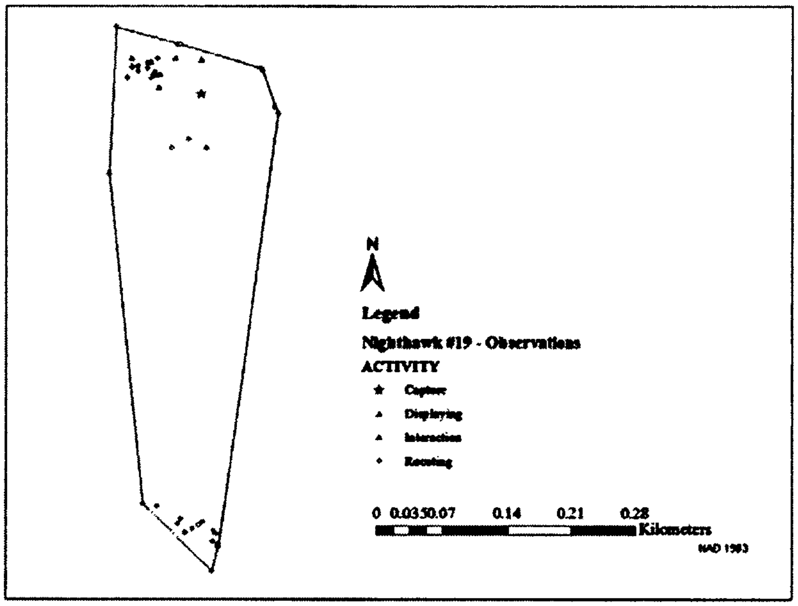


Figure 3.1. Size variation in the home size of Common Nighthawks. Using 95% MCP, these two home ranges included observations from all four activity periods. Bird #2 had a home range 12 times larger (145 ha) than #24 (12 ha).



a)



b)

Figure 3.2. Multiple activity centres differentiated by different time blocks. A) Observations as a function of time block. During the day, the individual was more often found in the south activity centre. B) Different activities observed depict a defended territory in the northern core area.

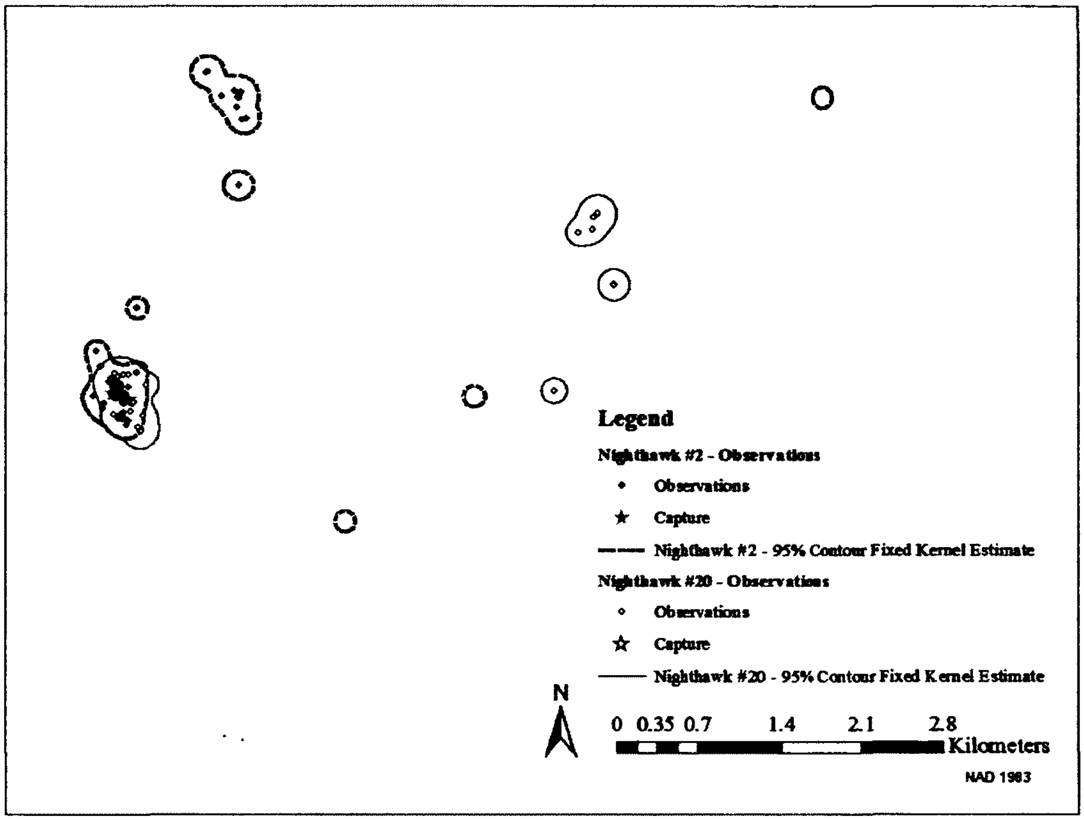


Figure 3.3. Multiple activity centres used by two nighthawks. Using 95% contours determined by fixed kernel density estimators, each home range had two core areas. In these examples, the southern core areas were defended (= territories), but the north and northeast contours illustrate where the individuals regularly roosted during the day. The area between these core areas had a low probability (<5%) of use.

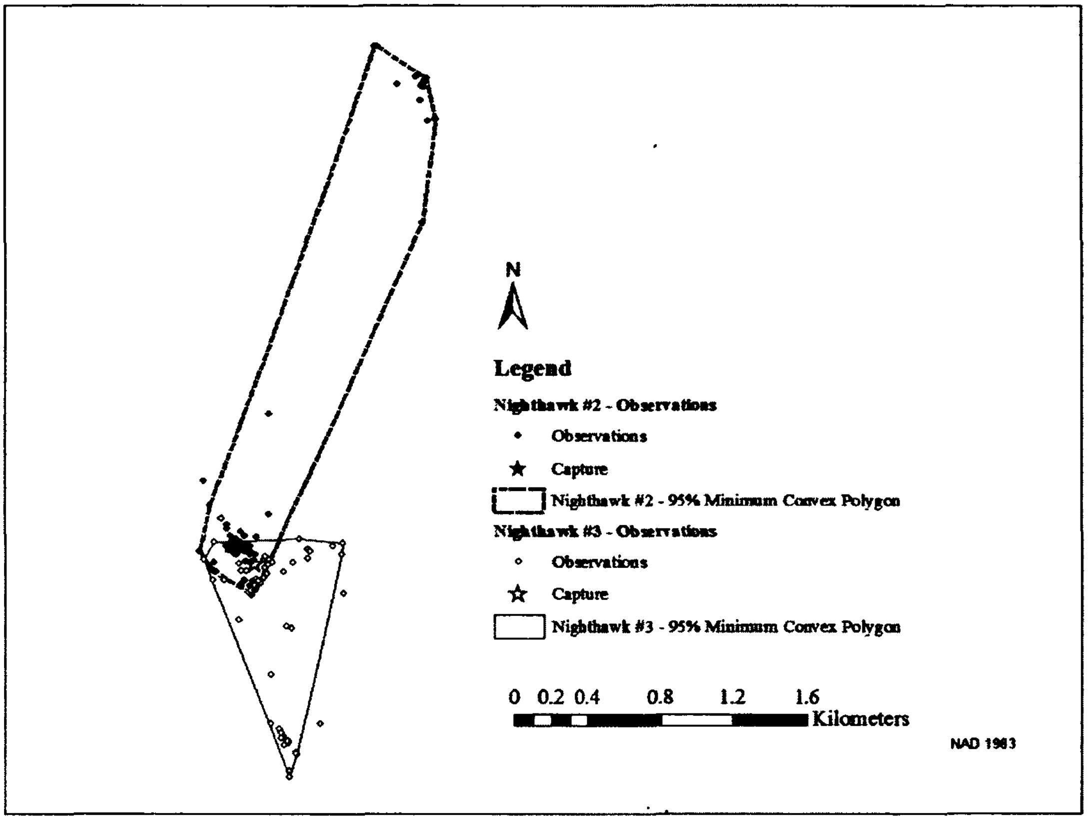


Figure 3.4. An example of two individuals with simultaneously overlapping home ranges.

large home ranges. Using Nice's (1941) territory types, these eight nighthawks occupied Type B territories, as they mated and nested in the area, but foraged elsewhere. These observations suggest that foraging areas are not defendable or predictable due to their large area, and that nest sites may be limiting and therefore worth defending.

Within the large home ranges, I found seven tagged nighthawks with spatially and temporally differentiated home ranges. These individuals occupied distinct activity areas that were separated by areas of low use, while five tagged birds used areas within their home range more homogeneously. Core activity areas likely result in larger home ranges because of low use areas interspersed between high use areas. This pattern has not previously been documented for nighthawks, but it is common for other birds including diverse species, such as Burrowing owls (*Athene cunicularia*, Haug and Oliphant 1990), and Northern Flickers (*Colaptes auratus*, Elchuck and Wiebe 2003), which are similar in size to nighthawks, and Bank Swallows (*Riparia riparia*, Garrison 1999), which have a similar foraging strategy.

Previous studies likely underestimated nighthawk home range size because it was assumed that birds remained on their display grounds during the day and night. However, an alternative explanation is that home ranges which showed spatially distinct activity areas were the result of selective use of available habitat and that home range size is dependent on habitat, which varies between studies (Pasinelli 2000). I found that core activity areas were often habitat patches unlike the surrounding landscape. While surrounded by native prairie, I commonly found tagged roosting nighthawks in a patch of dead aspen, an area littered with scrap metal, an oil compressor station, and a large pile of extracted tree stumps. Anecdotally, all of these habitat patches appeared to provide many potential roost sites similar in colouration to nighthawks and many flat narrow platforms, two of the characteristics described for roosts of nightjars (Holyoak 2001). Variation in home range size may depend on available habitat and habitat configuration (i.e., patches, Fraser and Stutchbury 2004). If activity centres are dependent on habitat type, nighthawks may require a larger area than just their display territory to fulfill basic needs, especially in patchy grassland ecosystems. Similarly, lesser nighthawks (*Chordeiles acutipennis*), rarely exhibit intraspecific territorial behaviour because they fly long distances to access the widely spaced resource habitat patches (Caccamise 1974).

Male home ranges throughout my study area exhibited varying degrees of overlap, based on both radio-telemetry data and observations. In one instance, I observed two males equipped with transmitters roosting within 6 m of each other, while a female nested between them. Possibly an intruding male was seeking extrapair copulations with the resident female. In general, extrapair mating is common among birds (Lindstedt et al. 2007), but it has not yet been reported for nighthawks. More in depth observation and genetic study may reveal information about extrapair mating in nighthawks and explain home range overlap in this context.

The home range overlap I documented is also consistent with high intraspecific competition, which can result in unpaired males, otherwise known as floaters, who do not possess territories, (Bayne and Hobson 2001, Mazerolle and Hobson 2004). Floater behaviour is widespread among birds and these males are often immature or less experienced (Bayne and Hobson 2001). Floaters often have home ranges that encompass one or more conspecific's territories (Zack and Stutchbury 1992), hence overlap of some home ranges maybe the result of floating males.

I observed considerable variation in home range use and size, but the observed home ranges still fit into Nice's classification system for territories. The majority of radio-tagged nighthawks possessed home ranges similar to Territory B because they likely mated and nested within defended areas, but most birds foraged over the reservoir. The home range overlap could indicate roosting territories, Territory F, because the high number of quality roost sites could allow for higher densities of roosting nighthawks. Most of the observed home ranges are likely examples of merged territory types B and F.

I found that nighthawks which I captured in mist nets were more likely to use home ranges that I could estimate the size of (and remain on the study area) than nighthawks caught using spotlights. Using the mist net technique, I expect I was more likely to catch nighthawks with home ranges because nets were set up near displaying birds, which is more indicative of a defended territory than just a roosting bird. Only males were radio-tagged and captures occurred throughout the entire breeding season, so it is unlikely that sex or seasonal differences account for differing movement patterns. I recommend that studies whose purpose is to assess home range or habitat use by territory holders should use mist nets and territorial playback calls to capture nighthawks rather than spotlighting to catch roosting birds because roosting birds may not represent territorial birds.

3.4.1 Limitations

Given the small number of observations I made, I only reported the estimated home range areas as 95% MCP's because this method requires fewer observations than others. While MCP's are the most commonly used estimate to compare home range size between studies (Harris et al. 1990), MCP's do not reveal as much detail about an animal's use of space as kernel-based estimators (Kernohan et al. 2001). Despite best efforts, more tagged birds and a more even distribution of observations across behavioural periods would produce more detailed information about space use and lead to more rigorous analysis regarding home range size and spatial patterns.

My average home range size undoubtedly remains an underestimate of true home range size even though it is 3-4 times larger than previously published estimates. First, I excluded five nighthawks from my analysis that were missing data collected during the true night period. The night roosts of these birds were likely a substantial distance away from their other activity centres and my general study area, and therefore in reality had much larger home ranges than I was able to document. Furthermore, I could not include foraging areas in home range estimates because birds foraged over the reservoir where I could not accurately track their locations. Of eleven tagged birds, only one bird was consistently observed foraging in upland areas. It was never recorded foraging over the reservoir. If foraging areas and all night roosts could have been were included in my analysis, I am certain the estimates for average home range size would have been larger.

3.4.2 Future Directives

The home range sizes I documented differ from those from previous studies because my data are the first to be collected from radio-tagged nighthawks. It is possible to delineate the defended area of territories for nighthawks without telemetry, but day and true night activities may take place away from the defended territories and it is virtually impossible to find and distinguish between individual birds without transmitters. Based on my results, I recommend that future home range and habitat studies require telemetry to allow finding nighthawks during different temporal and activity periods.

There are many gaps in knowledge about this widely distributed species and some aspects of nighthawk ecology make research on the species challenging. While some studies have examined roosting habitat (Fisher et al. 2004), home range size (Armstrong 1962), foraging strategies (Brigham 1990, Brigham and Fenton 1991), prey detection (Brigham and Barclay 1995), diet (Todd et al. 1998), and thermoregulation (Brigham 1993, Brigham et al. 1995, Fletcher et al. 2004), research on nighthawks is typically constrained by small sample sizes (Rottenberry and Wiens 1980, Debinski and Brussard 1994, Saab 1999). I found that both home range size and boundaries were highly variable and like other studies, my results must be interpreted cautiously due to small sample sizes. However, despite this, some clear spatial patterns emerged that should encourage future research because they may have important management implications for this declining species. With habitat loss as a potential limiting factor for nighthawks, understanding habitat requirements and space use is crucial for conservation. Future studies should consider trapping bias and larger study areas to maximize the confidence of outcomes.

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4.0 GENERAL CONCLUSIONS

4.1 Space Use

I found that Common Nighthawks were associated with specific landscape factors and habitat features relative to the available habitat. Three habitat variables were important in both local and landscape level models. Areas with high grassland cover, particularly in combination with low levels of aboveground vegetation and close proximity to water were good predictors of the presence of nighthawks during surveys.

In addition to landscape variables, environmental conditions also influenced the results of surveys and were important at all spatial scales examined. Nighthawks were more likely to be recorded on warmer nights. Light levels also factored into nighthawk activity because increased cloud cover and the amount of moon face illuminated (i.e. higher light levels) were related to a greater likelihood of nighthawks being detected around each survey point (i.e. local scale).

My observations of radio-tagged nighthawks suggest that home ranges were up to triple the size of previous home range size estimates. Large home ranges resulted in part from the spatial-temporal differentiation that some radio-tagged birds demonstrated. In many instances, individuals roosted, foraged, and displayed in spatially separate locations. My spatial analysis also showed that displaying males displayed considerable home range overlap. This was unexpected given that the species has previously been described as aggressively territorial.

Territorial males caught in mist nets were more likely to possess established home ranges compared to birds caught on gravel roads using the spotlight method, which were generally wide ranging without predictable movement patterns. These data suggest that nighthawks observed roosting on roads may not occupy home ranges.

4.2 Conservation Implications

Nighthawk populations have been declining by approximately 7.5% each year and the species was recently assessed as Threatened in Canada (COSEWIC 2007). While there is considerable published natural history information about nighthawks, there are few specific data about reproduction, survival, migration, and habitat use (Poulin et al 1996).

Understanding patterns of space use like habitat associations and home range characteristics are needed to allow meaningful management recommendations for populations and species. Particularly for declining species, like nighthawks, habitat management may be crucial for their persistence, because habitat loss is often a limiting factor.

Grassland habitat is likely a limiting factor for many species of grassland birds, including nighthawks, mostly due to conversion for agriculture (Jones and Bock 2002, Veech 2006, COSEWIC 2007). My study is consistent with this hypothesis because nighthawks were positively associated with grassland landcover and low aboveground productivity, attributes characteristic with grazed native prairie found in south western Saskatchewan, compared to cropland which is usually characterized by uniform growth with high aboveground productivity.

In addition to a widespread decline in grassland birds, Breeding Bird Surveys have found declines in many aerial insectivorous birds like swallows, chimney swifts

(*Chaetura pelagica*, COSEWIC 2007), flycatchers, and nightjars (*Caprimulgus vociferous*, COSEWIC 2009). The decline in the aerial insectivore guild may be attributed to several different factors, but an overall decrease in insect abundance is likely at least partly responsible given that diet is the common feature between these species. An abundance of flying insects is often associated with certain habitat features, such as water bodies. Water bodies are important foraging areas for nighthawks in some areas (Brigham 1990, Aldridge and Brigham 1991, Brigham and Fenton 1991, Brigham and Barclay 1995). Both my telemetry data and habitat models support a strong association with water. The telemetry data indicate that the majority of the radio-tagged nighthawks habitually foraged over water and my habitat model found nighthawks were likely found in close proximity to water.

Many of the same habitat variables (i.e. proportion of grassland, vegetation productivity, proximity to water) were included in both local and landscape habitat models, which emphasizes their strong association with nighthawk habitat. However, proximity to water and vegetation productivity were ranked differently between models, which may reflect a difference in scale effect. Based on my results, nighthawks respond to scale differences in habitat, which should be incorporated into management plans (Fletcher and Koford 2002).

Typically considered a highly territorial species with small home ranges, my data show that nighthawks in prairie regions appear to require large areas to fulfill their basic needs. It can not be assumed that sighting a roosting or displaying nighthawk means that there is a small home range surrounding the individual. Near (<10 km) or adjacent landscape features to defended territories, like water bodies, also need to be included into management plans because they likely provide other needs like foraging areas for birds.

4.3 Future Directives

My research identified several broad landscape features associated with the presence of nighthawks, but much is still unknown about habitat use patterns, from site-specific details like nest site characteristics, foraging areas, and roost characteristics, to landscape factors like fragmentation, landcover types, and human development.

Using telemetry, I found home range patterns that were different than previous studies (Armstrong 1965, Wedgwood 1973). However, due to limited sample sizes, more data are needed to make generalized conclusions about patterns of average size and variation, territory overlap, and spatial-temporal differentiation

Habitat features and home range characteristics need to be linked to demographic parameters like survival and reproduction, which can then potentially be extrapolated to provide information about population dynamics.

Future studies should use protocols specific to nighthawks, including nighthawk playback surveys to elicit responses.

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