Am. Midl. Nat. (2018) 180:216–232

Common Nighthawks (Chordeiles minor) in the Western Corn Belt: Habitat Associations and Population Effects of Grassland and Rooftop Nesting Habitat Conversion

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ABSTRACT.—Grassland habitat in the Northern Prairie region of North America has been greatly reduced since historical times, and conversion to agricultural row-crop production has recently intensified this decline. Common Nighthawk (*Chordeiles minor*) nesting habitat includes grasslands and flat, gravel rooftops, but relative occurrence of nighthawks in these habitats in the Northern Prairie region has not been previously quantified. We conducted point counts at 396 sites within two study areas in South Dakota, Nebraska, and Iowa; an eastern region dominated by row-crop agriculture and a western region with more grassland within the landscape. We compared land cover at points where nighthawks were present between the two regions and found higher incidences of cropland and grassland in the western region and higher developed land cover in the eastern region. We also compared land cover surrounding points where birds were present vs. absent for both regions combined and found greater cropland around points without birds and greater developed land cover around points with birds. We used Generalized Linear Models (GLMs) with binomial distributions to examine nighthawk presence relative to landscape variables, and ranked models with AICc. In the eastern study region, developed land cover was positively associated with nighthawk presence and cropland showed a weak negative trend with nighthawk presence. Nighthawks in the western region showed a positive association with cropland; suggesting that cropland has a positive effect on nighthawk occurrence, presumably by providing foraging opportunities, if grassland is present within the landscape at sufficient levels. If 2006-2015 regional conversion rates of grasslands and gravel rooftops continue, Markov models project suitable breeding habitat will decrease to levels where nighthawks might be extirpated as breeding birds from urban regions of the Western Corn Belt by 2026 and with substantial population reductions over the entire Northern Prairie region by 2106.

INTRODUCTION

Since the 1960s populations of many North American farmland and grassland bird species have decreased. During that time aerial insectivorous birds have declined by an average of about 40% (Nebel *et al.,* 2010; Sauer *et al.,* 2017; Stanton *et al.*, 2018). Because aerial insectivores are a diverse guild, the decrease is possibly linked with declines in flying insects (Hallman *et al.*, 2017), which, in turn, may be associated with nonselective pesticide spraying (Wedgewood, 1991) or land cover change (Nebel *et al.,* 2010), among other factors (Stanton *et al.*, 2018). The decline of aerial insectivores potentially has large-scale impacts, as they provide important ecosystem services, such as agricultural and urban pest control (Sekercioglu 2006, Kunz *et al.*, 2007, Philpott *et al.*, 2009).

The Common Nighthawk (*Chordeiles minor*) is an aerial insectivore and has a wide breeding distribution in North America; yet is subject to population declines. They are listed as a Threatened species in Canada (COSEWIC 2007). North American Breeding Bird Survey data (Sauer *et al.,* 2017) indicate a declining population trend for Common Nighthawks (hereafter referred to as "nighthawks"), with a 1.9 % decline annually from 1966-2015 for

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North America and a 1.0 % decline annually for South Dakota, our primary study area. The South Dakota trend for 1980-2006 was -4.3%/y, showing an accelerated decline relative to 1966-1979 (-0.9%/y, Sauer *et al.,* 2007), although this decline has slowed to -1.52%/y for 2005-2015 (Sauer *et al.,* 2017). Populations throughout most of the Western Corn Belt states (*i.e.,* Minnesota, Iowa, North Dakota, and South Dakota) share the same downward trend in populations (Sauer *et al.,* 2017), with the greatest declines in the eastern states within the region (*e.g.,* Minnesota, -3.6%/y), where row-crop land cover density is highest (Wright and Wimberly, 2013).

Nighthawk nesting habitat includes grasslands, open forests and urban rooftops (Brigham *et al.,* 2011). Preference for habitat can be influenced by long-term pressures, such as habitat disturbance or changes in food resources. Due to changing land-use practices, natural grassland nesting sites for nighthawks in the Northern Prairie region are in decline (Tallman *et al.,* 2002; Ng, 2009), and this trend has accelerated recently with grassland conversion to row crops due to higher prices for corn and soybeans (Wright and Wimberly, 2013). Coupled with higher commodity prices are the higher costs for establishing land easements to help protect grasslands from conversion (Walker *et al.,* 2013). The study area of the project, southeastern South Dakota, northeastern Nebraska and northwestern Iowa, is currently dominated by row-crop agriculture (Spess Jackson *et al.,* 1996; Tallman *et al.,* 2002) and is within the area with the greatest recent loss of grassland in the Western Corn Belt region (Wright and Wimberly, 2013; Gage *et al.,* 2017). Row-crop agriculture is associated with low biodiversity in agricultural areas within grassland biomes worldwide (Weibull *et al.,* 2003; Scherr and McNeely, 2008). Grassland habitats suitable for nighthawks (Fuhlendorf *et al.,* 2006) are more common in western than in eastern regions of the Northern Prairie (Wright and Wimberly, 2013; Ahlering and Merkord, 2016).

Recent studies of nighthawk population ecology in central North America have been conducted in large continuous expanses of grassland (Ng, 2009; Lohnes, 2010), but not in smaller, patchy grasslands characteristic of agriculturally dominated landscapes. Potential nest sites in both natural and urban habitats occur within the study area and their relative use by nighthawks presumably represents adjustments to prevailing land cover attributes. Natural nest sites typically occur on the ground in grasslands, open forests, or sandbars (Brigham, 1989; Wedgewood, 1991). In contrast urban nests are typically located on flat gravel rooftops (Brigham, 1989; Brigham *et al.,* 2011). The variety of nest sites available in the study area provides nighthawks with the opportunity for choices to optimize different crucial nest attributes (*e.g.,* surrounding land cover, thermal conditions).

Because nighthawks are aerial, opportunistic feeders (Caccamise, 1974), their diet is based upon insect prey availability (Todd *et al.,* 1998) and is expected to differ between grassland, open woodland, and urban habitat types. Changes in Missouri River flow patterns following the completion of dams in the 1950s have resulted in declines of aquatic macroinvertebrates in Missouri River habitats in South Dakota (Hay *et al.,* 2008; U.S. Army Corps of Engineers, 2012) and have reduced sandbars and open early successional stage forests (Dixon *et al.,* 2012) available for nighthawk nesting habitat (Brigham *et al.,* 2011). Therefore, the combination of river regulation and agricultural land conversion in the study area bordering the Missouri River has likely reduced foraging and nesting habitats. These changes might contribute to nighthawks seeking alternative nesting sites, such as urban rooftops. Conversion and loss of natural habitats within the Northern Prairie study area might thus contribute to greater use of urban habitats by nighthawks and potentially to regional population declines for this species, assuming that urban habitats are population sinks or do not support as many nighthawks as an unaltered landscape. This study compares nighthawk habitat associations in two parts of the study area, a western region, where grasslands are more common, and an eastern region which is almost exclusively dominated by row-crop agriculture. Grassland conversion rates are greater in western than in eastern portions of the study area because much of the eastern region's grasslands have already been converted to row crops (Wright and Wimberly, 2013; Gage *et al.,* 2017).

Changes in roofing practices are an added challenge to nighthawk nesting success in the study regions and elsewhere. Building owners are increasingly converting their flat, gravel rooftops to other materials that provide little camouflage for the eggs and produce temperatures that are too hot for successful egg incubation (Marzilli, 1989; COSEWIC, 2007). Therefore, the overall goal of this study was to examine nighthawk occurrence as a function of land cover attributes, which differed between eastern and western sections of the study area. Within this overall goal, the present study had two major objectives: (1) to determine the regional distribution of nighthawks, and (2) to estimate the effect of changing land use patterns on nighthawk habitat associations and population persistence.

METHODS

We chose two regions within the study area to compare nighthawk habitat associations, an eastern region dominated by row-crop agriculture and a western region with more grassland within the landscape. We conducted surveys at 396 points (348 in the eastern region and 48 in the western region) during two successive breeding seasons (Jun.-Jul., 2013-2014) to determine nighthawk occurrence patterns. Survey points were located within the Missouri Alluvial Plain, James River Lowland, Loess Prairies, and Southern Missouri Coteau Slope Level IV ecoregions (Bryce *et al.*, 1998). The western region (42.9°N- 43.0°N, 98.1°W-98.4°W) covered an extent of 9100 ha and the eastern region (42.6°N-43.0°N, 96.5°W-97.5°W) covered an extent of 155,600 ha (Fig. 1). The two study regions differed in size because sampling the variety of land cover types present on the landscape required more area at eastern sites due to the dominance of row-crop agriculture. The total areas surveyed (assuming a 400 m radius around survey points) were 11.6% of the total land area in the eastern study region and 29.2% of the total land area in the western study region. We

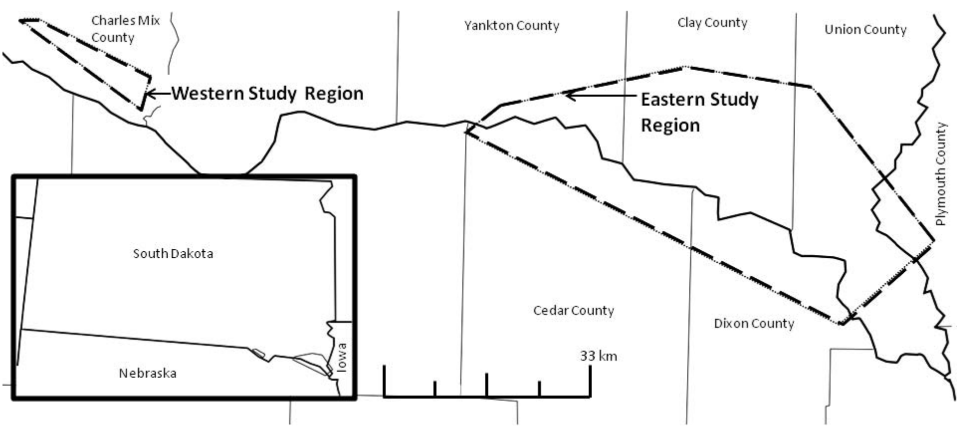

FIG. 1.—Western and eastern study regions in South Dakota, Iowa and Nebraska. Inset map shows study regions in southeastern South Dakota

combined and modified survey methods of the North American Breeding Bird Survey (U.S. Geological Survey, 2014), Nightjar Survey Network (2012), and Ng (2009) into our point count protocol. North American Breeding Bird Surveys (BBS) are conducted during the day, whereas the Nightjar Survey Network protocol is designed for nocturnal nightjars. Because nighthawks are crepuscular, we used the Ng (2009) nighthawk survey methods for the timing and conduct of our point counts and conducted surveys from 1 h before to 1 h after sunset. We used the environmental data collection methods from the BBS and Nightjar Survey Network protocols.

Preliminary observations of nighthawks suggested that birds in the eastern study region occurred primarily in towns whereas birds in the western study region were not restricted to towns and were more widespread across the landscape. Therefore, we centered the two study regions around areas where nighthawks had been documented previously but expanded the study regions to include surrounding landscapes including substantial representation of all available land cover types in both study regions. This strategy for establishing our study regions helped ensure that nighthawks would be present, but that minimal bias would be introduced as all habitats in the surrounding landscape were included within the point count surveys.

Our original survey design was based upon stratified random sampling, by dividing survey points among the ecoregions and dominant land cover types identified on Google Earth. However, once we began our point counts and "ground-truthed" our points, we realized that some adjustments needed to be made. We initially established survey points at 800 m intervals (*i.e.,* Breeding Bird Survey protocol, U.S. Geological Survey, 2014), which roughly corresponded to the approximately 800 m distance between territories of adjacent males (G.N. Newberry, pers. observ.), along all public roads within the study areas. The BBS distribution of survey points has been shown to sufficiently represent surrounding landscape (Veech *et al.*, 2017). This strategy of survey point distribution, however, placed the majority of points in cropland in the eastern study area, and we found very few nighthawks in cropland. Consequently, we eliminated many sections of cropland-dominated areas so that points were more evenly distributed among the different land cover types in both eastern and western study regions.

For both study areas, but especially in the eastern study region, where row crops were the overwhelmingly dominant landscape feature, we eliminated cropland survey points by either skipping some survey points along a route until we reached a point with more varied surrounding habitats, or by eliminating entire survey routes that passed though mainly row-crop landscapes. A random assortment of points would have been dominated by cropland and under-sampled other available habitats. As a result of this strategy for distribution of survey points, the dominant cropland was well-represented, but other habitats were also adequately sampled. Land cover types were more evenly distributed across the landscape in the western study region, and such heterogeneous landscapes are increasingly rare in the Western Corn Belt. As a consequence, the western study region was smaller and required fewer survey points to represent available land cover types in this region adequately.

We conducted point counts along roads, which are largely linear in eastern South Dakota, with routes consisting of 13-20 points along approximately 10-20 km transects, depending on the distance between survey points. We conducted as many point counts as possible within the 2 h sampling session, depending on distance between points, road conditions, and weather. Surveys lasted 3 min at each point, using playback (Ng, 2009) of nighthawk "boom calls" and vocalizations starting 1 min into the survey and lasting for 2 min. We did not conduct surveys if the wind speed exceeded 10 km/h, rain exceeded a sprinkle, or if noise was excessive (*e.g.,* continuous vehicle traffic). We conducted point counts at each survey point once per year and recorded whether nighthawks were present or absent, behavior (*i.e.,* calling overhead, territory defense) and environmental data (*i.e.,* temperature, sky and wind conditions, moon phase, and noise level).

Because our data are presence/absence data and because we based our methods in part on the playback methods of Ng (2009), we did not incorporate detection probability in our analysis. Instead to determine the effects of the environmental variables on nighthawk detection at survey points, we employed three Generalized Linear Models (GLM) with binomial distributions (Zuur *et al.,* 2009) using the R 3.3.2 MuMIn package to analyze the association of nighthawk presence (as a dependent variable) with weather (*i.e.,* temperature, short-term temperature change, sky and wind conditions), temporal factors (*i.e.,* moon phase and time before or after sunset), and other variables (*i.e.,* site and noise level). Statistical significance for all tests was defined at $P < 0.05$. We considered a bird present if it was present at a point in either year on any date. We were also very conservative in our approach to counting birds detected on successive points. If a nighthawk was detected on a previous survey point, any birds detected on successive points were not counted if they were coming from the direction of the previous point where they had been counted. This was fairly easy because of the tendency of nighthawks to vocalize steadily.

We quantified land cover characteristics surrounding survey points where birds were present and absent. Using satellite imagery (Google Earth, 2016), we quantified rooftop area (m^2) as a land cover type and identified 224,129 m^2 of flat rooftop in 4 towns (North Sioux City, Elk Point, Vermillion, and Yankton, South Dakota) in the study area by the shape of the rooftop in the imagery. Flat, gravel rooftops were not present in the study regions outside of these four towns. Rooftops on satellite imagery can be categorized into rubberized material which appears black, gravel which appears mottled gray, and new poly-synthetic materials which appear white. We determined that, in 2016, 106,945 m^2 of the total rooftop area was gravel and confirmed this categorization at a sample (95,174 m^2) of rooftops to which we had access by visiting the roof. For all other land cover types, we used raster-based 30 m resolution ArcGIS land cover data (Boryan *et al.,* 2011) (*i.e.,* National Land Cover Dataset; USDA, 2015) to quantify land cover surrounding survey points. To gain a general picture of the landscapes of the two regions, we also quantified land cover characteristics for reference points spaced 2.5 km apart and arranged on a grid (*i.e.,* 168 in the eastern region and 53 in the western region). We chose a 400 m buffer distance for both point counts and reference points based upon observed 500-800 m distances between territorial males (G.N. Newberry, pers. observ.) and the minimum 800 m distance between survey points. Because successive survey points were often 800 m apart, any buffer distances greater than 400 m run the risk of substantial overlap of land cover data between points; therefore, we limited land cover analyses to this single buffer distance. We lumped the land cover into categories that could be "ground truthed" by sight at our point counts: (1) row crop agriculture (termed hereafter as "cropland"), (2) water or wetland (termed hereafter as "water;" we lumped these two habitats as nighthawks tend to forage on emergent aquatic insects above both of these habitats), (3) grassland, hay crop, or pasture (termed hereafter as "grassland"), (4) developed urban, residential, or industrial (termed hereafter as "developed"), (5) flat, gravel rooftop (termed hereafter as "gravel rooftop"), and (6) deciduous, evergreen, or shrub forest (termed hereafter as "woodland").

We used two-tailed two-sample Welch's *t*-tests because the variances were unequal in R 3.3.2 to compare arcsin-square root transformed proportional land cover for each land cover type between study regions. We used several methods for these between-study region comparisons: between survey points where nighthawks were present and reference points and between all survey points and reference points. We also compared proportional land cover between points where birds were present vs. absent for both regions combined and for each region separately. In addition we used two separate GLMs with binomial distributions (Zuur *et al.,* 2009), one for each study region, to analyze nighthawk presence (as the dependent variable) as a function of the six land cover type variables with the R 3.3.2 MuMIn package. Following GLM analyses, we used AICc to rank land cover models within each region for each land cover type and for every combination of all six land cover types (Burnham and Anderson, 2002; Burnham and Anderson, 2004).

We constructed first order Markov state-transition probability models (Urban and Wallin, 2006) to project trends in grassland land cover for the western study region and for the entire state of South Dakota from 2006-2106. We ran the latter model to capture statewide land cover conversion trends, including ecoregions where grassland conversion rates are lower than for our western study region. We separated out grasslands protected via easements, Conservation Reserve Program (CRP), and federal and state ownership (Bauman *et al.,* 2016). Because most easements are long-term agreements and we cannot predict the future of easement policy or how they might be modified by land owners, we assumed grasslands protected via easements or federal/state ownership would continue in their present state and CRP conversion to agricultural lands would continue at the 2006-2015 regional CRP-conversion rate until 2106. We built the Markov model for the western study region by measuring land cover at reference points from 2006-2015 using USDA CropScape data (U.S. Department of Agriculture, 2016). We then compiled transition and input matrices for the Markov models using a steady-state solution (Urban and Wallin, 2006) by calculating percent land cover and 2006-2015 regional conversion rates (U.S. Department of Agriculture CropScape data; U.S. Department of Agriculture, 2016) for each of the five remaining land cover types, making simplified assumption that 2006-2015 regional conversion rates would continue into the future. Because developed, water, and woodland land cover types occurred at low percentages statewide, those categories we lumped with the other non-row crop and non-grassland categories in the Markov model as "other." Based upon Wright and Wimberley's (2013) 2006-2011 row-crop to grassland conversion area of 73,00 ha for South Dakota, the annual row-crop to grassland conversion rate was set to 0.01% and 0.001% for our western study area and for South Dakota, respectively.

In addition we built a first order Markov model to project trends in conversion of gravel rooftops to other materials in the eastern study region. To compile the input matrix for the Markov model (Urban and Wallin, 2006), we digitally measured and then calculated the percentage of gravel rooftop area in the eastern study region ($n = 56$) using 2006-2015 satellite imagery (Google Earth, 2016). Black rubberized rooftops were pooled and the new white poly-synthetic rooftop categories that had been converted from gravel from 2006-2015 into an "other rooftop" category in the Markov model. Reflecting a long-term trend (Marzilli, 1989; COSEWIC, 2007), it was assumed there was no conversion from the "other" rooftop category to gravel on existing roofs, and that new buildings would have the newer synthetic materials.

RESULTS

We detected totals of 29 birds at 48 survey points in the western region and 92 birds at 348 survey points in the eastern region over the two years of the study. Birds were present during both years at 5.9% of survey points, present during 1 y only at 12.5% of survey points and not present during either year at 81.6% of survey points. No effects of environmental or other variables on nighthawk occurrence were found (P > 0.05). Therefore, moon phase, weather, and other factors (*e.g.,* background noise) did not significantly affect nighthawk detections for the point counts. As a result, these variables were not included in further models for land cover and nighthawk habitat associations.

When we compared mean proportions of land cover at reference points between the two study regions (Fig. 2a), we found greater proportions of cropland (t_{104} = 1.983, P < 0.001), developed (t_{200} = 1.972, P < 0.001), and water (t_{131} = 1.978, P = 0.005) land cover types in the eastern region and greater grassland (t_{99} = 1.984, P < 0.001) and woodland (t_{103} = 1.983, P = 0.043) proportions in the western region. Because the region is dominated by agriculture (Wright and Wimberly 2013), and previous studies have established nighthawks' avoidance of agriculture (Brigham *et al.*, 2011), we attempted to avoid an overrepresentation of cropland and small patches of grazed grassland near cropland and include more representation of other land cover types used by nighthawks, namely developed areas and aquatic habitats (Brigham *et al.*, 2011), in our survey points. As a result, for the comparison between all bird survey points and all reference points for the two study areas combined (Fig. 2b), we found significantly greater proportions of cropland (t_{377} = -5.385, P < 0.001) and grassland (t_{401} = -2.916, P = 0.004) land cover types in reference points, greater proportions of water (t_{522} = 3.299, P = 0.001) and developed (t_{529} = 5.722, P < 0.001) land cover types in bird survey points, and no difference between survey points and reference points for woodland and gravel rooftop land cover types (P > 0.05). Since cropland and

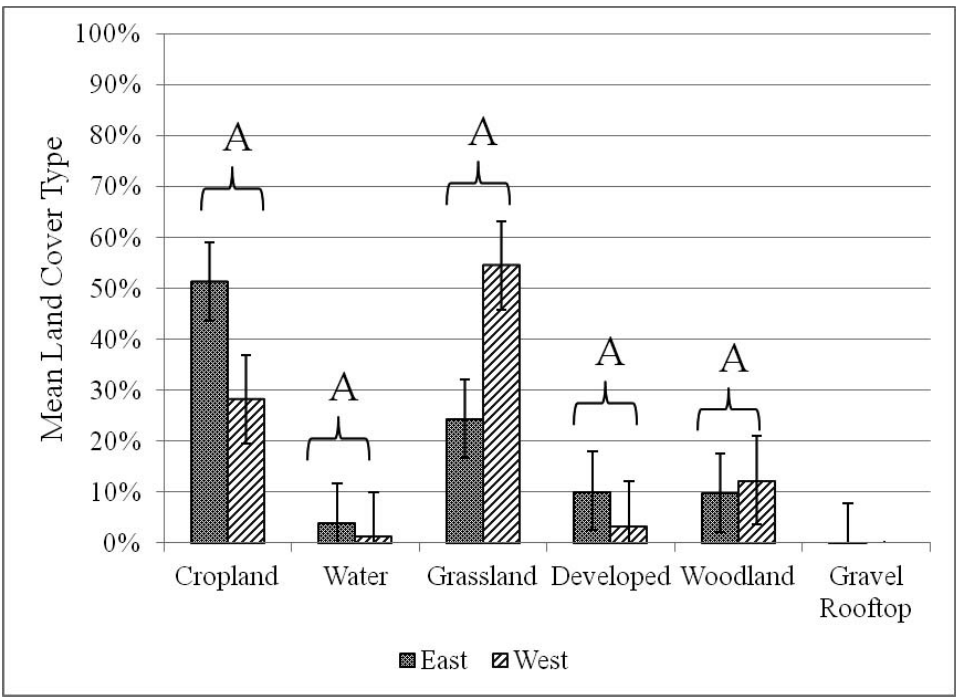

FIG. 2A.—Mean percent (±SE) land cover surrounding reference points in the two study regions. Significant between-region differences are denoted by A (for P < 0.05) for two-tailed two-sample Welch's *t*-tests

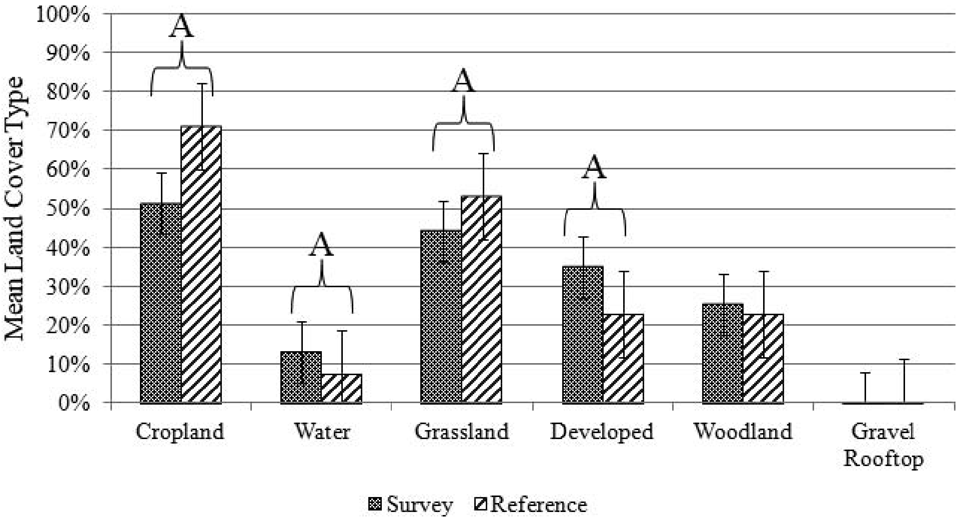

FIG. 2B.—Mean percent (±SE) land cover surrounding reference points and survey points in the two study regions combined. Significant between differences are denoted by A (for P < 0.05) for two-tailed two-sample Welch's *t*-tests

grassland were the two dominant land cover types in both our survey and reference points, we felt our surveys still effectively sampled those land cover types.

We also compared proportions of land cover at points where birds were present between the two study regions (Fig. 3) and found greater proportions of developed (t_{59} = 2.000, P < 0.0001), water (t_{297} = 1.968, P < 0.001), and gravel rooftop (t_{56} = 2.003, P = 0.0005) land cover types in the eastern region and greater proportions of cropland (t_{35} = 2.030, P < 0.001) and grassland (t_{33} = 2.035, P < 0.0001) land cover types in the western region.

When we compared mean proportion of land cover at points where birds were present vs. absent for both study areas combined (Fig. 4a), we found greater proportions of cropland (t_{129} = 2.569, P = 0.011), water (t_{222} = 5.034, P < 0.001), grassland (t_{121} = 2.434, P = 0.016), and woodland (t_{143} = 3.900, P < 0.001) were found at points where birds were absent. Greater developed (t_{83} = -7.082, P < 0.001) and gravel rooftop (t_{76} = -2.885, P = 0.005) land cover types were also found at points where birds were present. For the eastern study region separately (Fig. 4b), we found greater proportions of cropland (t_{95} = 4.352, P < 0.001), water (t_{132} = 3.991, P < 0.001), grassland (t_{89} = 3.829, P < 0.001), and woodland (t_{95} = 4.138, P < 0.001) land cover types where birds were absent and greater proportions of developed (t_{61} = -8.532, P < 0.001) and gravel rooftop (t_{56} = -2.935, P < 0.05) land cover types where birds were present. For the western study region (Fig. 4c), we found greater proportions of cropland where birds were present than absent (t_{39} = -2.811, P < 0.001), but no significant differences between the other land cover types (P >0.05).

For the eastern study region, GLMs showed developed land cover had a positive relationship with nighthawk presence, but cropland showed a weak negative trend with nighthawk presence (Table 1). For AICc models, the model containing only developed land cover was the best fitting model for nighthawk presence for the eastern study region (AICc = 218.3, weight = 1). All other models showed AICc weights of 0 and ΔAICc values greater than 67. These data highlight the importance of developed areas in the eastern region for

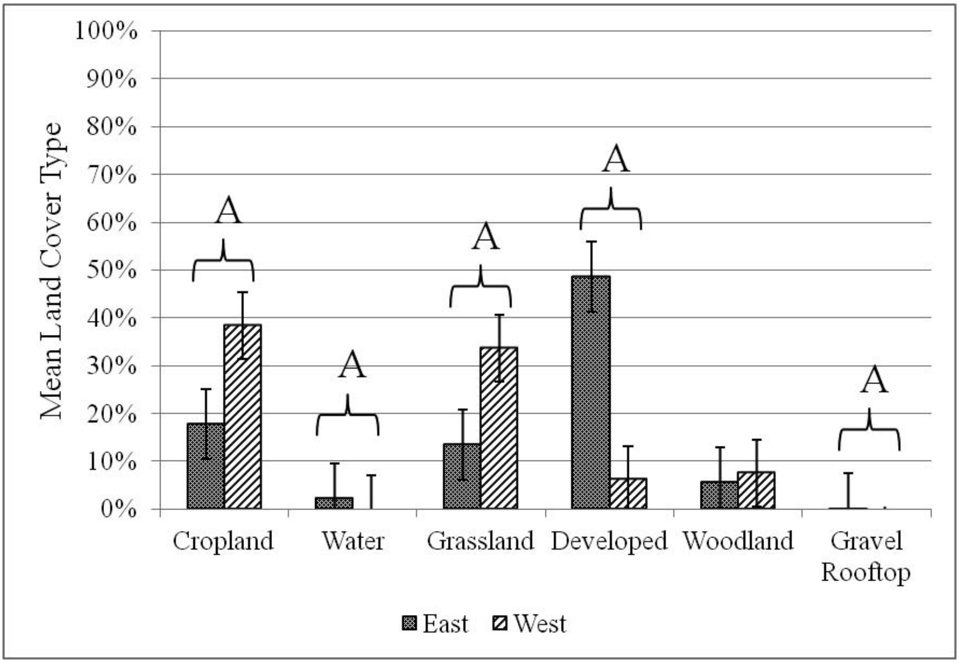

FIG. 3.—Mean percent (±SE) land cover surrounding points where birds were present in the two study regions. Significant between-region differences are denoted by A (for P < 0.05) for two-tailed two-sample Welch's *t*-tests

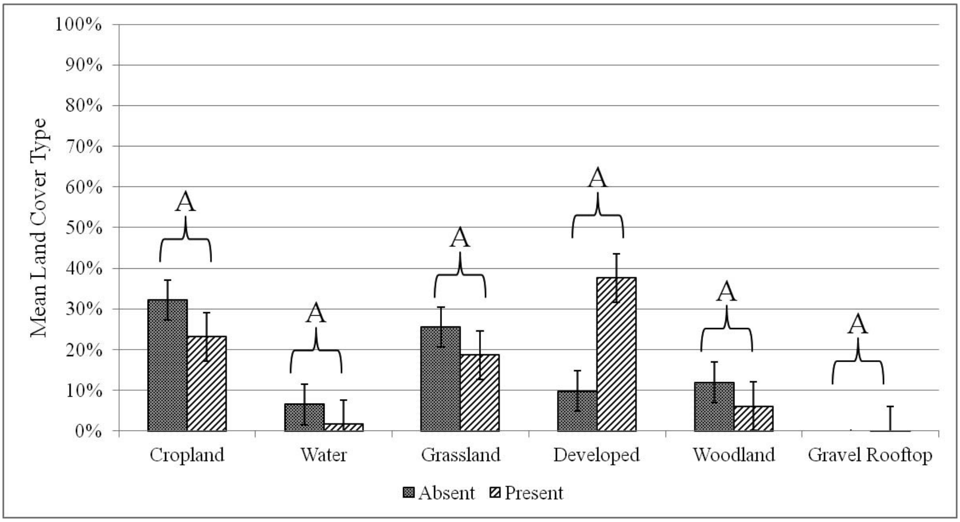

FIG. 4A.—Mean percent (±SE) land cover surrounding points where birds were present and where birds were absent for the two study regions combined. Significant differences are denoted by A (for P < 0.05) for two-tailed two-sample Welch's *t*-tests

TABLE 1.—Summary of Generalized Linear Models (GLM) with binomial distributions for nighthawk presence (as the dependent variable) as a function of land cover category variables by study region. There were no gravel rooftops in the western study region

Study Region	Variable	*Coef*	*Z*-value	*Df*	P-value	AICc	delta	Weight
Eastern	% Developed	5.609	3.798	347	**0.0001**	218.3	0.00	1
	% Gravel Rooftops	1803	0.018	347	0.9860	286.3	67.97	0
	% Cropland	-2.254	-1.902	347	0.0572	300.9	82.63	0
	% Grassland	-2.404	-1.022	347	0.3068	305.0	86.73	0
	% Woodland	-4.155	-0.846	347	0.3977	305.2	86.85	0
	% Water	-5.122	-1.860	347	0.0629	307.1	88.76	0
	Intercept	-1.519	-2.058	347	**0.0396**	314.5	96.17	0
Western	% Cropland	3.693	2.268	47	**0.0233**	66.9	0.00	0.744
	% Water	-1051	-0.007	47	0.9942	71.3	4.39	0.083
	Intercept	-3.049	-1.484	47	0.1377	72.25	5.18	0.056
	% Woodland	-1.942	0.790	47	0.4295	73.85	6.95	0.023
	% Grassland	-0.419	1.058	47	0.2901	74.13	7.22	0.020
	% Developed	-1.904	-0.158	47	0.8745	74.23	7.32	0.019

nighthawk habitat. In the western region, the model containing only cropland was the top ranked land cover model (AICc = 66.9, weight = 0.744), with all other land cover models showing AICc weights less than 0.094 and ΔAICc values greater than four. For the western study region, only cropland had a positive relationship with nighthawk presence (Table 1).

Markov model projections for grassland conversion in the western study region, using the 2006-2015 annual regional conversion rate of 0.5 %, showed that grassland would be reduced by 5 % by the year 2055, and by 15 % by the year 2106 (Fig. 5a). This level of conversion would reduce 2106 grassland land cover in the western study region to the current level of grassland land cover in the eastern study region (22%), where nighthawk

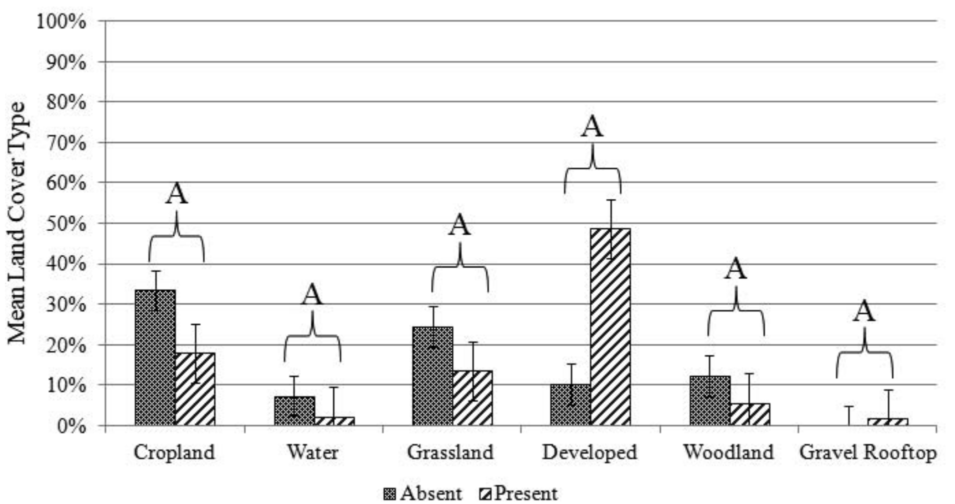

FIG. 4B.—Mean percent (±SE) land cover surrounding points where birds were present and where birds were absent for the eastern study region. Significant differences are denoted by A (for P < 0.05) for two-tailed two-sample Welch's *t*-tests

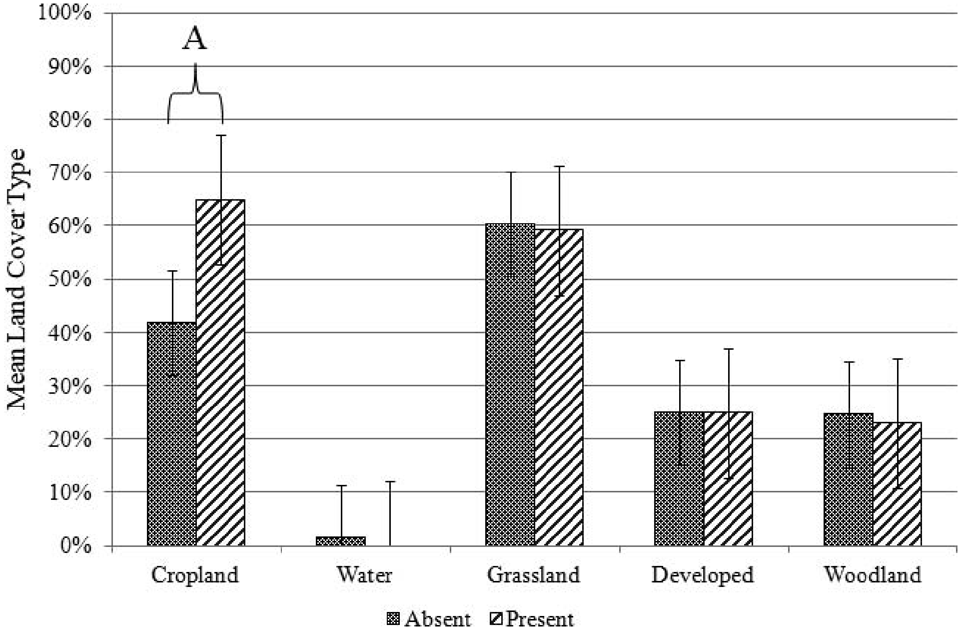

FIG. 4C.—Mean percent (±SE) land cover surrounding points where birds were present and where birds were absent for the western study region. Significant differences are denoted by A (for $P < 0.05$) for two-tailed two-sample Welch's *t*-tests

presence was positively associated only with developed habitats. The 2006-2015 annual grassland conversion rates for the western study region are greater than the conversion rates for South Dakota as a whole, but lower than those for some other Western Corn Belt regions (Wright and Wimberly, 2013 [2006-2011 1.0%-5.4% annual conversion]; Gage*, et al.,* (2017) [2009-2015 2.0% annual conversion]). An annual projected statewide grassland conversion rate of 0.01 % for South Dakota resulted in the Markov models projecting grassland land cover for the state would be reduced by 6% by the year 2106 (Fig. 5b).

We determined the annual gravel-to-other rooftop type conversion rate for 2006-2015 at eastern study sites was 0.7%. At this conversion rate, Markov models predicted gravel rooftops would be reduced by 54% by 2106 if gravel materials are not phased out by the roofing industry. However, rooftops are typically replaced every 7-10 years based upon customer recommendations by roofing companies (Progressive Materials, 2016; Roofcalc, 2016). If gravel rooftops in the eastern study region are replaced by other rooftop materials according to this schedule, then it is possible that gravel rooftops will disappear from eastern study sites within the next 10 y. Gravel rooftops are already absent from the relatively small urban areas in the western study region.

DISCUSSION

Nighthawk presence in the eastern study region was positively associated with developed land cover (Table 1). This was not true for the western study region where the small developed areas lacked gravel rooftops; highlighting the importance of gravel rooftops

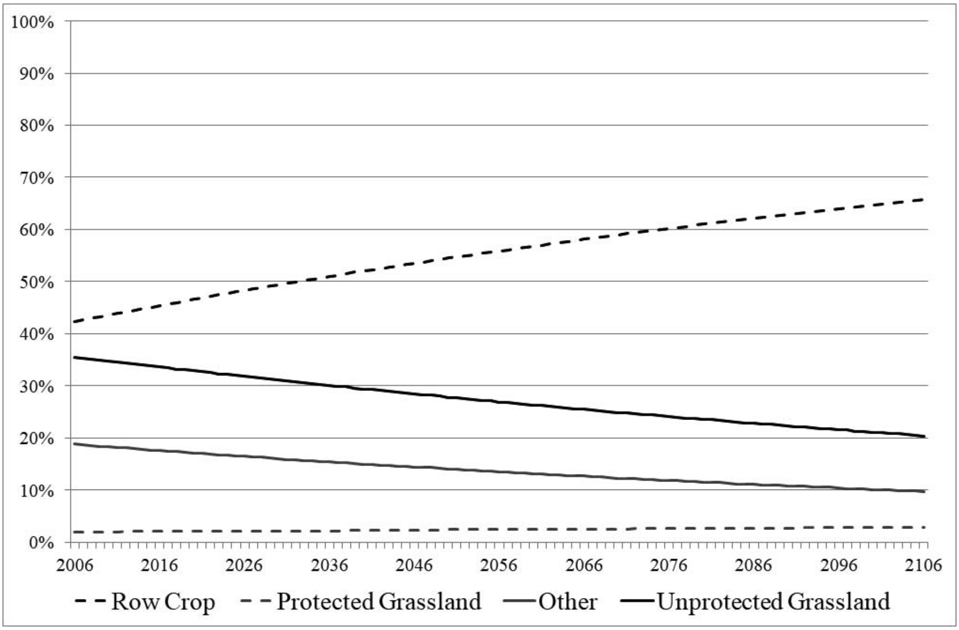

FIG. 5A.—Markov model predictions for trends in row-crop, grassland area and other land cover types at western sites in this study

within developed areas for nighthawks. Nighthawk occurrence was weakly negatively associated with cropland at eastern study sites (Table 1), where grassland patches were generally small and occupied only 24% of the landscape area. Indeed, the proportion of cropland in the eastern region was 2-fold greater than in the western region (Fig. 2a). Moreover, nighthawk presence showed a significant positive association with cropland in the western study region (Table 1), which has greater grassland and less cropland on the landscape than the eastern study region (Fig. 2a) and had greater cropland where nighthawks were present than absent (Fig. 4b). This result indicates that nighthawks can coexist with cropland in a more patchwork, heterogeneous landscape as long as grasslands are in the mix. The divergent responses of nighthawk occurrence to cropland in the two study regions is consistent with the idea that grassland conversion in the western study region has not yet reached a level where nighthawks are forced to seek other nesting and/or foraging habitats; therefore, birds are distributed more broadly across the landscape than in the eastern study region. Moreover, previous nighthawk research (Brigham *et al.*, 2011) indicates that grassland is an important habitat. Our data did not show a direct positive effect of grassland on nighthawk occurrence, but they did show that the effects of cropland were reversed from negative to positive with increased grassland within the landscape. This result suggests that cropland provides a benefit to nighthawks in these landscapes, presumably by providing foraging opportunities in open environments, but that grassland also provides an indirect benefit to nighthawks by allowing them to persist in these heterogeneous landscapes along with croplands.

Current land use trends in the Northern Prairie region include conversion of gravel rooftops to newer synthetic materials (Brigham *et al.*, 2011) and net conversion of grasslands

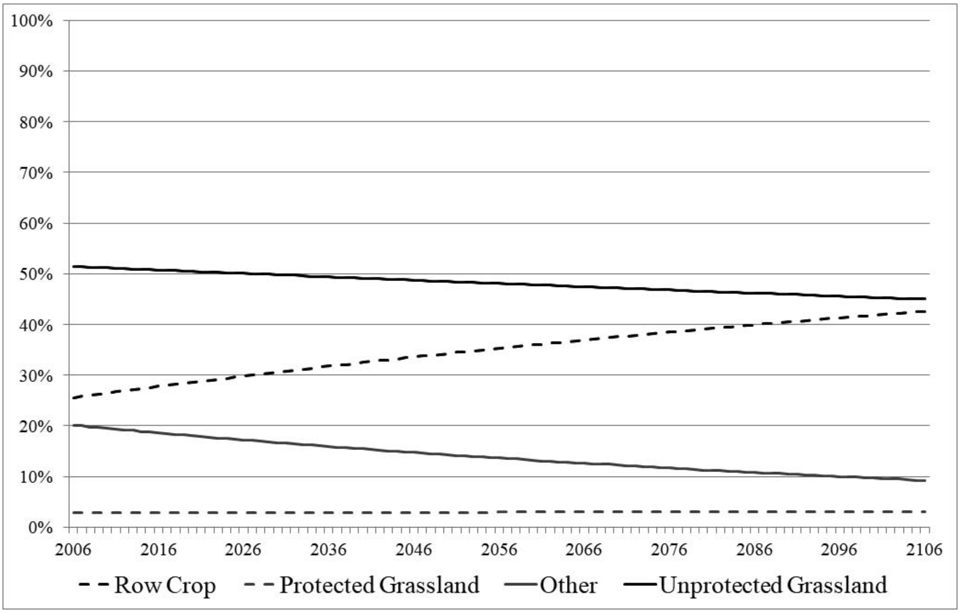

FIG. 5B.—Markov model predictions for trends in row-crop, grassland area and other land cover types for South Dakota

to row-crops (Wright and Wimberly, 2013; Gage *et al.*, 2017). Given that these trends reduce habitats favorable to nighthawk nesting and foraging, these data reveal multiple challenges for nighthawk populations in the Western Corn Belt. Nighthawk habitat associations in the present study are generally consistent with those from other studies across their range where nighthawks are positively associated with open habitats, including open forests, grasslands, and bare ground, during the breeding season (Brigham *et al.*, 2011). For example Ng (2009) demonstrated nighthawk abundance was positively associated with grassland cover and proximity to water in a grassland-agriculture landscape in Saskatchewan. In the Central Plains, nighthawks are primarily associated with short-grass prairie but also occur in lower numbers in dry-land agricultural habitats (winter wheat and sorghum); although not in Conservation Reserve Program grasslands (McLachlin, 2007). Grassland conversion to shrubland habitat in New Mexico resulted in decreases in nighthawk abundance (Pidgeon *et al.*, 2001). Lohnes (2010) showed grassland habitats, especially those with short grasses or open sandy and rocky areas, were important to nighthawks in tallgrass prairie landscapes in eastern Kansas. Viel (2014) studied nighthawk habitat associations in agricultural and developed landscapes in Wisconsin and demonstrated negative associations with agricultural land cover and positive associations with developed land cover with gravel rooftops. In contrast to this latter study, nighthawks in British Columbia preferred natural habitats (*i.e.*, open pine forest) to urban sites with gravel rooftops for nesting and roosting if sufficient natural habitat was available (Brigham, 1989). Collectively, these studies highlight the importance of grassland habitat with bare or sparsely vegetated areas to nighthawks, but also suggest urban habitats with gravel rooftops are important, especially in areas where abundant natural grasslands or other suitable habitats are not available within the landscape.

Nighthawks are capable of nesting in a number of habitat types (*e.g.,* sandbars, open forests, grasslands, and gravel rooftops; Brigham *et al.,* 2011). However, the present study showed different habitat associations in the two study regions, corresponding to a possible area threshold for natural nesting habitats (*e.g.,* grassland, sandbar, and open forest), below which nighthawks are forced to occupy urban habitats with gravel rooftops. At eastern study sites, where gravel rooftops occur and grasslands occupy a small proportion of the landscape and only in small parcels, nighthawk presence was positively associated with developed areas and gravel rooftops and weakly negatively associated with cropland. These results suggest this sub-population has adjusted to occupy urban areas with gravel rooftops as natural nesting habitat has declined. Such an area threshold for suitable natural nesting habitat is consistent with the findings of Brigham (1989), where nighthawks did not use available gravel rooftops when sufficient natural habitats also occurred in the area, and Viel (2014), where nighthawks were positively associated with urban areas in an intensively managed agricultural landscape.

Current land cover proportions of grasslands in the western study region appear sufficient to attract nighthawks during the nesting season and nighthawks appear more evenly distributed across the land cover categories in the western study region. This suggests birds at western study sites used a wide variety of habitats (including row crops) adjacent to grassland in this area where row-crop agriculture is not the dominant landscape feature. However, Markov models, assuming current regional rates of grassland conversion to row-crops, along with the small proportions of protected grasslands, suggest that continued loss of grasslands will reduce grassland land cover by 2106 to levels similar to those at eastern study sites, where nighthawks occur almost exclusively in developed areas with gravel rooftops. Because the small developed areas in the western study region have no gravel rooftops, this region seems unlikely to support a nighthawk population by the year 2106. Such a conclusion is consistent with the concept of extinction thresholds (Fahig, 2001). Moreover, recent economic pressures (*i.e.,* high prices for corn and soybeans stimulated by the biofuel industry and the low enrollment of CRP lands) in the Western Corn Belt (Wright and Wimberly, 2013) make it unrealistic to expect existing unprotected grasslands will be protected without increases in grassland easement acquisition by governmental and non-governmental conservation agencies. Our modeling strategy assumes a constant rate of land use change which is influenced by a recent emphasis on biofuels, and this emphasis will likely change over the next century. Nevertheless, the finding that at current rates of land use change, the heterogeneous landscape of the western study region, which is amenable to nighthawks, will change to a row-crop dominated landscape that nighthawks do not use (outside of developed areas), is useful for conservation planning for this species.

Gravel rooftops can provide refugia for nighthawks displaced by grassland conversion to row-crop dominated landscapes (Brigham *et al.,* 2011; Viel 2014). However, as a worst-case scenario, if gravel rooftops are replaced by newer synthetic materials at the typical time frames for roof replacement, gravel rooftops might disappear from the row-crop dominated landscapes of the eastern study region within the next 10 y. Even if gravel is not replaced by the newer synthetic materials, Markov models based on recent transition rates project gravel rooftops will drop to less than 30% of all flat rooftops in the region by 2106. Given that similar landscapes characterize much of the Western Corn Belt states (*i.e.,* Minnesota, Iowa, South Dakota, and North Dakota), these data suggest nighthawks in this region face serious future threats to population persistence. In addition, urban areas are subject to the increasing prevalence of nestling and fledgling predation by crows and other species, which has likely contributed to declines of urban nighthawk populations in North America (Marzilli, 1989;

Wedgwood, 1991; COSEWIC, 2007; Latta and Latta, 2015). Moreover, the increasing temperatures expected under climate change scenarios, particularly in urban areas (Bonan, 2002), might also compromise nighthawk nesting success in exposed rooftop habitats (Fisher *et al.,* 2004; Newberry and Swanson, 2018). Given urban nighthawk population trends and the longevity and increased energy efficiency of newer rooftop materials, it might be impractical to suggest gravel rooftops can be conserved as an important nesting habitat, especially for a single species. Policies promoting continued existence of gravel rooftops or alternative roofing practices, such as ecoroofs, which provide small rooftop patches of suitable nesting habitat in urban settings (Lewis, 2016), might be the only course of action to maintain urban nighthawk populations within the Western Corn Belt region. Additionally, future studies could be helpful in identifying a threshold for gravel rooftop cover that could maintain a nighthawk population, irrespective of the other urban pressures.

Regions of North America that are mostly unsuitable for row-crop agriculture, such as the western plains, offer areas where grassland and open forest habitats persist at higher levels of landscape cover than in the Western Corn Belt. The continued persistence of nighthawks in such areas is supported by the statewide grassland conversion Markov models for South Dakota (Fig. 5b), which suggest areas of the Northern Plains unsuitable for row-crop agriculture will provide sufficient grassland breeding habitat for nighthawk populations into the future. As a result, we expect regional range shifts westward in nighthawk populations. Consistent with this idea, nighthawk abundances have increased in western South Dakota and the western Great Plains since the 1960s (Sauer *et al.,* 2017). Moreover, climate change may be causing areas along the western edge of he Western Corn Belt to become more arid in the future; thus, areas with recent expansion of row-crops might convert back to rangeland in the future (Seager *et al.,* 2018) Thus, we recommend conservation efforts for Northern Plains nighthawks be concentrated in these areas.

Acknowledgments.—We are grateful to Dr. R. Mark Brigham for providing advice on point count methods for this species. We thank Drs. Mark D. Dixon, Erica L. Mize, and Erliang Zeng for their advice on statistics. We also thank technician Will Culver III for his work on the project. DLS was supported by the U.S. National Science Foundation OIA-1632810. Funding was provided by South Dakota Game, Fish and Parks Wildlife Diversity Small Grants, Prairie Biotic Inc., University of South Dakota Biology Department, University of South Dakota Research and Creativity Grant, University of South Dakota John W. Carlson Research Grant, and South Dakota Ornithologists' Union Nathanial R. Whitney Memorial Research Grant. No funding organization influenced the manuscript, and none required approval of the manuscript. This research was conducted under the University of South Dakota Institutional Animal Care and Use Protocol (IACUC No. 23-05-13-16C, 15-05-16-19C). Nebraska, Iowa, and South Dakota do not require permits for point counts.

LITERATURE CITED

AHLERING, M.A. AND C. L. MERKORD. 2016. Cattle grazing and grassland birds in the northern tallgrass prairie. *J. Fish Wildl. Manag.*, **80**:643–654.

BAUMAN, P., B. CARLSON, AND T. BUTLER. 2016. Quantifying undisturbed (native) lands in eastern South Dakota. South Dakota State University Public Report.

BONAN, G.B. 2002. Urban ecosystems. *In:* Ecological climatology: concepts and applications. Cambridge University Press, Cambridge, UK.

BORYAN, C., Z. YANG, R. MUELLER, AND M. CRAIG. 2011. Monitoring US agriculture: The US Department of Agriculture, National Agricultural Statistics Service, Cropland Data Layer Program. *Geocarto Int.*, **26**:341–358.

BRIGHAM, R. M. 1989. Roost and nest sites of Common Nighthawks: are gravel roofs important? *Condor*, **91**:722–724.

BRIGHAM, R. M., J. NG, R. G. POULIN, AND S. D. GRINDAL. 2011. Common Nighthawk (*Chordeiles minor*). *In*: P. G. Rodewald (ed.). The Birds of North America. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, DC, doi:10.2173/bna.213.

BRYCE, S., J. M. OMERNIK, D. E. PATER, M. ULNER, J. SCHAAR, J. FREEOUF, R. JOHNSON, P. KUCK, AND S. H. AZEVEDO. 1998. Ecoregions of North Dakota and South Dakota. Jamestown, ND: Northern Prairie Wildlife Research Center Online.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, NY.

———. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol Method Res.*, **33**:261–304.

CACCAMISER, D. F. 1974. Competitive relationships of the Common and Lesser Nighthawks. *Condor*, **76**:1–20.

COSEWIC 2007. COSEWIC assessment and status report on the Common Nighthawk *Chordeiles minor* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 25 pp.

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. *Environ. Manage.*, **49**:990–1008.

FAHIG, L. 2001. How much habitat is enough? *Bio. Conserv*, **100**:65–74.

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.

FUHKENDORF, S. D., W. C. HARRELL, D. M. ENGLE, R. G. HAMILTON, C. A. DAVIS, AND D. M. LESLIE, JR. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.*, **16**:1706–1716.

GAGE, A. M., S. K. OLIMB, AND J. NELSON. 2016. Plowprint: tracking cumulative cropland expansion to target grassland conservation. *Gr. Plains Res.*, **26**:107–116.

GOOGLE EARTH. 2016. Image Landsat. (accessed October 20, 2016). https://www.google.com/earth/explore/products/desktop.html

HALLMAN, C. A., N. SORG, E. JONGELANS, E. SIEPEL, H. HOFLAN, AND H. SCHWAN. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE,* **12**:e0185809.

HAY, C. H., T. G. FRANTI, D. B. MARX, E. J. PETERS, AND L. W. HESSE. 2008. Macroinvertebrate drift density in relation to abiotic factors in the Missouri River. *Hydrobiologia*, **598**:175–189.

KUNZ, T. H., E. BRAUN DE TORREZ, D. BAUER, T. LOBOVA, AND T. H. FLEMING. 2011. Ecosystem services provided by bats. *Ann. N. y. Acad. Sci.* **1223**:1–38.

LATTA, S. C. AND K. N. LATTA. 2015. Do urban American Crows (*Corvus brachyrhynchos*) contribute to population declines of the Common Nighthawk (*Chordeiles minor*)? *Wilson J. Ornithol.*, **127**:528–533.

LEWIS, A. 2016. Ecoroofs in Multnomah County, Oregon as habitat for the Oregon Vesper Sparrow and Common Nighthawk. Master's Thesis. University of Oregon, Eugene, OR.

LOHNES, R. G. 2010. Nest site selection and nest thermal properties of Common Nighthawks on the tallgrass prairie of Kansas. Master's Thesis. Cornell University, Ithaca, NY.

MARZILLI, V. 1989. Up on the roof. *Maine Fish Wildl.*, **31**:25–29.

MCLACHLAN, M., M. CARTER, C. RUSTAY, AND P. L. J. VENTURE. 2007. Effects of the Conservation Reserve Program on priority mixed-grass prairie birds. USDA Natural Resources Conservation Service, WA.

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**:1.

NEWBERRY, G. N. AND D. L. SWANSON. 2018. Elevated temperatures are associated with stress in rooftop-nesting Common Nighthawk (*Chordeiles minor*) chicks. *Conserv. Physiol.*, in press.

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, SK.

NIGHTJAR SURVEY NETWORK. 2012. Survey Instructions. The College of William and Mary and the Virginia Commonwealth University, The Center for Conservation Biology, Williamsburg, VA. http://www.nightjars.org/participate/survey-instructions

PHILPOTT, S. M., O. SOONG, J. H. LOWENSYEN, A. L. PULIDO, D. T. LOPEZ, D. F. FLYNN, AND F. DECLERK. 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecol. Appl. 19*:1858–1867.

PIDGEON, A. M., N. E. MATHEWS, R. BENOIT AND E. V. NORDHEIM. 2001. Response of avian communities to historic habitat change in the northern Chihuahuan Desert. *Conserv. Biol.*, **15**:1772–1788.

PROGRESSIVE MATERIALS. 2016. Flat Roof Options. http://www.pmsilic1.com/flat-roof-options/

ROOFCALC. 2016. Roof Calculator. http://RoofCalc.org.

SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI, JR. AND W. A. LINK. 2007. The North American Breeding Bird Survey, Results and Analysis 1966–2012. Version 2007.10, USGS Patuxent Wildlife Research Center, Laurel, MD.

SAUER, J. R., 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, MD.

SCHERR, S. J. AND J. A. MCNEELY. 2008. Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes. *Philos T R Soc B*, **363**:477–494.

SEAGER, R., J. FELDMAN, N. LIS, M. TING, A. P. WILLIAMS, J. NAKAMURA, H. LIU, AND N. HENDERSON. 2018. Whither the 100th Meridian? The Once and Future Physical and Human Geography of America's Arid–Humid Divide. Part II: The Meridian Moves East. *Earth Interact* **22**:1–24.

SEKERCIOGLU, C. H. 2006. Increasing awareness of avian ecological function. *Trends Ecol. Evol. 21:* 464–471.

SPESS JACKSON, L., C. A. THOMPSON, AND J. J. DINSMORE. 1996. The Iowa breeding bird atlas. University of Iowa Press, IA.

STANTON, R. L., C. A. MORRISSEY, AND R. G. CLARK. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. *Agr. Ecosyst. Environ.*, **254**:244–254.

TALLMAN, D. A., D. L. SWANSON AND J. S. PALMER. 2002. Birds of South Dakota. South Dakota Ornithologists' Union, SD.

TODD, L. D., R. G. POULIN, AND R. M. BRIGHAM. 1998. Diet of Common Nighthawks (*Chordeiles minor*: Caprimulgidae) relative to prey abundance. *Am. Midl. Nat.*, **139**:20–28.

URBAN, D. L. AND D. O. WALLIN. 2006. Introduction to Markov Models. *In:* S. E. Gergel and M. Turner (eds.). Learning landscape ecology: a practical guide to concepts and techniques, Springer, NY.

U.S. ARMY CORPS OF ENGINEERS. 2012. Missouri River recovery program. http://www.facebook.com/MoRiverRecovery/info and http://www.moriverrecovery.org/

U.S. DEPARTMENT OF AGRICULTURE. 2016. National Agricultural Statistics Service CropScape – Cropland Data Layer. http://nassgeodata.gmu.edu/CropScape/

U.S. GEOLOGICAL SURVEY. 2014. Instructions for conducting the North American Breeding Bird Survey. USGS Patuxent Wildlife Research Center, Laurel, MD. https://www.pwrc.usgs.gov/bbs/participate/instructions.html.

VEECH, J. A., K. L. PARDIECK, AND D. J. ZIOLKOWSKI, JR. 2017. How well do route survey areas represent landscapes at larger spatial extents? An analysis of land cover composition along Breeding Bird Survey routes. *Condor*, **119**:607–615.

VIEL, J. M. 2014. Habitat preferences of the Common Nighthawk (*Chordeiles Minor*) in cities and villages in southeastern Wisconsin. Master's thesis. University of Wisconsin, Milwaukee, WI.

WALKER, J., J. J. ROTELLA, C. R. LOESCH, R. W. RENNER, J. K. RINGELMAN, M. S. LINDBERG, R. DELL, AND K. E. DOHERTY. 2013. An integrated strategy for grassland easement acquisition in the Prairie Pothole Region, USA. *J. Fish Wildl. Manag.*, **4**:267–279.

WEDGEWOOD, J. A. 1991. Common Nighthawks in Saskatoon. Saskatchewan Natural Historical Society, SK.

WEIBULL, A.-C., Ö. ÖSTMAN, AND Å. CRANQVIS. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodivers. Conserv.*, **12**:1335–1355.

WRIGHT, C. K. AND M. C. WIMBERLY. 2013. Recent land use change in the Western Corn Belt theatens grasslands and wetlands. *Proc. Natl. Acad. Sci. U.S.A.*, **110**:4134–4139.

ZUUR, A., E. N. IENO, N. WALKER, A. A SAVELIEV AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, NY.

SUBMITTED 20 FEBRUARY 2018 ACCEPTED 26 JUNE 2018