

Common Nighthawks (*Chordeiles minor*) in Agricultural Landscapes: Genetic Structure of Populations Restricted to Urban Rooftop Nesting

SARAH E. MAYS¹, GRETCHEN N. NEWBERRY, LYNN RILEY, HUGH B. BRITTEN AND DAVID L. SWANSON

Department of Biology, University of South Dakota, Vermillion 57069

ABSTRACT.—Agricultural development may produce highly fragmented landscapes, which can influence population genetic structure for organisms restricted to insularized breeding habitats. Common Nighthawks (*Chordeiles minor*) in agriculturally dominated landscapes nest on urban gravel rooftop and might be subject to reduced gene flow among isolated urban sites. We conducted an analysis of the genetic variability and population genetic structure of Common Nighthawks nesting on rooftops in four towns in southeastern South Dakota, an area that has experienced extreme conversion of native prairie to agriculture. Using sequence data from a 725 bp region of the *cytochrome b* (*cytb*) mitochondrial gene sampled from 37 individuals representing a total of 30 different nests collected in summers 2014–2016, we found evidence of a recent population bottleneck and reduced mtDNA variability. The spatial dispersion of the 14 detected haplotypes and the presence of nine haplotypes unique to one of the four sampled towns further suggested a lack of panmixia among these nighthawks. These data are consistent with a hypothesis of habitat fragmentation due to agricultural expansion resulting in population isolation within this species of conservation concern.

INTRODUCTION

Since the 1980s aerial insectivorous birds have experienced one of the most prominent population declines of any bird guild (Sauer *et al.*, 2007; Nebel *et al.*, 2010). This decline may result in large-scale ecological impacts given insectivores provide important ecosystem services, such as agricultural and residential pest control. Caprimulgiformes, a large taxon that includes aerial insectivores, such as the Common Nighthawk (*Chordeiles minor*), is one of the least studied avian clades worldwide due to the nocturnal and crepuscular nature of its member species (Cleere, 1998). Common Nighthawks are one of the more studied species of Caprimulgidae, yet much of the information relative to their natural history is anecdotal (Brigham *et al.*, 2011).

Common Nighthawks have a wide breeding distribution in North America but have experienced local population declines. The species is listed as Threatened on the Canadian Species at Risk Public Registry and by the Committee on the Status of Endangered Wildlife in Canada (Brigham *et al.*, 2011) and is declining in other portions of North America, including the Upper Midwestern United States (Sauer *et al.*, 2017). Due to current land use practices, natural nighthawk nesting sites (*i.e.*, open woodlands and grasslands) in the Upper Midwestern United States have declined substantially from their historical extent (Tallman *et al.*, 2002; Wright and Wimberly 2013). For example the focal area of this study, southeastern South Dakota, is currently dominated by row-crop agriculture but was historically covered by grasslands (Spess Jackson *et al.*, 1996; Tallman *et al.*, 2002). North American Breeding Bird Survey data from 1966–2015 indicate a declining population trend for Common Nighthawks, with a 1.9% decline annually across North America and a 1.0% decline

¹ Corresponding author: Entomology and Nematology, University of Florida, Gainesville, 32608; email: sarah.maestas@ufl.edu

annually for South Dakota (Sauer *et al.*, 2017). The annual South Dakota trend from 2005–2015 was -1.5% , showing an accelerated decline relative to 1966–1979 (-0.9% annually; Sauer *et al.*, 2007). This accelerating population decline for South Dakota is coincident with a period of climate change associated with earlier springs that might affect insect phenology (Swanson and Palmer, 2009), as well as conversion of grasslands and other habitats to row-crop agriculture (Wright and Wimberly, 2013). Our southeastern South Dakota study area lies on the border between the Eastern Tallgrass Prairie Bird Conservation Region (BCR) to the east and the Prairie Pothole BCR to the west (Bird Studies Canada-NABCI 2014). Common Nighthawk populations in the Eastern Tallgrass Prairie BCR show the same downward trend at -0.5% annually for 2005–2015, while the trend for the Prairie Pothole BCR shows an increase of $+1.95\%$ for 2005–2015 (Sauer *et al.*, 2017), suggesting a potential westward shift in the regional population to areas where grassland land conversion is less severe (Wright and Wimberly, 2013).

Natural nest sites of Common Nighthawks typically occur in grasslands or open woodlands with minimal disturbance (*e.g.*, low agricultural conversion, limited pesticide use; Brigham, 1989; Wedgewood, 1991). Such nesting habitat is preferred over closed forests to allow for higher wind speeds that facilitate heat loss and provide more favorable nesting microclimates (Fisher *et al.*, 2004). Common Nighthawks sometimes use flat, graveled, urban rooftops for nesting (Brigham *et al.*, 2011). Most observations and nests of common nighthawks in South Dakota are in grasslands, open woodlands, or towns with flat gravel rooftops (Drilling *et al.*, 2016), and in our study area, they are almost exclusively birds of towns with flat gravel rooftops (Newberry and Swanson, 2018). Environmental disturbance of natural nesting sites in agricultural landscapes and abundant insect prey surrounding urban light fixtures may influence nest choice for Common Nighthawks (Brigham, 1989). Natural habitat preferences for nighthawks include high levels of grassland cover (Ng, 2009), suggesting early 20th Century and additional ongoing conversion of eastern South Dakota's tallgrass prairie to agriculture (Tallman *et al.*, 2002) might be causing Common Nighthawks to be displaced to urban settings (Newberry and Swanson, 2018). Urban nests are typically located on flat, graveled rooftops, but these sites are not used uniformly throughout the range and appear to be rarely used if sufficient natural nesting sites are available (Brigham, 1989; Brigham *et al.*, 2011). Preferences for nesting habitat can be influenced by long-term pressures, including habitat disturbance and nest microclimate changes, as well as by proximate pressures, such as food availability (Chalfoun and Schmidt, 2012). The use of gravel roofs suggests abundant prey in urban settings (*e.g.*, around light fixtures) might outweigh costs associated with urban nest sites (Brigham, 1989), including increased predation risk from urban generalist predators, such as raccoons, corvids, and domestic cats (Marzilli, 1989; Wedgewood, 1991).

Landscape-level changes in the distribution of suitable habitat for the Common Nighthawk may drive nesting habitat fragmentation. Such fragmentation can potentially contribute to isolation of populations, leading to reduced gene flow across the region and lower genetic variability in somewhat disjunct population segments. Common Nighthawks generally show high nesting site fidelity (Gross, 1940; Dexter, 1952, 1956, 1961), and urban nesting nighthawks will often return year-after-year to the same rooftop (Brigham *et al.*, 2011). Moreover, nighthawk nesting home range sizes in urban settings (mean < 20 ha) tend to be substantially smaller than those in natural habitats, and much smaller than distances among adjacent towns with gravel rooftops in the agricultural landscapes of the southeastern South Dakota study area (Brigham *et al.*, 2011). Nighthawks in southeastern South Dakota also tend to avoid agricultural habitats and occur in much higher

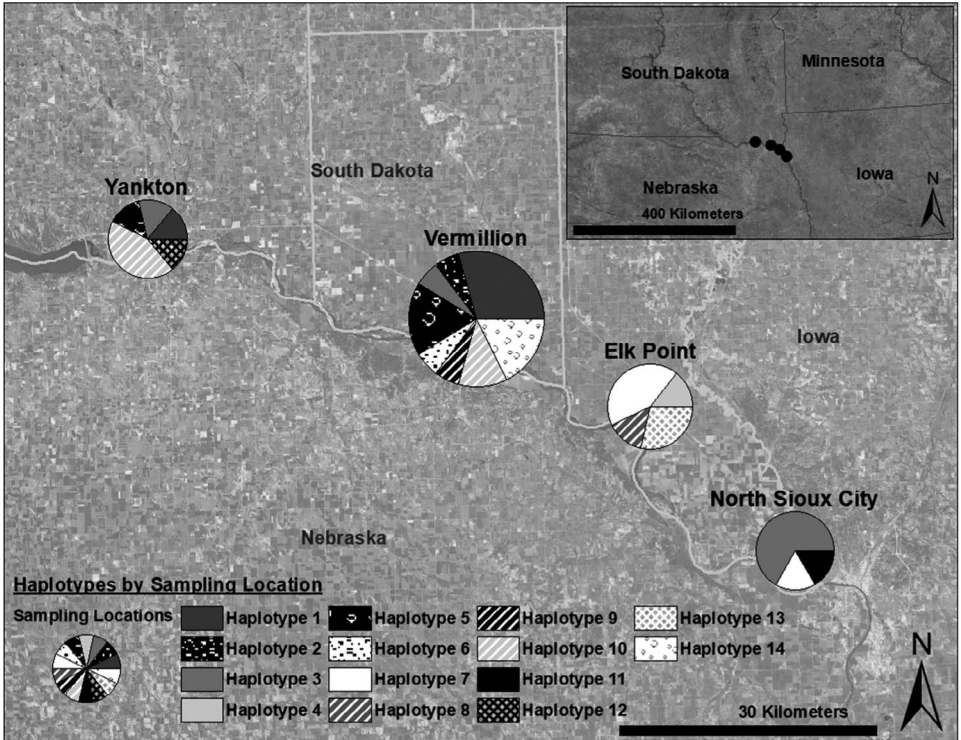


FIG. 1.—Common Nighthawk nest sample locations in southeastern South Dakota. Pie charts at each location provide the frequencies of *cytb* haplotypes for each sampled city. Size of pie charts demonstrates relative sample sizes at each location

abundances in (Newberry and Swanson, 2018). These features combine to raise the possibility that nighthawk habitats in southeastern South Dakota may be sufficiently fragmented to produce genetic differentiation among populations from different urban locations. Finally, nighthawk life history traits may exacerbate the genetic effects of habitat fragmentation in our study area. Nighthawks have low fecundity, with each female generally producing only a single clutch of two eggs each year (Brigham *et al.*, 2011). Low fecundity slows population recovery after declines and lowers genetically effective population sizes, thereby accelerating the loss of genetic diversity due to genetic drift. Without the countervailing force of gene flow, genetic drift will lead to increasing genetic differentiation among isolated subpopulations, as we hypothesize might be present in southeastern South Dakota.

The objective of this study was to determine population genetic structure and level of genetic variability in Common Nighthawks nesting on rooftops in four towns (Elk Point, North Sioux City, Vermillion, and Yankton) in southeastern South Dakota. All of these towns are separated from each other by 20–40 km and are surrounded by an agriculturally dominated (row crop) landscape (Fig. 1). These agricultural landscapes do not provide appropriate nesting habitat for nighthawks and nighthawks in this region are almost exclusively restricted to urban habitats (Newberry and Swanson, 2018). To the best of our knowledge, a population genetics study has not been conducted on Common Nighthawks

from this part of their distribution, where they encounter fragmented natural habitats and rely on rooftops for nesting.

MATERIALS AND METHODS

Four urban locations in southeastern South Dakota, U.S.A., were sampled: North Sioux City (Lat. 42.5272, Long. -96.4831), Elk Point (Lat. 42.6833, Long. -96.6836), Vermillion (Lat. 42.7794, Long. -96.9292), and Yankton (Lat. 42.8711, Long. -97.397). To identify nest areas for sampling, we used Google Earth to survey for flat, gravel rooftops in each location near point count sites where nighthawks were observed on previous surveys (Newberry and Swanson, 2018). The identified rooftops were then visited and searched systematically for nesting birds by laying out a grid with 1 m x 1 m squares on graveled areas of the rooftop and walking all gridlines until adult birds flushed. When adults flushed, the area from which they flushed was carefully searched for eggs or chicks.

Due to the fairly high anthropogenic traffic on urban rooftops (e.g., maintenance workers, window washers) (Gotmark, 1992), nests were monitored every 6-7 d instead of the typical 4-5 d interval (Johnson, 1979) to avoid unnecessary disturbance. Dead chicks, unhatched eggs, blood from living chicks, as well as incidental fecal and feather samples were collected from 12 rooftop nest sites at four different locations (Fig. 1). Two adults found dead were also collected. Over the three years of the study, samples were collected from a total of 66 different individuals from a total of 40 nests. We were unable to track unique females' nests across years in our study, because Common Nighthawk nests are very simply constructed and are not found in the same locations on each rooftop between years. The numbers of unique nests sampled per year are given in Table 1.

Chicks were removed from the nest at 7-14 d after hatching to collect blood samples (<100 µl) by pricking the brachial vein with a 26 gauge needle and collecting blood in a heparinized capillary tube. Following collection of the blood sample, pressure was applied to the bleeding site with a cotton ball until the bleeding stopped. Chicks were then returned to the nest. These sampling methods (Wingfield *et al.*, 1994) are standard for drawing small volumes of blood from birds and are approved methods in the Ornithological Council's *Guidelines to the Use of Wild Birds in Research* (Fair *et al.*, 2010). Blood samples were stored on ice in microcentrifuge tubes while in the field. Upon return to the laboratory, the blood samples were centrifuged for 10 min at 3000 X g at 4 C, plasma was removed for other studies, and red blood cells, as well as other samples, were stored at -80 C until later analyses.

Genomic DNA was extracted from all nighthawk tissue samples using the Qiagen DNeasy® Blood and Tissue kit (Qiagen, Inc., Valencia, California). Approximately 25 mg tissue samples from chicks and eggs were extracted following the DNeasy® animal tissue spin-column protocol. Chick tissue samples were digested overnight. Egg tissue samples were digested for 2-4 h. Approximately 25 mg fecal samples and feather samples were extracted following a modified DNeasy® tissue extraction protocol. Ten microliter blood samples were extracted following the DNeasy® animal blood spin-column protocol. A negative extraction control containing only extraction reagents was included with each set of samples that were extracted. Extracted DNA was stored in elution buffer at -20 C prior to use for polymerase chain reaction (PCR).

DNA was amplified via PCR using primers for the mitochondrial DNA (mtDNA) *cytochrome-b* gene region (*MT-CYB* L14764 and *MT-CYB* H16060) (Han *et al.*, 2010) and Taq PCR master mix (Qiagen, Inc., Valencia, California) following Han *et al.*, (2010). Extraction negative controls were included in PCR to verify that there was no contamination during the extraction procedure. PCR negative controls containing water and PCR reagents but no

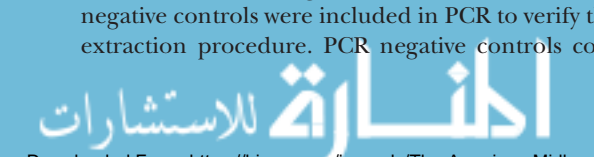


TABLE 1.—Number of Common Nighthawk samples collected and number of samples successfully extracted and sequenced by location, sample type, and collection year

Location	Type	# samples collected by year (# unique nests)			# samples sequenced by year (# unique nests)		
		2014	2015	2016	2014	2015	2016
Elk Point	Chick	0	0	1(1)	0	0	1(1)
	Egg	0	0	6(3)	0	0	5(3)
	Blood	0	0	2(1)	0	0	1(1)
	Fecal	0	0	1(1)	0	0	0
North Sioux City	Chick	0	0	1(1)	0	0	1(1)
	Egg	3(2)	7(4)	2(1)	3(2)	1(1)	0
	Blood	0	0	1(1)	0	0	1(1)
	Feather	0	0	1(1)	0	0	1(1) ¹
	Fecal	0	0	2(2)	0	0	0
	Adult	0	1	0	0	0	0
Vermillion	Chick	1(1)	3(2)	5(5)	1(1)	3(2)	4(4)
	Egg	3(2)	3(2)	2(2)	3(2)	2(2)	2(2)
	Blood	0	0	10(6)	0	0	2(2)
	Feather	0	0	1(1)	0	0	0
	Fecal	0	0	1(1)	0	0	0
	Adult	0	0	1	0	0	1
Yankton	Chick	0	0	1(1)	0	0	0
	Egg	0	2(1)	3(3)	0	2(1)	3(3)
	Blood	0	0	1(1)	0	0	1(1)
	Feather	0	0	1(1)	0	0	0
	Feather	0	0	1(1)	0	0	0

sample DNA were also run. All PCR products were run on a 1.5% agarose gel using GelRed™ pre-stain loading buffer (Biotium, Inc., Fremont, California) to confirm successful amplification. DNA extractions, PCR amplification, and gel electrophoresis were carried out in separate areas with designated equipment to prevent contamination. PCR products were cleaned in preparation for sequencing using ExoSAP-IT (Affymetrix, Inc., Cleveland, Ohio) to remove excess primers and nucleotides, and sent to the Arizona State University School of Life Sciences DNA Laboratory for unidirectional sequencing using the *MT-CYB* H16060 primer. Blood, feather and fecal samples were only sequenced from nests if tissue or egg samples were not recovered or successfully sequenced. No individuals were represented by sequences from multiple sample types.

Sequence results were cleaned using FinchTV 1.4.0 (Geospiza, Inc., Seattle, Washington) and aligned using ClustalW in BioEdit 7.2.5 (Hall, 1999). A BLAST search revealed that our sequences were similar to two Common Nighthawk sequences in GenBank; one of these sequences (Accession # FJ588441.1) was identical to one of our haplotypes over the relevant 725bp region, and the other (Accession # EU166983.1) was 99.7% similar to another haplotype, with two base pair changes. Haplotype diversity estimates, gene flow and genetic differentiation analyses, identification of synonymous and non-synonymous substitutions as well as Tajima's D test for selective neutrality were carried out in DnaSP 5.10.01 (Librado and Rozas, 2009). Nucleotide diversity (π) values were based upon variation at synonymous sites. The statistical parsimony haplotype network was estimated using Population Analysis with Reticulate Trees (PopART) software (<http://popart.otago.ac.nz>).

TABLE 2.—Genetic variability estimates at the *cytb* locus at four sample locations for the Common Nighthawk in southeastern South Dakota

Population	Sequences	Segregating sites (S) synonymous, non-synonymous	Haplotypes (h)	Haplotype diversity (Hd)	Avg. nucleotide differences (K)	Nucleotide diversity (π)
Elk Point	7	10, 3	4	0.81	5.81	0.0250
North Sioux City	6	8, 0	3	0.60	2.87	0.0156
Vermillion	17	14, 1	8	0.88	4.68	0.0231
Yankton	7	8, 1	5	0.86	4.00	0.0203
Total Data	37	17, 4	14	0.92	4.81	0.0233

RESULTS

We sampled 66 individuals from a total of 40 different nests over the course of the study. Of the 66 sampled individuals, 38 from 30 different nests were successfully genotyped. The *cytb* primers amplified a region of about 1140 base pairs (bp) for most samples. We acknowledge that sample sizes per location are low as a result of the relative rarity of the study organism and sample degradation on exposed roof tops. After alignment, all sequences were trimmed and a 725 bp region was used for analysis. One sequence from the only successfully amplified feather sample was much shorter than the rest (<500 bp) and was not included in the genetic analysis.

A total of 14 different haplotypes (h) were present across all sampling locations, with differing numbers of haplotypes present at each location (Table 2). Vermillion had the greatest number of haplotypes recovered; likely due to the larger sample size from Vermillion. Of the eight haplotypes detected in Vermillion (Haplotypes 1, 2, 3, 5, 6, 9, 10, and 14), four (Haplotypes 1, 3, 5, and 10) were shared with the Yankton location, and one was shared with both the North Sioux City and Yankton locations (Haplotype 3, Fig. 1). Haplotype 3 was the only haplotype shared by Yankton and North Sioux City. Overall, nucleotide diversity (π) for all 37 sequences was low (0.023). Haplotype diversity is the probability that two randomly selected haplotypes in a population are different. Elk Point, Vermillion, and Yankton locations had similar haplotype diversity (Table 2). The North Sioux City location had slightly lower haplotype diversity (Table 2). Overall haplotype diversity was 0.92 across all four study towns and ranged from 0.60 (North Sioux City) to 0.88 (Vermillion) (Table 2).

A Chi-square test for differences in haplotype frequencies across the four sample sites was significant ($\chi^2 = 67.20$, $P = 0.003$) indicating that haplotypes are unevenly distributed among the four sampling locations (Hudson *et al.*, 1992). Relatively low F_{st} values indicate low genetic differentiation between sample sites (Table 3). The most differentiated pair of sites was Elk Point and Yankton ($F_{st} = 0.18$). The most similar pairs of sites were Vermillion and North Sioux City, and Vermillion and Yankton ($F_{st} = 0.05$ for both pairs). Tajima's D test indicated selective neutrality (Tajima's $D = -0.15$, $P > 0.1$) (Tajima, 1989).

The TCS statistical parsimony network illustrates the most parsimonious relationships between the haplotypes and the locations at which each haplotype was found (Fig. 2). The network and Figure 1 show that five haplotypes were represented in two or three locations, but the majority of haplotypes ($N = 9$) were exclusive to one location.

DISCUSSION

Because nighthawks in the study area occur almost exclusively in towns and seldom are detected in the agricultural landscape matrix among towns (Newberry and Swanson, 2018),

TABLE 3.—Pairwise F_{ST} values between Common Nighthawk sample locations below diagonal based on *cytb* sequences. Approximate distances in kilometers between each sample city are above diagonal

	Elk Point	North Sioux City	Vermillion	Yankton
Elk Point	-	24	23	62
North Sioux City	0.08	-	46	84
Vermillion	0.13	0.05	-	40
Yankton	0.18	0.08	0.05	-

this raises the possibility that such widespread habitat conversion to agriculture and the subsequent use of urban rooftop nesting sites could result in habitat fragmentation and population subdivision with some loss of genetic variability. Our analysis of a 725 bp region of the *cytb* gene in Common Nighthawks sampled from southeastern South Dakota supports

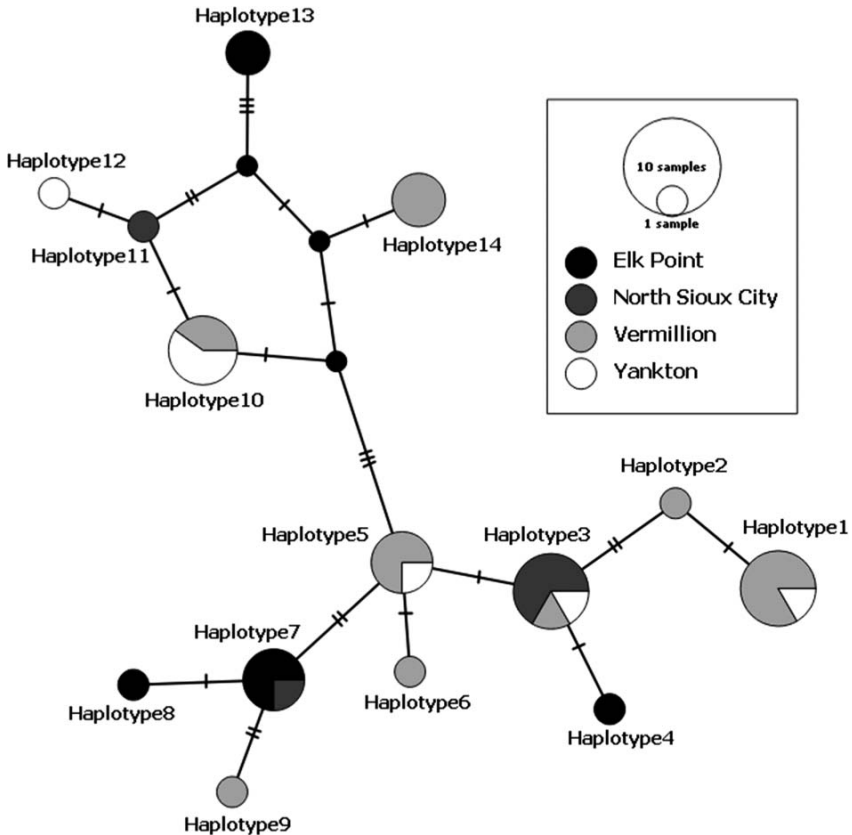


FIG. 2.—Statistical parsimony network based on 1000 iterations for 725 bp sequences of the *cytb* locus in Common Nighthawks sampled from four southeastern South Dakota cities. Size of circles represent number of samples of each haplotype and shading represent sample locations for each haplotype. Slashes across branch network lines represent single nucleotide changes between haplotypes. Small filled circles without haplotype labels are hypothetical haplotypes within the network that were not detected in our samples

this hypothesis. Mitochondrial nucleotide diversity (π) is comparatively low in our samples (overall $\pi = 0.023$). In contrast, Moom and Árnason (2001) estimated Razorbill (*Alca torda*) and Common Guillemot (*Uria aalge*) nucleotide diversity from across the Atlantic Ocean at 1.26 and 0.50, respectively. Similarly, Szczys *et al.* (2017) found nucleotide diversity ranged from 0.25 to 1.36 across 12 eastern North American sites at which Common Terns (*Sterna hirundo*) were sampled. On the other hand, some bird populations, like western North American Golden Eagles (*Aquila chrysaetos canadensis*) and Taiwanese endangered Black-faced Spoonbill (*Platalea minor*) have much lower diversity estimates, of $\pi = 0.0013 - 0.0025$ (Craig *et al.*, 2016) and 0.00033 (Yeung *et al.*, 2006), respectively. Ecological and demographic data point to a recent population bottleneck for the Common Nighthawk in southeastern South Dakota. Our estimate of Tajima's D (Tajima, 1989) suggests a stable population size, however our estimate of D may lack the statistical power to detect bottlenecks in the sampled populations. Our results suggest reduced mtDNA sequence diversity, but not to the extent seen in some other birds of conservation concern. Low fecundity (Brigham *et al.*, 2011) in our study population may amplify the effects of population bottlenecks by slowing demographic recovery and contributing to genetic drift.

In addition to significant differences in *cytb* haplotype frequencies among the four sampled locations, the spatial distribution of the 14 haplotypes suggests that there is somewhat restricted gene flow between sites. Less than a third (5 of 14) of the haplotypes were recovered from multiple sites; one (Haplotype 3) was recovered from three sites and four (Haplotypes 1, 5, 7 and 10) were recovered from two sites each (Figs. 1, 2). Among the Elk Point samples, four haplotypes were detected among the seven samples; three of these were unique to that site and the fourth was shared only with the North Sioux City sample (Fig. 1) and is identical to GenBank Accession # FJ588441.1, an individual collected at an overwintering site in the Cayman Islands, indicating that it is likely a common haplotype in Common Nighthawk populations. Even more notable is the fact that very few nighthawks were found in Elk Point, likely due to a lower availability of gravel rooftops at this location (1092 m² vs. 18,581 to 65,476 m² in the three other towns). The seven Elk Point samples came from five nests, likely belonging to four different females, one of which is thought to have renested in 2016 after an initially unsuccessful nest. All females were presumed to be mating with the same male (GN, pers. obs.). Haplotype 7 was detected in two nests (both presumed to belong to the same female that renested) and the other three haplotypes were unique to their nests. This indicates that the four females present were unrelated to each other (assuming the Haplotype 7 bird renested in 2016; alternatively, the second Haplotype 7 nest may represent a fifth, related female), and maternally unrelated to nighthawks at any other sampled location except North Sioux City. The North Sioux City site had only three haplotypes, one of which was unique to that site (Fig. 1). In contrast we detected eight haplotypes from the Vermillion site, five of which were unique to that location.

An analysis of the spatial distribution of unique haplotypes is dependent on the proportion of nests discovered and successfully genotyped during sampling. We successfully obtained genotypes from 30 of the 40 nests sampled during the study, so it is possible that we may have missed some genotypes at some locations that could have been shared with other locations. On the other hand, unsampled nests could have contained unique haplotypes that might have been missed. We estimated our sampling coverage as 68.9% of expected nests based on point counts that identified 87 birds breeding in the study areas and a 1:1 sex ratio (*i.e.*, 43.5 nests if every female nests once).

The significant Chi-square test for differences in haplotype frequencies across the four sample sites suggests haplotypes are unevenly distributed among the four sampling locations

(Hudson *et al.*, 1992). However, relatively low F_{st} values (Table 3) indicate that gene flow has occurred between the populations at least in past generations. Most of the locations with the smallest pairwise F_{st} estimates are the locations nearest each other geographically, with lower gene flow occurring between the more widely separated locations (Table 3). The parsimony network (Fig. 2) corroborates our hypothesis of a recent population bottleneck and restricted gene flow between sites for Common Nighthawks in southeastern South Dakota. Under a scenario of complete genetic isolation over many generations, we expect each location to have its own set of very similar haplotypes separated from the other locations by several mutations. In contrast, under panmixia with very little genetic isolation among sites, we expect more shared haplotypes across sites and fewer site-specific haplotypes. The lack of clustering by town in our haplotype network (Fig. 2) and wide dispersion of site-specific unique haplotypes (Fig. 1) suggest a more evenly mixed regional population in which bottlenecks and genetic drift have recently acted to reduce overall genetic variability and to confine nine of the haplotypes to single sites. Overall, these results are consistent with a hypothesis of formerly continuous habitat that has been fragmented due to land-use changes over the last several generations.

We detected population-level differences that may be important for conservation efforts for the Common Nighthawk in southeastern South Dakota. Although based on relatively small sample sizes, our genetic results suggest that the Elk Point samples have the highest level of genetic differentiation from the other sites and contain a nearly unique set of mtDNA haplotypes despite our small sample size ($n = 7$) from Elk Point. There may be an historic artifact of differential habitat use exacerbated by a relatively recent population bottleneck and genetic isolation driving this result. Specifically, we speculate that this pattern may be due in part to a combination of factors: land use change, historic nesting sites and life history traits. In addition to increasing sample size in future sampling, the use of nuclear markers, such as microsatellites, might allow finer-scale resolution of the timing and severity of these environmental and demographic effects, so future studies using such markers seem worthwhile.

Common Nighthawks use grassland, open forest, sandbars, and flat, gravel rooftops for nesting habitat in the Northern Plains (Brigham *et al.*, 2011). As open forest and sandbar habitat in the region were reduced (due primarily to the construction of the Missouri River dams in the 1950s; Dixon *et al.*, 2012), and grasslands were converted to row-crop agriculture (Wright and Wimberly, 2013), this left flat, gravel rooftops associated with urban areas as the sole nesting habitat in agriculture-intensive regions of the Northern Prairie (Newberry and Swanson, 2018). Common Nighthawks can have large home ranges in natural grassland habitats (*i.e.* 86 ± 99 ha; Ng, 2009) and smaller home ranges in urban settings (*i.e.*, 10.5 ha, Wedgewood, 1973; 10.4 ha, Armstrong, 1965). Moreover, nighthawk females exhibit some nest site fidelity (Gross, 1940; Dexter, 1952, 1956, 1961). We emphasize female ecology in this regard, because mtDNA loci, such as *cytb*, are maternally inherited and reflect the demography and movement of female lineages within populations. When home ranges shrink in fragmented urban habitats and females return to the same nest site each year, there is little interchange among breeding adult females among towns. It is possible that dispersal of young females away from nest sites might increase genetic mixing among populations, but essentially no data on dispersal from nest sites exist for nighthawks (Brigham *et al.*, 2011). It is more likely that dispersal is mostly within rather than among towns, as suitable nesting habitat (*i.e.*, gravel rooftops) is highly localized in this area (Newberry and Swanson, 2018). As a result each town could represent a distinct genetic profile, which is consistent with our data. Coupled with nest site fidelity, shrinking home

ranges, and historic habitat use, land use change might be further complicating efforts to restore genetic connectivity and genetic variability among regional nighthawk populations.

Acknowledgments.—We would like to thank B. Fischer for her assistance with laboratory procedures. This project was funded by the South Dakota Department of Game Fish and Parks (Common Nighthawks (*Chordeiles minor*) in agricultural landscapes: Thermal microclimates, nesting productivity and population genetic structure) and the University of South Dakota, Department of Biology.

LITERATURE CITED

- ARMSTRONG, D. P., E. H. RAEURN, R. G. POWLES, M. HOWARD, B. CHRISTENSEN, AND J. G. EWEN. 2002. Obtaining meaningful comparisons of nest success: data from New Zealand Robin (*Petroica australis*) populations. *New Zeal. J. Ecol.*, **26**:1–13.
- BIRD STUDIES CANADA AND NABCI. 2014. Bird Conservation Regions. Published by Bird Studies Canada on behalf of the North American Bird Conservation Initiative. <http://www.birdscanada.org/research/gislab/index.jsp?targetpg=bcr> Accessed: 14 September 2017.
- BRIGHAM, R. M. 1989. Roost and nest sites of Common Nighthawks: Are gravel rooftops important? *Condor*, **91**:722–724.
- , J. NG, R. G. POULIN, AND S. D. GRINDAL. 2011. Common Nighthawk (*Chordeiles minor*). In: RODEWALD, P. G., (ed.) *The Birds of North America*. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists' Union, Washington DC, USA. doi:10.2173/bna.213.
- CHALFOUN, A. D. AND K. A. SCHMIDT. 2012. Adaptive breeding-habitat selection: is it for the birds? *The Auk*, **129**:589–99.
- CLEERE, N. 1998. Nightjars: a guide to the nightjars, nighthawks and their relatives. Yale University Press, New Haven, Connecticut, USA, 1st ed. p. 31.
- CRAIG, E. H., J. R. ADAMS, L. P. WATTS, M. R. FULLER, AND D. M. WHITTINGTON. 2016. Nuclear and mitochondrial DNA analyses of Golden Eagles (*Aquila chrysaetos canadensis*) from three areas in western North America; Initial results and conservation implications. *PLOS ONE*. DOI:10.1371/journal.pone.0164248.
- DEXTER, R. W. 1952. Banding and nesting studies of the Eastern Nighthawk. *Bird-Banding*, **23**:109–114.
- . 1956. Further banding and nesting studies of the Eastern Nighthawk. *Bird-Banding*, **27**:9–16.
- . 1961. Further studies on nesting of the Common Nighthawk. *Bird-Banding*, **32**:79–85.
- DIXON, M. D., W. C. JOHNSON, M. L. SCOTT, D. E. BOWEN, AND L. A. RABBE. 2012. Dynamics of plains cottonwood (*Populus deltoides*) forests and historical landscape change along unchannelized segments of the Missouri River, USA. *Environmental Management*, **49**:990–1008.
- DRILLING, N. E., R. A. SPARKS, B. J. WOJDESKI, AND J. P. BEASON. 2016. South Dakota Breeding Bird Atlas II: Final Report. Tech. Rep. M-SDBBA2-07. Rocky Mountain Bird Observatory, Brighton, Colorado.
- FAIR, J. M., E. PAUL, J. JONES, A. B. CLARK, C. DAVIE, AND G. KAISER. 2010. Guidelines to the Use of Wild Birds in Research, 3rd ed. Ornithological Council, Washington, D.C., USA.
- FISHER, R. J., Q. E. FLETCHER, C. K. R. WILLIS, AND R. M. BRIGHAM. 2004. Roost selection and roosting behavior of male Common Nighthawks. *Am. Midl. Nat.*, **151**:79–87.
- GOTMARK, F. 1992. The effects of investigator disturbance on nesting birds. In: D. Power (ed.), *Current Ornithology*, Vol. 9. Springer, USA. p. 63–104.
- GROSS, A. O. 1940. Eastern nighthawk. In: A. Brent (ed.), *Life Histories of North American Cuckoos, Goatsuckers, Hummingbirds, and their Allies*. *United States National Museum Bulletin.*, **176**:206–234.
- HALL, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acid. S.*, **41**:95–98.
- HAN, K., M. B. BOBBINS, AND M. J. BRAUN. 2010. A multigene estimate of phylogeny in the nightjars and nighthawks (Caprimulgidae). *Mol. Phylogenet. Evol.*, **55**:443–453.
- HUDSON, R. R., D. D. BOOS, AND N. L. KAPLAN. 1992. A statistical test for detecting geographic subdivision. *Mol. Biol. Evol.*, **9**:138–151.

- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *The Auk*, **96**:651–661.
- LIBRADO, P. AND J. ROZAS. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, **25**:1451–1452.
- LIU, M. AND D. L. SWANSON. 2014. Stress physiology of migrant birds during stopover in natural and anthropogenic woodland habitats of the Northern Prairie region. *Conserv. Phys.*, **2**:1–14.
- MARZILLI, V. 1989. Up on the roof. *Maine Fish and Wildlife*, **31**:25–59.
- MOUM, T. AND E. ÁRNASON. 2001. Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. *Mol. Ecol.*, **10**:2463–2478.
- NEBEL, S., A. M. MILLS, J. D. MCCrackEN, AND P. D. TAYLOR. 2010. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conserv. Ecol.*, **5**(2):1.
- NEWBERRY, G. N. AND D. L. SWANSON. 2018. Common Nighthawks (*Chordeiles minor*) in the Western Corn Belt: habitat associations and population effects of grassland and rooftop nesting habitat conversion. *Am. Midl. Nat.*, **180**:216–332.
- NG, J. W. 2009. Habitat use and home range characteristics of Common Nighthawks (*Chordeiles minor*) in mixed-grass prairie. Master's thesis. University of Regina, Regina, SK, Canada.
- SAUER, J. R., J. E. HINES, AND J. E. FALLON. 2007. The North American breeding bird survey, results and analysis. 1966–2006, Version 10.13.2007 (Archived). Laurel, MD:USGS Patuxent Wildlife Research Center. <https://www.mbr-pwrc.usgs.gov/bbs/> (last accessed 4 April 2017).
- , D. K. NIVEN, J. E. HINES, D. J. ZIOLKOWSKI, JR., K. L. PARDIECK, J. E. FALLON, AND W. A. LINK. 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017 USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- SPESS JACKSON, L., C. A. THOMPSON, AND J. J. DINSMORE. 1996. The Iowa breeding bird atlas. University of Iowa Press, Iowa City.
- SWANSON, D. L. AND J. S. PALMER. 2009. Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change. *J. Field Ornithol.*, **80**:351–363.
- SZCZYS, P., S. A. OSWALD, AND J. M. ARNOLD. 2017. Conservation implications of long-distance migration routes: regional metapopulation structure, asymmetrical dispersal, and population declines. *Biol. Conserv.*, **209**:263–272.
- TAJIMA, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**:585–595.
- TALLMAN, D. A., D. L. SWANSON, AND J. S. PALMER. 2002. Birds of South Dakota. South Dakota Ornithologists' Union, Aberdeen, p. i–vii, 197.
- WEDGEWOOD, J. A. 1973. Nighthawks in the city. *Blue Jay*, **31**:82–88.
- . 1991. Common Nighthawks in Saskatoon. Regina, SK: Saskatchewan Natura Historical Society.
- WINGFIELD, J. C., C. M. VLECK, AND M. C. MOORE. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *J. Exp. Zool.*, **264**:419–428.
- WINGFIELD, J. C., C. R. SUYDAM, AND K. HUNT. 1994. The adrenocortical responses to stress in Snow Buntings (*Plectrophenax nivalis*) and Lapland Longspurs (*Calcarius lapponicus*) at Barrow, Alaska. *Comp. Biochem. Phys. C*, **108**:299–306.
- WINGFIELD, J. C., K. HUNT, C. BRUENER, K. DUNLAP, G. S. FOWLER, L. FREED, AND J. LEPSOM. 1997. Environmental stress, field endocrinology and conservation biology. p. 95–131 *In*: J. Clemmons and R. Buchholz (eds.), Behavioral Approaches to Conservation in the Wild. Cambridge University Press, Cambridge, UK.
- WRIGHT, C. K. AND M. C. WIMBERLY. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *P. Natl. Acad. Sci. USA*, **110**:4134–4139.
- YEUNG, C. K.-L., C.-T. YAO, Y.-C. HSU, J.-P. WANG, AND S.-H. LI. 2006. Assessment of the historical population size of an endangered bird, the black-faced spoonbill (*Platalea minor*) by analysis of mitochondrial DNA diversity. *Anim. Conserv.*, **9**:1–10.

Copyright of American Midland Naturalist is the property of University of Notre Dame / American Midland Naturalist and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.