

BUTEO ECOLOGY: AN INTENSIVE STUDY OF SWAINSON'S HAWKS ON THE
NORTHERN GREAT PLAINS

BY

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TABLE OF CONTENTS

ABSTRACT	vii
CHAPTER 1: <i>BUTEO</i> NESTING ECOLOGY: EVALUATING NESTING OF SWAINSON’S HAWKS ON THE NORTHERN GREAT PLAINS	1
ABSTRACT.....	3
INTRODUCTION.....	4
METHODS.....	6
RESULTS.....	10
DISCUSSION.....	13
CONCLUSION.....	17
LITERATURE CITED.....	18
CHAPTER 2: SPATIAL ECOLOGY AND ADULT SURVIVAL OF SWAINSON’S HAWKS (<i>BUTEO SWAINSONI</i>) IN THE NORTHERN GREAT PLAINS	30
ABSTRACT.....	32
INTRODUCTION.....	33
STUDY AREA.....	35
METHODS.....	36
RESULTS.....	40

DISCUSSION.....	43
LITERATURE CITED.....	48
CHAPTER 3: DIET COMPOSITION AND PROVISIONING OF SWAINSON'S HAWK NESTLINGS IN THE NORTHERN GREAT PLAINS.....	64
ABSTRACT.....	67
INTRODUCTION.....	69
METHODS.....	72
RESULTS.....	76
DISCUSSION.....	78
CONCLUSION.....	82
LITERATURE CITED.....	83

ABSTRACT

BUTEO ECOLOGY: AN INTENSIVE STUDY OF SWAINSON'S HAWKS ON THE
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Swainson's hawks (*Buteo swainsoni*) are long-distance migratory raptors that nest primarily in isolated trees located in areas of high grassland density. In recent years, anthropogenic conversion of grassland habitat has raised concerns about the status of the current breeding population of the hawk in the northern Great Plains. In 2013, we initiated a study to investigate the influence of intrinsic and extrinsic factors influencing Swainson's hawk nesting ecology in north-central South Dakota and south-central North Dakota. Using ground and aerial surveys, we located and monitored nesting Swainson's hawk pairs: 73 in 2013 and 120 in 2014. Apparent nest success was 40% in 2013 and 58% in 2014. Overall, 163 chicks fledged; 1.63 fledglings per successful pair in South Dakota and 1.68 fledglings per successful pair in North Dakota. We captured and radio marked 15 breeding Swainson's hawks to evaluate home range size during the breeding season. We estimated 95 % and 50% minimum convex polygon home ranges for 10 breeding Swainson's hawks in 2013 (1.91 km² and 0.24 km²) and 9 in 2014 (2.10 km² and 0.58km²); males and female home ranges were similar ($P = 0.12$). We used Program MARK to evaluate the influence of land cover on nest success resulting in two competing models. Model S_{State} indicated that nest success differed between states, which was 0.35 (95% CI = 0.28–0.43) and 0.19 (95% CI = 0.12–0.30) in North Dakota and South Dakota,

respectively. Model $S_{\text{Dist2Farm}+\%\text{Hay}}$ indicated that nest survival was greater in closer proximity to farms and with decreased percent hay cover. We used logistic regression analysis to evaluate the influence of landscape variables on nest site selection; percent row crop negatively affected nest site selection whereas percent housing development positively affected nest site selection. Home range sizes in our study area were smaller than previously documented and analysis of covariance model results indicated that home range size was influenced by the percent of grassland and development within their breeding home ranges. Our results indicate that Swainson's hawks maintain a high degree of breeding site fidelity and that home range size is influenced positively by the presence of grasslands and negatively by percent development. We suggest that tree belts associated with farmsteads, whether occupied or not, provide critical breeding sites for Swainson's hawks in the northern Great Plains.

CHAPTER 1: *Buteo* nesting ecology: evaluating nesting of Swainson's hawks on the northern Great Plains

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Buteo nesting ecology: evaluating nesting of Swainson's hawks on the
northern Great Plains

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Abstract

Swainson's hawks (*Buteo swainsoni*) are long-distance migratory raptors that nest primarily in isolated trees located in areas of high grassland density. In recent years, anthropogenic conversion of grassland habitat has raised concerns about the status of their current breeding population in the northern Great Plains. In 2013, we initiated a study to investigate the influence of intrinsic and extrinsic factors influencing Swainson's hawk nesting ecology in north-central South Dakota and south-central North Dakota. Using ground and aerial surveys, we located and monitored nesting Swainson's hawk pairs: 73 in 2013 and 120 in 2014. Apparent nest success was 40% in 2013 and 58% in 2014. Overall, 163 chicks fledged; 1.63 fledglings per successful pair in South Dakota and 1.68 fledglings per successful pair in North Dakota. We used Program MARK to evaluate the influence of land cover on nest success, which resulted in two competing models. Model S_{State} indicated that nest success differed between states, which were 0.35 (95% CI = 0.28–0.43) and 0.19 (95% CI = 0.12–0.30) in North Dakota and South Dakota, respectively. Model $S_{\text{Dist2Farm}+\% \text{Hay}}$ indicated that nest survival was greater in closer proximity to farms and with decreased percent hay cover. We used logistic regression analysis to evaluate the influence of landscape variables on nest site selection; percent row crop negatively affected nest site selection whereas percent housing development positively affected nest site selection. We suggest that tree belts associated with farmsteads, whether occupied or not, provide critical breeding sites for Swainson's hawks in the northern Great Plains.

Introduction

Swainson's hawks (*Buteo swainsoni*) are long-distance migratory raptors that nest primarily in areas consisting of isolated tree stands scattered among open grassland areas [1–3]. Due to the broad distribution of Swainson's hawks across much of the central and western United States and Canada, numerous studies have been conducted documenting reproduction across much of their range [1, 2, 4–9]. Swainson's hawks nest in high densities in the Prairie Pothole Region of the Great Plains [1, 11–12]. However, continued grassland loss has resulted in the Swainson's hawk being listed as a Species of Concern by state and federal agencies [11–13].

The Conservation Reserve Program was established by the Farm Service Agency to remove fields with highly-erodible soils out of production and reestablish permanent cover to control soil erosion. They created contracts to pay a fee to farmers to not farm their land and re-establish grasslands across the United States [14]. However, with CRP payments unable to compete with rising commodity prices, CRP reenrollment continues to decline. Estimates of CRP lands lost from 2007–2013 were 931,000 ha in North Dakota and South Dakota [14] and an additional net loss of non-CRP grasslands of 271,000 ha from 2006–2011 [15]. Continued expansion of intensive agricultural practices raises concerns about potential impacts to nesting ecology of grassland nesting raptors [e.g., 9].

In the northern Great Plains, extrinsic factors influencing nest survival of Swainson's hawks have received little attention [1]. These extrinsic factors (e.g., habitat,

predation, competition, and climate) have the potential to positively [3, 16] or negatively [17] affect nest success rates. Habitats surrounding nest sites could impact survival by displacing prey communities, increasing or changing predator populations, or increasing competition. Farming and ranching practices on remaining grasslands also are a potential concern; increased cattle production and infrequent haying could alter foraging habitats [18]. However, agriculturally rich habitats may increase productivity rates more than habitats lacking agriculture and potentially provide a stabilized prey base [16, 19–20].

Swainson's hawks have been documented nesting in areas dominated by grasslands [1–2] as well as agriculturally dominated landscapes [1, 3, 21–22]; however, limited information exists concerning the influence of habitat variables on nest site selection in the northern Great Plains. Research conducted in agriculturally intensive areas have documented that Swainson's hawks have increased productivity in agriculture rich landscapes and in some cases have selected for these agricultural landscapes [1, 16, 21–22]. The effects of specific crop types (e.g., row crop, small grain crop) on nest survival and nest site selection are currently unknown. Previous studies have focused on nest site characteristics and habitat around the nest on a micro- scale [e.g., 9]. Evaluating the effects of habitat on a larger scale (e.g., home range), could provide additional understanding of land cover effects on nest survival and nest site selection [5, 17].

Documenting nesting ecology of Swainson's hawks occupying the northern Great Plains could provide insight into the effects of grassland loss on this species. Therefore, our first objective was to evaluate the influence of extrinsic (e.g., percent row crop, distance to farm) variables on nest survival of Swainson's hawks in the northern Great Plains. We expected that with high occurrences of grassland to row crop conversion over

the last 10 years that row crop production would have a negative effect on nest survival and that grassland would increase nest survival rates. Our second objective was to evaluate the influence of habitat variables on nest site selection. We predicted that due to the increase in crop production and the lack of trees on this landscape, Swainson's hawks would select for areas with high percentages of grassland and trees while selecting against areas of row crop production.

Materials and Methods

Study Area

The 11,137 km² study area consisted of four counties located in south-central North Dakota and north-central South Dakota (Fig. 1). McPherson County, South Dakota and Dickey, McIntosh, and Logan counties, North Dakota, lie within the Northern and Northwestern Glaciated Plains level III ecoregion [23]. This moraine landscape contains numerous pothole wetlands scattered among the rolling terrain, which is typical of the Missouri Coteau region [10, 23]. Land use in the four counties consisted of cultivated land (62.5%), grassland (17.4%), and development (13.7%), with the remaining land constituting forested cover (3.6%) and wetlands (2.8%; [24]). Average high and low temperatures for the months of April through July ranged from 11.6° C to 29.3° C and –0.5° C to 14.4° C, respectively. Average annual precipitation was 45–53 cm and the majority of precipitation events occurred during May to September [25]. Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern reedgrass (*Calamagrostis stricta*), prairie cordgrass (*Spartina*

pectinata) big bluestem (*Andropogon gerardi*), western wheatgrass (*Pascopyrum smithii*), porcupine grass (*Stipa spartea*), and little bluestem (*Schizachyrium scoparium*; [23]). Tree species were primarily cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*; [10]).

Nest Monitoring

We began searching for active nests on 1 May of each breeding season targeting all tree sites (e.g., shelterbelts, farmsteads, riparian areas) in the study area. We attempted to locate all active nest structures from roads before tree foliage obscured our ability to locate nests. If we located a nesting pair when tree growth obscured our view, we gained landowner permission and located nest sites by foot. We used vehicles to systematically drive all accessible roads in each county; roads that were not accessible by vehicle were traveled by foot. We used aerial surveys to cover remaining areas inaccessible by vehicle or foot. We considered nest sites active if there was evidence of nesting behavior (e.g., copulation, incubation; [1]). All active nest site locations were recorded using handheld Garmin GPSMAP 62 Global Positioning System (GPS; Garmin Ltd.) units and were then entered into ArcGIS 10.1 [26]. We monitored nest sites from roads (distance ≤ 600 m) using binoculars and spotting scopes at least once every two weeks throughout each breeding season (1 May–15 Aug). When the nestlings became visible in the nests, we entered nest structures using ladders or climbing equipment. At each nest we recorded the number of nestlings and each chick was then fitted with a numbered aluminum United States Fish and Wildlife Service lock-on band if they were

≥ 14 days of age. The species of the nest tree was identified, and we used clinometers and rangefinders to estimate nest height above the ground and the height of the nest tree.

Young were considered successfully fledged when nestlings reached 80% (~34 days) of average fledging age (~43 days; [27]).

Our nest monitoring protocol for this study followed the guidelines established by [28], all animal handling methods followed the guidelines approved by The Ornithological Council [29] and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Approval No. 13-002A). Data collection was authorized by South Dakota Game, Fish, and Parks, North Dakota Game and Fish, and United States Fish and Wildlife Service. Access to private lands was granted by individual landowners for data collection. All data collected on public land was conducted with permission from South Dakota Game, Fish, and Parks, North Dakota Game and Fish, and United States Fish and Wildlife Service. No endangered or threatened species were involved in this study.

Statistical Analysis

Habitat Measurements

We used the Cropland Data Layer (CDL; [24]) to evaluate land cover at nest sites. We reclassified the CDL layers from 2013 and 2014 for each state to represent the land cover variables we assessed as biologically significant from published literature [3]; row crop, grain crop, alfalfa/hay, grassland, water, trees, and housing development. We generated random points using the Random Point Generator tool in ArcGIS 10.1 to simulate random nest sites for logistic regression analysis. If a generated random point

was not located at a visible tree, it was repositioned to the nearest available tree to simulate a nest site. We clipped reclassified CDL layers to 1200-m buffers around each random and nest site using Geospatial Modeling Environment [30] and calculated land cover percentages for extrinsic variables using ArcGIS 10.1. We selected the 1200-m (4.5 km²) buffer because it was twice the size of the average estimated home range size for breeding Swainson's hawks in the region (2.07 km²; [31]). For nest survival, we also assessed distance to landscape features (meters); distance to farms, distance to wetlands, and distance to roads using ArcGIS 10.1. We used the Focal Statistics tool in the Spatial Analyst package to calculate the number of inter- and intraspecific raptor nests within the 1200-m buffers. We used analysis of variance (ANOVA) to determine differences in mean land cover values between states and years. All statistical tests were conducted using program R [32] with an experiment-wide error rate of 0.05.

Nest Survival Analysis

We selected a suite of 12 predictor variables from field observations consisting of land cover, distance to landscape features, and number of nearest raptor nests as potential factors effecting nest survival (Table 1). We used Pearson's correlation for evidence of multicollinearity and excluded covariates from the same model if $r \geq |0.7|$. We considered nests successful if they fledged ≥ 1 young and used nest survival models in Program MARK [33] with the logit-link function to evaluate the effect of predictor variables on nest survival throughout the nesting season. We created 17 models from field observations that we believed were biologically significant and used Akaike's Information Criterion (AIC_c) corrected for small sample size to select models that best described the data [34]. We considered models as competing models if they differed by

$\leq 4 \Delta AIC_c$ [35] from the top model and used Akaike weights (w_i) as an indication of support for each model. We evaluated whether competing models contained covariates where β -estimates did not have 95% confidence intervals that encompassed zero [36–37]. There is currently no goodness-of-fit test for nest survival; therefore, we investigated model robustness by artificially inflating \hat{c} (i.e., a model term representing over dispersion) from 1.0 to 3.0 (i.e., no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in Quasi-AICc (QAICc; [37–38]).

Nest Site Selection

We used logistic regression and Akaike's Information Criterion (AIC) to determine the effects of intrinsic and extrinsic variables on nest site selection. We generated 190 random nest sites to use as pseudo-absent points. We created 11 *a priori* models from published literature (Table 5; [1, 3]) to estimate the influence of our selected predictor variables (Table 1). We considered models as competing models if they differed by $\leq 4 \Delta AIC$ [35] from the top model and used Akaike weights (w_i) as an indication of support for each model. Predictive capacities of significant models were tested using receiver operating characteristics (ROC) values. We followed guidelines stated by [39] and considered acceptable discrimination for ROC values between 0.7 and 0.8 and excellent discrimination between 0.8 and 1. We used an Odds-ratio test to evaluate the effect of variables in the optimal model on nest site selection.

Results

We located and monitored Swainson's hawk nests in south-central North Dakota (ND) and north-central South Dakota (SD) : 73 (40 in ND and 33 in SD) in 2013 and 120 (83 in ND and 40 in SD) in 2014. Breeding adults were observed arriving on the study area on 28 April 2013 and 26 April 2014. In 2013, apparent nest success was 24% in South Dakota and 58% in North Dakota, resulting in 29 successful breeding attempts (21 in ND and 8 in SD) that produced 30 fledglings in North Dakota and 14 fledglings in South Dakota. In 2014, apparent nest success was 40% in South Dakota and 64% in North Dakota, resulting in 69 successful breeding attempts (53 in ND and 16 in SD) that produced 94 fledglings in North Dakota and 25 fledglings in South Dakota. In South Dakota, Swainson's hawks fledged 1.75 and 1.56 fledglings per successful nest in 2013 and 2014, respectively. In North Dakota, Swainson's hawks fledged 1.43 and 1.77 fledglings per successful nest in 2013 and 2014, respectively.

Mean percentages of grain crop ($F_{2,192} = 5.60, P = 0.02$) and housing development ($F_{2,192} = 7.33, P = 0.007$), distance to farm ($F_{2,192} = 12.50, P < 0.001$), and number of nearest raptor nests ($F_{2,192} = 8.46, P = 0.004$) were greater around nest sites in North Dakota than South Dakota (Table 2). Mean percent hay land ($F_{2,192} = 25.71, P < 0.001$) was greater around nest sites in South Dakota than North Dakota (Table 2); remaining habitat variables did not differ between states ($F_{2,192} \leq 3.24, P \geq 0.07$).

Percent row crop and grass covariates were negatively correlated ($r = -0.84$); thus, no models were created including both variables. Nest survival analysis indicated that model S_{State} was the top-ranked model ($w_i = 0.74$), providing strong evidence for inter-state variation (Table 3). The 95% confidence intervals of the β estimate for state (0.76, 95% CI = 0.35–1.17) did not encompass zero; the probability of nest survival

throughout the duration of the study was 0.35 (95% CI = 0.28–0.43) in North Dakota and 0.19 (95% CI = 0.12–0.30) in South Dakota. The second-ranked model $S_{\text{Dist2Farm}+\% \text{Hay}}$ was 2.8 ΔAIC_c from the top model and indicated that nest success increased when nests were closer to farmsteads and in areas with lower percent hay land. The 95% confidence intervals of the β estimates for Dist2Farm (–0.34, 95% CI = –0.0006 to –0.0001) and %Hay (–0.03, 95% CI = –0.06 to –0.007) did not encompass zero; nest survival estimates using this model were 0.34 (95% CI = 0.27–0.42). When adjusting \hat{c} from 1.0 to 3.0 to test for over dispersion, interpretation of our top model S_{State} did not change and it remained the top-ranked model when $\hat{c} = 2.0$ (moderate dispersion; QAIC_c wt = 0.49) and through $\hat{c} = 3.0$ (extreme dispersion; QAIC_c wt = 0.33).

At 193 nest sites, American elm was the most common tree species (47%) used followed by green ash (22%); eastern cottonwood, 17%; box elder, 6%. eastern red-cedar (*Juniperus virginiana*), peachleaf willow (*Salix amygdaloides*), Russian olive (*Elaeagnus angustifolia*), and chokecherry (*Prunus virginiana*) accounted for the remaining 9% of nest trees. Average tree height used for nesting was 10.9 m (SE = 0.56) and nest height averaged 9.0 m (SE = 0.54). The highest recorded nest was 23.4 m (eastern cottonwood) and the lowest recorded nest height was 1.7 m (peachleaf willow).

Percent row crop, trees, and housing development, was the top-ranked model ($w_i = 0.85$) for predicting nest site selection of Swainson's hawks; predictive capability of the model was excellent (ROC = 0.91; Table 4). Logistic odds-ratio estimates from the top-ranked model indicated the odds of nest site selection were 0.98 (95% CI = 0.97–0.99) times less for every percent row crop increase and 1.43 (95% CI = 1.18–1.75) times greater for every percent increase in housing development. All 95% confidence intervals

for parameter estimates for percent housing development ($\beta = 0.35$, $SE = 0.10$) and percent row crop ($\beta = -0.01$, $SE = 0.005$) did not overlap zero, indicating significant influence on Swainson's hawk nest site selection. Although the percentage of trees was included in the top-ranked model, the logistic odds ratio (0.70, 95% CI = 0.47–1.02) did not differ from one indicating no effect.

Discussion

Our results suggest that reproductive success of this breeding population of Swainson's hawks is relatively low. The survival estimate during our study was lower than previously documented (81%; [2], 48%; [4], 44-58%; [9]), though available habitat varied greatly between our study and similar reproductive success studies. Our study contained more land dedicated to row crop production than studies conducted in Arizona [9], New Mexico [2], or Colorado [4]. While direct comparisons among studies are difficult, our results indicate that there may be a relationship between agricultural intensity and its effect on other extrinsic variables (e.g., prey availability, disturbance) that may ultimately be responsible for low nest survival rates in this region. Nest survival results indicate that this population is currently declining in the northern Great Plains which is contrary to current research that indicates increasing or stable Swainson's hawk populations (e.g., [4]). However, caution should be taken when interpreting these results because this was only a two year study and variation in raptor nest success has been documented temporally in other studies (e.g., [40]).

Apparent nest success was similar to studies in California (65%; [8]), Colorado (54%; [41]), and North Dakota (54-69%; [1]). However, other studies have documented

apparent nest success rates 20-30% higher than what we documented [2, 5, 42–44].

Apparent nest success may provide a positively biased estimate of actual nest success and may only be appropriate when used to assess long-term trends in highly detectable nesting species [45]. Therefore, we believe that it is appropriate to only compare studies using similar approaches to estimate nest success (e.g., Mayfield method, logistic-exposure models) and caution should be taken when interpreting apparent nest success results from short-term studies.

We observed fluctuations in nest survival throughout our study, which has been frequently documented in *Buteo* reproductive rates (e.g., [40]). We documented poor reproductive success in South Dakota in 2013 and we suspect that there was an intrinsic factor (i.e., West Nile virus; WNV) responsible for the decreased nest success. Disease is an intrinsic factor of interest because of its lethality in avian species [46–48]. Concurrent research conducted in this study area documented cases of WNV in ferruginous hawk (*Buteo regalis*) fledglings [48]. Additionally, nest cameras from a concurrent study displayed Swainson's hawk chicks exhibiting similar WNV symptoms (e.g., lethargy, head-bobbing, lack of appetite) experienced by the ferruginous hawk chicks before their subsequent death. However, due to rapid decomposition, we were not able retrieve the carcasses to confirm cause-specific mortality.

Our second competing model contained two variables that influenced nest success, distance to farm and percent hay cover. Nests that were located closer to farms had an increased probability of survival. Similarly, Swainson's hawks selected nest sites in developed areas. We observed Swainson's hawks selecting nest sites near farm sites and areas of disturbance similar to Swainson's hawks in central North Dakota [1],

California [5], and Oklahoma [3]. The availability of nest trees increased due to the implementation of tree plantings in the northern Great Plains in order to control soil erosion and provide protection from the wind [1]. We observed that Swainson's hawks nested near farm sites similar to that documented during the early 1980s [1]. Even though farms have decreased 18% in South Dakota and North Dakota from 1980–2009 [49], they seem to provide optimal breeding territories for Swainson's hawks by providing mature trees for nesting, similar to findings in North Dakota [1]. Farm sites may provide a disturbance that predators (i.e. red-tailed hawks) and competitors avoid (e.g., daily farming operations) as well as providing optimal foraging habitats (e.g., frequently mowed grass increasing prey vulnerability); thus, farm sites may be a potential limiting factor for Swainson's hawks in this region. Because Swainson's hawks are less prone to disturbance compared to other *Buteo* species (e.g., ferruginous hawks), they are more likely to adapt and select for this habitat, which may be high quality habitat [1]. However, our results indicate there may not be a benefit from a high percentage of agriculture in our study area compared to that of southeastern Alberta where productivity of Swainson's hawks was higher in agriculturally rich areas [16, 19]. In relation to nest survival we found that row crop percent was not different between failed and successful nests and only accounted for one-quarter of land cover within nest buffers in a landscape containing >60% cultivated land.

Nest site selection was not influenced by percent hay cover, however, nest survival was negatively affected by percent hay cover. Contrary to our findings, Swainson's hawks have been observed selecting for hay fields around nest sites [9, 50]. Our study area contained other habitats that were available for foraging (e.g., grassland,

pasture, farm sites) compared to Swainson's hawks in California that selected for alfalfa and fallow fields [50]. Grasslands and other non-cropland areas around nest sites may provide habitats that make prey more accessible to Swainson's hawks when compared to other habitats [43]. Prey accessibility has been hypothesized to drive Swainson's hawk foraging rather than prey densities in a particular habitat [43]. We found that Swainson's hawks in our study nested in areas of relatively low hay cover. However, we observed Swainson's hawks switching to foraging primarily in hay fields when vegetation height in other habitats made them inaccessible (e.g., row crops, grain crops) for hunting, particularly during the brood rearing period (25 Jun–15 Aug). This also resulted in increased raptor densities in foraging areas, which would make nests more susceptible to avian predation. We frequently observed multiple pairs and species of raptors foraging in the same hay field. However, more research on predator and prey accessibility in this study area is needed to understand the magnitude of this effect on Swainson's hawk nest survival.

Swainson's hawks in our study selected American elm trees as their preferred nest trees. These findings contradict those of [1] who observed that American elm trees only accounted for less than 1% of nest trees used as Swainson's hawk nest sites in south-central North Dakota. Eastern cottonwood trees, which made up 45% of nest trees used in 1977–79 [1], only accounted for 17% of nest trees in our study. Shelterbelts in this region consisted primarily of American elm and green ash; nest tree selection reflected this availability, whereas eastern cottonwoods were located primarily in isolated patches around or near wetlands. Wetlands have declined by 7.4% the last 25-32 years across the Dakota Prairie Pothole Region (eastern North Dakota and South Dakota; [51]) due to

agricultural expansion. This factor may have contributed to a shift in nest tree species since the last study conducted in 1984 [1].

Swainson's hawks chose nest sites based on habitat characteristics at the local-level preferring nest sites with a low amount of row crop [3, 9, 21–22]. However, our results indicate a selection against agricultural areas associated with row crop production. In North Dakota and South Dakota, grassland conversion to row crop agriculture has been occurring at an annual rate of 1% – 5% since 2006 [15], translating to an increase of 8% – 43% in row crop production over the last 8 years. Even with this recent increase in row crop acres on the landscape, Swainson's hawks still occupied areas with high amounts of grassland cover and relatively low amounts of row crop.

Conclusion

Our study provides updated information on nesting ecology of Swainson's hawks in the northern Great Plains; a landscape that has undergone significant land use changes in the last decade. Distance to farm and percent hay cover explained some of the variation in our low estimates of nest survival. However, there may be underlying biological or environmental factors affecting overall nest survival. Swainson's hawks selected for nest sites that contained high percentages of housing development and low percentages of trees and row crops. Given the apparent relationship between percent housing development and distance to nearest farm in our respective analysis, we suggest that farmsteads, whether occupied or not, provide critical breeding sites. Removal of large, mature shelterbelts due to agriculture expansion may also negatively affect Swainson's hawks. This research documents the response of Swainson's hawks during a

time of rapid agriculture expansion. Our results are contrary to previous research and indicated a declining Swainson's hawk population in the northern Great Plains. We suggest that long-term monitoring of this population may provide for a more accurate evaluation of the factors affecting the nesting ecology of Swainson's hawks in this altered landscape.

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Figure 1. Swainson's hawk nest ecology study area in south-central North Dakota and north-central South Dakota, USA.

Swainson's hawk (*Buteo swainsoni*) study area (shaded) in Logan, McIntosh, and Dickey County, North Dakota and McPherson County, South Dakota, USA, 2013–2014.

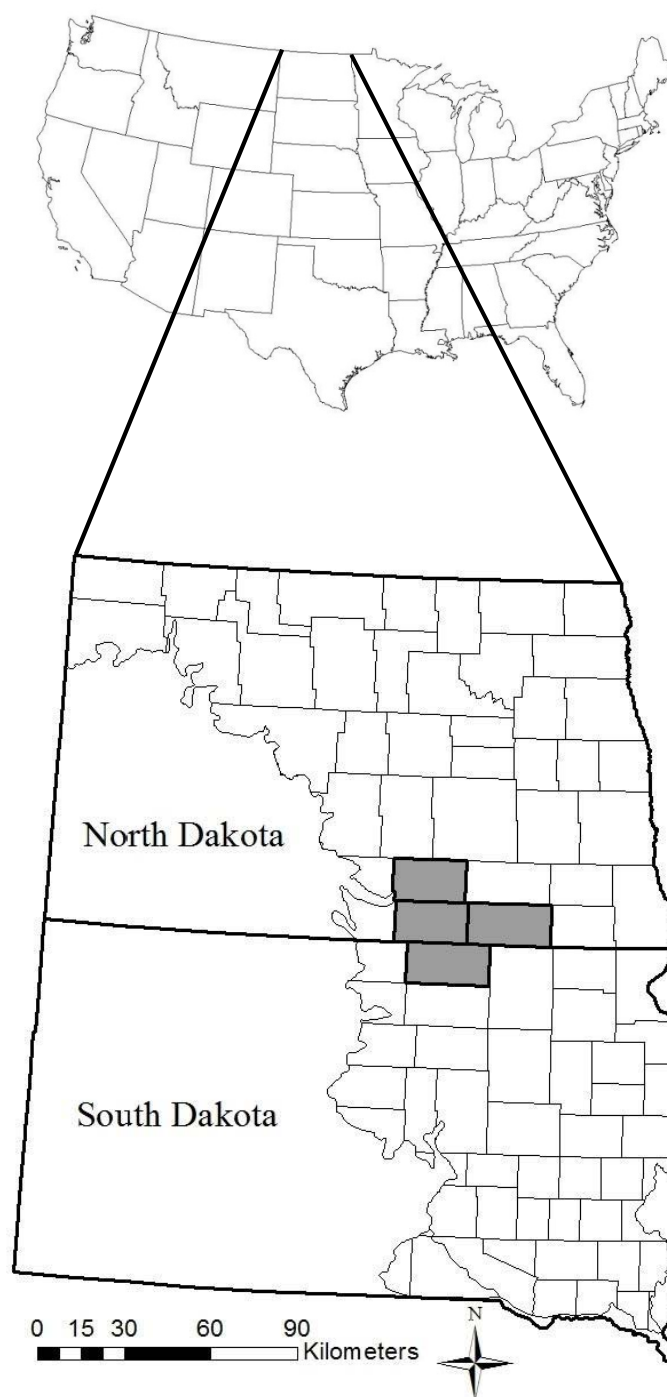


Table 1. Final variables measured within 1200-m buffers of nest sites used to model the influence of intrinsic and extrinsic factors on Swainson’s hawk nest survival and nest site selection in the northern Great Plains, USA, 2013–2014.

Variable Name	Definition
Row Crop	Total corn and soybean cover (%)
Grain Crop	Total grain crop cover (%)
Hay	Total alfalfa/grass hay cover (%)
Grass	Total grassland and pasture (%)
Water	Total wetland cover (%)
Trees	Total tree cover (%)
Housing development	Total farm sites (%)
Distance to farm*	Distance to nearest farm site (m)
Distance to road*	Distance to nearest road (m)
Distance to wetland*	Distance to nearest wetland (m)
Number of nearest raptor nests*	Number of raptor nests within 4.5 km ² of nest site
Year*	Year 1 or 2 of study
State*	North Dakota or South Dakota

* Excluded from nest site selection analysis

Table 2. Mean and standard error (SE) for land cover and distance to landscape features for Swainson's hawk nests in north-central South Dakota and south-central North Dakota, USA, 2013–2014.

Variable Name	South Dakota (N = 73)		North Dakota (n = 120)	
	\bar{x}	SE	\bar{x}	SE
Row Crop (%)	23.72	2.31	26.84	1.82
Grain Crop (%)	5.63*	0.74	8.36*	0.88
Hay (%)	12.60*	0.96	7.22*	0.54
Grass (%)	48.28	2.32	46.55	1.77
Water (%)	5.73	0.92	6.73	0.64
Trees (%)	0.37	0.06	0.43	0.05
Housing development (%)	3.63*	0.13	4.23*	0.16
Distance to Wetland (m)	511.21	43.77	337.47	31.13
Distance to Road (m)	134.64	13.73	131.81	11.15
Distance to Farm (m)	1031.08*	117.27	668.33*	49.21
Number of Nearest Raptor Nests	1.31*	0.17	1.95*	0.17

* Means differed ($P < 0.05$) between states

Table 3. Nest survival models of Swainson's hawks during the 2013–2014 breeding season in South Dakota and North Dakota, USA.

Model	AIC _c ^a	ΔAIC _c ^b	w _i ^c	K ^d	Deviance
<i>S</i> State	566.19	0.00	0.74	2	562.19
<i>S</i> Dist2Farm+%Hay	569.09	2.91	0.17	3	563.08
<i>S</i> %Housing development+Dist2Farm	573.01	6.86	0.02	3	567.00
<i>S</i> Dist2Farm	573.02	6.88	0.02	2	569.03
<i>S</i> #NearestRaptorNests+Dist2Farm	573.72	7.52	0.02	3	567.72
<i>S</i> %Housing development	576.44	10.24	0.00	2	572.44
<i>S</i> Dist2Road	577.02	10.83	0.00	2	573.02
<i>S</i> Null	577.43	11.24	0.00	1	575.43
<i>S</i> Saturated Model	577.75	11.56	0.00	13	552.71
<i>S</i> %Hay+%Grass+%Trees	577.78	11.58	0.00	4	569.77
<i>S</i> #NearestRaptorNests	578.15	11.95	0.00	2	574.15
<i>S</i> %RowCrop+%GrainCrop+%Trees+%Housing	579.29	13.09	0.00	7	565.27
<i>S</i> Year	579.35	13.15	0.00	2	575.35
<i>S</i> Dist2Water	579.41	13.21	0.00	2	575.41
<i>S</i> %Water	579.43	13.23	0.00	2	575.43
<i>S</i> %RowCrop+%GrainCrop+% Housing development	579.76	13.57	0.00	4	571.76
<i>S</i> %RowCrop+%GrainCrop	580.20	14.01	0.00	3	574.20

^a Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).

^b Difference in AIC_c relative to min. AIC.

^c Akaike wt (Burnham and Anderson 2002).

^d Number of parameters.

Table 4. Akaike's Information Criterion (AIC) model selection of logistic regression models for nest site selection of Swainson's hawks in South Dakota and North Dakota, USA, 2013–2014.

Model Covariates	<i>K</i>	AIC	Δ AIC	w_i	ROC ^d
Row Crop + Trees + Housing development	4	424.34	0.00	0.85	0.91
Row Crop + Grain Crop + Hay + Water + Trees + Housing development	7	427.96	4.91	0.12	0.93
Trees + Housing development	3	432.23	8.11	0.03	0.88
Row Crop + Water + Trees	4	437.16	13.12	0.00	0.74
Grass + Hay + Trees	4	439.64	14.84	0.00	0.73
Row Crop + Hay	3	441.54	16.26	0.00	0.82
Trees + Water + Grass	4	442.39	17.61	0.00	0.64
Trees	2	442.50	17.60	0.00	0.77
Water + Trees	3	444.91	19.49	0.00	0.68
Null	1	447.77	22.75	0.00	0.70
Water	2	448.35	23.08	0.00	0.79

^a ROC = receiver operating characteristic curve. Values between 0.7 – 0.8 considered acceptable discrimination and between 0.8 – 1 were considered excellent discrimination (Hosmer and Lemeshow 2000)

**CHAPTER 2: SPATIAL ECOLOGY AND ADULT SURVIVAL OF SWAINSON'S
HAWKS (BUTEO SWAINSONI) IN THE NORTHERN GREAT PLAINS**

*This chapter was prepared for submission to the Journal of Raptor Research and was
coauthored by Shubham Datta, Jonathan A. Jenks, Robert W. Klaver, and Troy W.*

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SPATIAL ECOLOGY AND ADULT SURVIVAL OF SWAINSON'S HAWKS
(BUTEO SWAINSONI) IN THE NORTHERN GREAT PLAINS

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ABSTRACT

In recent years, anthropogenic conversion of grassland habitat has raised concerns about the status of breeding Swainson's hawks (*Buteo swainsoni*) in the Northern Great Plains. During 2013–2014, we captured breeding Swainson's hawks in north-central South Dakota and south-central North Dakota to estimate home range size, determine adult survival rates during the breeding season, and evaluate habitat use. We captured and radio-tagged 15 Swainson's hawks during the study and monitored 13 breeding adults in 2013 and 9 in 2014. Seven individuals captured in 2013 returned to the study area for the 2014 breeding season. Mean 95% and core (50%) minimum convex polygon home range estimates were 208.3 ha (SE = 56.2 ha, $n = 19$) and 68.9 ha (SE = 30.2 ha, $n = 19$), respectively, for the duration of the study. We used known-fate analysis in Program MARK to estimate adult survival during the breeding season. The top-ranked model indicated survival varied over time and was 0.95 (95% CI = 0.72–0.99) during the breeding season. Resource selection analysis indicated that Swainson's hawks did not select habitats in proportion to availability during 2013 ($\chi^2_{42} = 781.99$, $P < 0.001$) and 2014 ($\chi^2_{40} > 999.99$, $P < 0.001$). Breeding Swainson's hawks selected for trees and against wetlands and grassland habitat in 2013 and selected against grassland habitat in 2014. Home range sizes in our study area were smaller than previously documented and analysis of covariance model results indicated that home range size was influenced by the percent of grassland and development within their breeding home ranges. Our results indicate that Swainson's hawks maintain a high degree of breeding site fidelity and that home range size is influenced positively by the presence of grasslands and negatively by percent development.

In the Prairie Pothole Region of the Great Plains, Swainson's hawks nest in high densities (Lokemoen and Duebbert 1976, Gilmer and Stewart 1984, Hagen et al. 2005, South Dakota Game, Fish and Parks 2005). However, the status of breeding Swainson's hawks in the northern Great Plains has not been assessed for over 30 years (Gilmer and Stewart 1984). Swainson's hawks are considered a K-selected species; high survival, low reproductive rates, and delayed reproduction (Pianka 1970). Mass mortalities, such as those documented in their wintering range in Argentina (Goldstein et al. 1996), have been suggested as contributing to population declines across much of this hawk's range (Goldstein et al. 1999). Correlates of survival, both intrinsic and extrinsic, may be important parameters in assessing survival within a population. Intrinsic variables (e.g., individual health, age; McCleery et al. 2008) may affect survival during the breeding season which requires a large investment in reproduction. Extrinsic variables (e.g., habitat, competition; Horak and Lebreton 2008) also may affect survival due to variation in available foraging and nesting habitats.

In the Northern Great Plains Region, grassland conversion to row crop agriculture is occurring at a substantial rate (Wright and Wimberly 2013). This grassland loss has resulted in the Swainson's hawk being listed as a species of concern by state and federal agencies (Hagen et al. 2005, South Dakota Game, Fish and Parks 2005, United States Fish and Wildlife Service 2008, 2011). The Conservation Reserve Program (CRP) was established by the Farm Service Agency as a means to control grassland conversion by establishing a contract to pay a fee to farmers to not farm their land and re-establish grasslands across the United States (United States Department of Agriculture 2015). However, with CRP rent payments unable to compete with rising commodity prices, CRP

reenrollment continues to decline (United States Department of Agriculture 2015). Furthermore, the 2014 Farm Bill has decreased the cap of enrolled CRP acres from 36 million down to 24 million acres. Net loss estimates of CRP grasslands from 2007-2013 were 931,000 ha in North Dakota and South Dakota (United States Department of Agriculture 2015), and a net loss of non-CRP grasslands of 271,000 ha from 2006-2011 in North and South Dakota (Wright and Wimberly 2013). However, the published literature is conflicting on whether crop production is contributing to population declines across much of the Swainson's hawk range (Gilmer and Stewart 1984, Schmutz 1987, Bechard et al. 1990, Nishida et al. 2013).

Currently there is little to no information documenting home range size, survival, and habitat use of Swainson's hawks on the northern Great Plains. Likewise, landscape composition in north-central South Dakota and south-central North Dakota differs from that of previously documented home range studies in California (Andersen 1995, Babcock 1995), New Mexico (Gerstell and Bednarz 1999), and Washington (Bechard 1982). Unlike those studies, the northern Great Plains is dominated by a grassland ecosystem fragmented with areas of intensive agriculture (Lokemoen and Duebbert 1976, Gilmer and Stewart 1984). Resource selection of a particular habitat and variations in home range size can vary greatly due to a variety of factors such as habitat fragmentation (e.g., cropland, farming techniques), prey availability, nest location, and vegetation height (Bechard 1982, Schmutz 1987, Preston 1990, Babcock 1995). In California, Swainson's hawks maintain large home ranges due to the lack of available foraging habitats near nest sites (Babcock 1995). Descriptions of raptor habitat use indicate that foraging is not related to prey density but is affected by a suite of environmental factors

such as habitat characteristics and prey availability (Bechard 1982, Preston 1990). It is suggested that predators forage in habitats requiring the least amount of energy spent per hunting effort regardless of prey densities (Royama 1970). To address the lack of spatial ecology and survival information for Swainson's hawks in this region, we initiated a study in 2013 to monitor breeding adults via radio telemetry. The objectives of our study were to document home range sizes and survival of breeding Swainson's hawks, and provide up-to-date information on how this species uses available habitats at the home range scale in the prairie grasslands of the northern Great Plains.

STUDY AREA

The 11,137 km² study area consisted of four counties located in south-central North Dakota and north-central South Dakota (Figure 1). McPherson County, South Dakota and Dickey, McIntosh, and Logan counties, North Dakota, lie within the Northern and Northwestern Glaciated Plains level III ecoregion (Bryce et al. 1998). This moraine landscape contains numerous pothole wetlands scattered among the rolling terrain, which is characteristic of the Missouri Coteau Region (Lokemoen and Duebbert 1976, Bryce et al. 1998). Land use in the four counties included cultivated land (62.5%), grassland (17.4%), and development (13.7%), with the remaining land constituting forested cover (3.6%) and wetlands (2.8%; United States Department of Agriculture 2014b). Average high and low temperatures for the months of April through July ranged from 11.6° C to 29.3° C and -0.5° C to 14.4° C, respectively. Average annual precipitation was 45–53 cm, with the majority of precipitation events occurring during May to September (North Dakota State Climate Office 2010). Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern

reedgrass (*Calamagrostis stricta*), prairie cordgrass (*Spartina pectinata*) big bluestem (*Andropogon gerardi*), porcupine grass (*Stipa spartea*), and little bluestem (*Schizachyrium scoparium*; Bryce et al. 1998). Tree species were primarily cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*; Lokemoen and Duebbert 1976).

METHODS

We began searching for active nests on 1 May of each breeding season, targeting all tree sites (e.g., shelterbelts, farmsteads, riparian areas) in the study area. We attempted to locate all nest structures before tree foliage obscured our ability to locate nests. If we located a nesting pair when tree growth obscured our view from the road, we gained landowner permission and located nest sites by foot. We used vehicles to systematically drive all accessible roads in each county; roads that were not accessible by vehicle were traveled by foot. We used aerial surveys to cover remaining areas inaccessible by vehicle or foot. We considered nest sites occupied if there was evidence of nesting behavior (e.g., copulation, incubation; Gilmer and Stewart 1983). All active nest sites were recorded in handheld Global Positioning System (GPS) units, which were later logged into ArcGIS 10.1 (Esri, Inc., Redlands, CA). We targeted nesting pairs and actively trapped from 1 May to 10 June during the 2013 and 2014 breeding seasons. We used a modified bal-chatri trap (Berger and Mueller 1959) constructed using 1.27-cm mesh hardware cloth resulting in a hemi-cylindrical shape (30.5 cm long × 25.4 cm wide × 15.24 cm high) with 15.8-kg monofilament nooses approximately 4-4.5 cm in diameter. We baited traps with two live house mice (*Mus musculus*); trapping attempts were made

from vehicles in view of raptors on the side of roads, monitoring from close proximity for immediate radio tagging and release of captured raptors.

We fitted captured birds with Very High Frequency (VHF) radio transmitters (Model 1135; Advanced Telemetry Systems, Isanti, MN) with unique frequencies. We used a backpack style harness that attached the transmitter to the synsacrum of the bird (Rappole and Tipton 1991, Mallory and Gilbert 2008). We weighed each hawk and only radio-tagged individuals when the transmitter weight was less than 3% of total body mass (Philips et al. 2003). We sexed captured raptors using a combination of morphological measurements that included weight, footpad length, and wind chord length (Kochert and McKinley 2008). We classified birds as female or male if measurements in two of three categories were within the measurement ranges established for each gender by Kochert and McKinley (2008). All animal handling procedures followed guidelines of The Ornithological Council (Fair et al. 2010) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Approval No. 13-002A).

We located radio-tagged individuals using R-1000 handheld receivers (Communications Specialists Inc., Orange, CA), an R2000 receiver (Advanced Telemetry Systems), truck-mounted omni-directional antennas, and hand-held 4-element Yagi antennas. Each bird was located 2–3 times per week on a rotational daytime schedule using 8-hr intervals to avoid obtaining locations during the same interval on successive attempts (i.e., 0630–1430 and 1430–2230). We also intensively monitored birds twice throughout the breeding season, once during incubation and once after hatching (Bechard 1982, Andersen and Rongstad 1989, Babcock 1995). The intensive monitoring sessions consisted of recording a location every hour for 8 hrs. Sessions were conducted from

0600–1400 hr or 1400–2100 hr; ensuring that every bird had one morning and one evening session. The first round of intensive monitoring was conducted from 10 June – 25 June and the final round was conducted from 10 July – 25 July. To avoid autocorrelation of locations, ≥ 1 hr passed between successive relocations (Andersen and Rongstad 1989, Babcock 1995). This ensured that we collected enough locations throughout the season (>30 ; Seaman et al. 1999) and confirmed that locations collected 2–3 times per week provided an accurate representation of foraging patterns. Bird locations were only recorded if the bird was visually located (Babcock 1995) and birds were observed to be foraging (Bechard 1982). All locations were recorded on National Agriculture Imagery Program (NAIP; United States Department of Agriculture 2014a) maps created in ArcGIS 10.1 (ESRI, Inc., Redlands, CA). We recorded locations of individuals based on the approximate location of the bird over a specific landscape feature with the assistance of optics and rangefinders. The availability of roads around nest sites allowed us to be ≤ 800 m when recording locations and the availability of landscape features (e.g., tree belts, rock piles) increased our accuracy. Recorded locations were then referenced with ArcGIS 10.1 to determine the coordinates of each location. For each relocation we recorded additional field observations; date, time, habitat, behavior (e.g., hunting, perched), and any additional observed behaviors.

We estimated home range size for each bird by generating 95% minimum convex polygon (MCP) isopleths to delineate breeding home range as well as 50% MCP to define core use areas using the `adehabitatHR` package (Calenge 2011) in program R (R Core Team 2014). We used the Cropland Data Layer (CDL; United States Department of Agriculture 2014b) to evaluate land use within home ranges. We reclassified the CDL

layers from 2013 and 2014 for each county to represent the land cover variables we assessed as biologically significant from published literature (Bechard 1982); row crop, grain crop, alfalfa/hay, grassland, water, trees, and housing development. We clipped reclassified CDL layers to MCP home ranges for each animal using Geospatial Modeling Environment (Beyer 2012) and calculated land cover percentages for each land cover type using ArcGIS 10.1 (Esri, Inc., Redlands, CA).

We used the kernel overlap function in the `adehabitatHR` (Calenge 2006) package in program R to calculate utilization distribution overlap indices (UDOI; Fieberg and Kochanny 2005) for home ranges of birds that returned to the same nest sites in the second year of the study to evaluate breeding site fidelity. This method calculates the product of an animal's utilization distribution (UD) for each animal each year and then compares the distribution of the independent UD's to determine space-use overlap (Fieberg and Kochanny 2005). Home range overlap for UDOI analysis is equal to zero for no overlap and 100% (1.0) for complete overlap for uniformly distributed home ranges (Fieberg and Kochanny 2005). Home ranges for UDOI may be >1 if the two home ranges are non-uniformly distributed on the landscape associated with a high degree of overlap (Fieberg and Kochanny 2005).

We used analysis of covariance (ANCOVA) to relate variability in individual home ranges to habitat types (Table 1) within home ranges, and examined possible effects of habitat on home range size. We generated 13 models from field observations that we believed to be biologically significant in interpreting variation in home range size. We used Akaike's Information Criterion (AIC_c) corrected for small sample sizes to select models that best described the data (Burnham and Anderson 2002). We considered

models as competing models if they were $\leq 2 \Delta AIC_c$ from the top model and used Akaike weights (w_i) as an indication of support for each model.

We assessed habitat selection by comparing use and availability of habitat types at the individual home range level (design III; Manly et al. 2002). We used program R with the adehabitat library (Calenge 2006) to calculate selection ratios and chi-square tests for overall deviation from random use of habitat types. Use was defined as the location of the animal during the time of relocation and availability as the amount of a specific habitat available to an animal within its home range (Manly et al. 2002). A positive, negative, or neutral selection of a habitat was determined if the selection ratio (w) differed significantly from 1.0 (no overlap in 90% confidence intervals; Manly et al. 2002). Only relocations in which we observed active foraging or hunting attempts were included in resource selection analysis.

We used known-fate analysis in Program MARK (White and Burnham 1999) with the logit-link function to evaluate adult survival rates during the breeding season. Due to sample size, we limited our survival analysis to three potential models to evaluate adult survival of breeding Swainson's hawks; constant survival and models that included time and year effects. We used Akaike's Information Criterion (AIC_c) corrected for small sample size to select models that best described the data (Burnham and Anderson 2002). We considered models as competing models if they were $\leq 2 \Delta AIC_c$ from the top model and used Akaike weights (w_i) as an indication of support for each model.

RESULTS

During the 2013 and 2014 breeding seasons, we captured and radio-tagged 15 adult Swainson's hawks (8 male and 7 female). Captures occurred from 5 May to 10 June each year. Average weight, wing chord length, and footpad lengths for radio-tagged male Swainson's hawks were 853.9 g (SE = 33.1), 386.0 mm (SE = 3.8), and 71.5 mm (SE = 0.8), respectively. Radio-tagged females had an average weight, wing chord length, and footpad length of 1062.7 g (SE = 30.3), 413.4 mm (SE = 3.7), and 78.1 mm (SE = 0.8), respectively. Radio-tagged female Swainson's hawks were significantly larger than males in all measurement categories; weight ($t_{13} = 4.65$, $P \leq 0.001$), wing chord length ($t_{13} = 5.17$, $P \leq 0.001$), and footpad length ($t_{13} = 5.95$, $P \leq 0.001$).

We collected locations on 10 and 9 breeding adults in 2013 and 2014, respectively. An additional three birds were censored from home range analysis in 2013 due to mortality ($n = 1$), radio malfunction ($n = 1$), and non-breeding activity ($n = 1$). We collected a total of 742 visually observed foraging locations that were used in home range analysis; 433 in 2013 and 309 in 2014. Average number of locations per bird used to estimate home range size was 43 (SE = 6.2). Average 95% MCP home range size in 2013 was 205.4 ha (SE = 42.8, $n = 10$) and 211.1 ha (SE = 69.6, $n = 9$) in 2014, and did not differ between years ($t_{13} = 0.07$, $P = 0.95$) and averaged 208.3 ha (SE = 56.2, $n = 19$) for the duration of the study. Mean core home range (50% MCP) was 78.2 ha (SE = 33.5, $n = 10$) in 2013 and 59.7 ha (SE = 26.9, $n = 9$) in 2014. Core home ranges were not different between years ($t_{17} = -0.46$, $P = 0.65$) and averaged 68.9 ha (SE = 30.2, $n = 19$) over the course of the study. Overall, males ($\bar{x} = 245.3$ ha, SE = 37.8) exhibited a larger average 95% MCP home range than females ($\bar{x} = 175.9$ ha, SE = 64.1), however, they were not significantly different ($t_{15} = -0.94$, $P = 0.18$) from one another. Core areas were

marginally different ($t_{15} = 1.41$, $P = 0.08$) for males ($\bar{x} = 99.7$ ha, $SE = 32.0$) and females ($\bar{x} = 42.1$ ha, $SE = 24.4$).

Of the 13 breeding Swainson's hawks we initially captured in 2013, seven returned to the same nest sites the following year. UDOI estimates for four of the seven birds who returned in 2014 indicated an extremely high degree of overlap ($UDOI \geq 0.95$; Table 2) while the three remaining birds displayed a low degree of overlap ($UDOI \leq 0.29$; Table 2). Average UDOI values for all seven birds indicated a moderately high degree of home range overlap between years ($UDOI = 0.69$, $SE = 0.17$).

Swainson's hawk home ranges in 2013 were comprised primarily of grassland (44.0%), row crop (26.0%), and hay (13.9%; Table 2). Similarly in 2014, grassland (41.6%), row crop (28.9%), and hay (17.4%) accounted for the majority of land cover within home ranges (Table 3). Habitat within home ranges was similar between years ($t_{17} \leq 0.23$, $P \geq 0.26$) except for wetlands ($t_{10} = 2.55$, $P = 0.03$), which decreased within home ranges by 5.8% from 2013 to 2014.

Analysis of covariance models estimating the influence of land cover type on home range size indicated that the model [Grass + Development] was the most influential model on home range size of breeding Swainson's hawks ($w_i = 0.55$, $F_{2,16} = 8.60$, $P = 0.003$, $R^2 = 0.46$; Table 4). Weight of evidence supporting this model was 4.36 times greater than the second ranked model and 6.90 times \geq remaining models. Parameter estimates (Table 5) indicated that home range size was positively associated with percent grass and negatively associated with percent development. Swainson's hawk home ranges increased 3.4 ha for every 1% increase in percent grass and decreased 19.0 ha for

every 1% increase in percent development (Fig. 2). We did not consider any other competing models as all other models were $>2 \Delta AIC_c$ from the top model (Table 4).

Breeding Swainson's hawks did not randomly select habitats based upon their availability in 2013 ($\chi^2_{42} = 781.99, P < 0.001$) and 2014 ($\chi^2_{40} > 999.99, P < 0.001$). In 2013, Swainson's hawks selected trees ($w = 115, 90\% \text{ CI} = 21.3 - 209$) greater than expected and selected wetlands ($w = 0.06, 90\% \text{ CI} = 0.00 - 0.17$) and grassland ($w = 0.36, 90\% \text{ CI} = 0.18 - 0.53$; Table 6) habitats less than expected within their home range. In 2014, Swainson's hawks selected grassland ($w = 0.47, 90\% \text{ CI} = 0.35 - 0.60$; Table 6) less than what was available.

The top model in our survival analysis was S_{Time} ($w_i = 0.81$) providing a survival estimate of 0.95 (95% CI = 0.72 – 0.99) for the duration of both breeding seasons. All other models were $>2 \Delta AIC_c$ from the top model. This model indicated that adult survival varied with time and was represented by the one mortality event that we experienced during the entire study. We were unable to determine cause-specific mortality associated with our one mortality. We also censored two individuals from survival analysis due to transmitter malfunction and transmitter loss, respectively.

DISCUSSION

Previous studies examining home range size of Swainson's hawks have documented substantially larger breeding home ranges (Bechard 1982, Andersen 1995, Babcock 1995, Gerstell and Bednarz 1999) than documented during our study. In California, Swainson's hawk home ranges were 2,130 ha (Andersen 1995) and 4,038 ha (Babcock 1995) whereas they were 866 ha in Washington (Bechard 1982). Swainson's

hawk home ranges comparable to our study were documented in New Mexico (400 ha, Gerstell and Bednarz 1999); however, our home ranges were still only half the size reported by Gerstell and Bednarz (1999). To our knowledge, our findings are currently the smallest documented home ranges for breeding Swainson's hawks. Available habitats in previous studies provide evidence for the large variation in home range size (e.g., Babcock 1995). In California, Babcock (1995) and Andersen (1995) documented that tree fruit crops (nuts and citrus) dominated the landscape; therefore, Swainson's hawks were required to fly long distances to find available foraging habitat (e.g., nearest alfalfa field). Habitats within home ranges of Swainson's hawks in our study area were comprised of large proportions of grassland habitat that accounted for nearly half of the habitat types within their home ranges. Agricultural production also comprised a significant proportion of habitat within home ranges Swainson's hawks in our study. These results were similar to studies in Arizona (Nishida et al. 2013), Alberta, Canada (Schmutz 1987), and North Dakota (Gilmer and Stewart 1984) that observed Swainson's hawks commonly nesting in agriculturally rich landscapes.

Model results assessing the effects of habitat on home range size of Swainson's hawks indicated that percent of grass and development within home ranges had the greatest influence on home range size. Previous studies suggested home range size of Swainson's hawks was related to the availability of foraging habitat (Bechard 1982, Schmutz 1987, Preston 1990, Babcock 1995), which is likely a function of multiple factors such as prey density, vegetation height (e.g., prey accessibility), competition, and location of nest sites (Bechard et al. 1990, Restani 1991). Unlike Swainson's hawks in California (Babcock 1995), raptors in the Northern Great Plains maintained small home

ranges. However, because of low reproductive success of Swainson's hawks in this area (Inselman 2015), extremely small home ranges may be a function of raptor nesting density or Swainson's hawks may be occupying marginal habitats. Because Swainson's hawks arrive much later to this breeding area than other nesting raptors (i.e., red-tailed hawks, ferruginous hawks, great horned owls) in this area, all suitable habitats may already be occupied requiring Swainson's hawks to occupy poor quality habitat.

Decreasing home range size in relation to percent development was likely due to the selection of farmsteads as nesting sites (Gilmer and Stewart 1984). Even though farms have decreased 18% from 1980–2009 (United States Department of Agriculture 2010) in South and North Dakota, nest sites associated with farmsteads on these farms may provide optimal breeding territories for Swainson's hawks by providing mature nesting trees, which is similar to findings in North Dakota (Gilmer and Stewart 1984). Because Swainson's hawks are less prone to disturbance compared to con-specifics (e.g., Ferruginous hawks; *Buteo regalis*), they are more likely to adapt and select for this potentially high-quality habitat (Lokemoen and Duebbert 1976, Gilmer and Stewart 1984), which may provide them with the necessary biological needs in a small, localized area. The presence of roads on the landscape may also provide ideal foraging habitat. Road ditches are frequently mowed and hayed throughout the summer which may make prey more vulnerable to predation by raptors. Accessibility of prey may then attract foraging Swainson's hawks. Transmission line poles associated with roadways provides ideal perch sites that benefit these birds in a landscape where tree availability is limited. Our results suggest development (e.g., farm sites) provides a resource in nest trees that are limited in the prairie grassland ecosystem.

Grasslands, row crops, and hay fields comprised >80% of the available habitat within home ranges each year. Agricultural crops such as corn and soybeans may provide valuable foraging habitats during the early stages of nesting. Although Swainson's hawks used row crops proportionately, we observed that when vegetation reached heights that obscured the ground, birds would then switch to more suitable habitats with shorter vegetative height (e.g., harvested hay fields). Also, the large cattle ranching industry in this area provided grazed pastures that allowed accessibility to prey when hay and row crop vegetation was too tall for birds to effectively hunt. Swainson's hawks did, however, use grassland habitat less than its availability within home ranges in both years of the study. Swainson's hawks likely shifted foraging strategies to other habitat types when grassland vegetation was too tall for effective foraging. We observed that Swainson's hawks shifted foraging habitats almost exclusively to hay fields when hay harvesting began. Swainson's hawks also utilized wetland habitats proportionally less than what was available in 2013. Diets of Swainson's hawks have been tied to wetland dependent species (Murphy 2010); however, few foraging locations were recorded in or near wetland habitats. We also noticed a significant decrease in overall wetland habitat within home ranges in the second year of the study likely due to the loss of wetlands to agricultural practices (e.g., drain tile). In 2013, we saw significant use of trees within Swainson's hawk home ranges. This result was contrary to previous studies that suggested that Swainson's hawks used perching habitats substantially less than other *Buteo* spp. (e.g., Red-tailed hawks [*Buteo jamaicensis*]; Janes 1985, 1987). Janes (1985) also noted that Swainson's hawks occupied habitats that contained few perches and foraged primarily from the air. The selection of trees within Swainson's hawk home

ranges in our study could likely be biased high due to the lack of available trees in our study area. However, we frequently observed Swainson's hawks hunting from power poles and trees, which may indicate a shift in foraging strategies in the region.

We documented a high degree of home range overlap for four of seven breeding Swainson's hawks that used the same nest sites in subsequent years. Interestingly, three of the birds that returned to the same nest sites that exhibited a low degree of home range overlap had suffered nest failures the previous year, which may have led to their shift in breeding territory distribution and use. However, three of the four birds that exhibited a high degree of home range overlap had failed nest attempts in the first year of the study. This result is contrary to many studies that have reported that some bird species will leave a breeding territory if nesting attempts fail (e.g., Schroeder and Robb 2003). Breeding Swainson's hawks that occupy the same nesting territory regardless of nest survival may benefit from increased fitness by not having to search for new suitable habitat and potentially reduced competition for limited resources (e.g., nest sites).

Results of our survival analysis indicated high survival rates for breeding adults, which were comparable to studies conducted in California (0.85 – 0.90; Briggs et al. 2011) and western Canada (0.84; Schmutz et al 2006). Apparent survival of Swainson's hawks in California (Briggs et al. 2011) was negatively associated with reproductive parameters (e.g., number of offspring produced) and extrinsic factors which increased survival rates (e.g., agriculture). Similarly, Schmutz et al. (2006) indicated that high adult survival was attributed to the propensity of large raptors to endure stress associated with biotic and abiotic factors. The survival estimates of our study may underrepresent true survival rates of this population due to the limited sample size of Swainson's hawks

tagged during this study. Our results however, do represent the survival patterns frequently observed in other raptors (e.g., bald eagles [*Haliaeetus leucocephalus*]; Bowman et al. 1995); a K-selected species (Pianka 1970).

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Table 1. Final variables measured within 100% minimum convex polygon (MCP) home ranges of breeding Swainson's hawks in the northern Great Plains, USA, 2013–2014.

Variable Name	Definition
Row Crop	Total corn and soybean cover (%)
Grain Crop	Total grain crop cover (%)
Hay	Total alfalfa/grass hay cover (%)
Grass	Total grassland and pasture (%)
Water	Total wetland cover (%)
Trees	Total tree cover (%)
Development	Total farm sites and roads (%)

Table 2. Utilization distribution overlap index (UDOI) for seven breeding Swainson's hawks that occupied the same nest sites in 2013 and 2014.

Bird ID	2013	2014	UDOI ^b
	HR ^a	HR ^a	
149.053	404.21	244.80	1.12
149.254	171.69	642.78	0.23
149.272	284.53	19.28	0.29
149.312	157.07	192.21	0.95
149.333	3.47	39.74	0.15
149.365	344.20	175.77	1.17
149.374	145.79	24.17	0.95

^a 95% MCP home ranges (ha)

^b Indicates degree of overlap for home ranges; 0 (no overlap) and 1.00 (complete overlap; Fieberg and Kochanny 2005)

Table 3. Land cover variables (%; including mean and SD) measured within 100% MCP home ranges for breeding Swainson's hawks in south-central North Dakota and north-central South Dakota, 2013–2014.

Variable	2013 (<i>n</i> = 10)		2014 (<i>n</i> = 9)	
	\bar{x}	SE	\bar{x}	SE
Row Crop	26.02	5.14	28.91	6.58
Grain Crop	3.80	1.33	3.41	1.40
Hay	13.90	4.45	17.48	7.29
Grass	44.00	6.67	41.64	7.18
Water	7.04*	2.09	1.24*	0.51
Trees	0.27	0.08	0.64	0.35
Development	5.00	0.62	6.67	1.16

*Significant between years ($P < 0.05$)

Table 4. Top-ranked analysis of covariance models used to estimate home range size of breeding Swainson's hawks in north-central South Dakota and south-central North Dakota, 2013–2014.

Models	K^a	AIC_c^b	ΔAIC_c^c	w_i^d
Grass + Development	3	241.97	0.00	0.55
Grass + Water + Trees	4	244.92	2.95	0.13
Hay + Grass + Trees	4	245.83	3.86	0.08
Trees + Development	3	245.91	3.94	0.08
Row Crop + Development	3	246.02	4.05	0.07
Row Crop + Grain Crop + Hay + Grass + Water + Trees + Development	8	248.16	6.19	0.02
Water + Trees	3	248.60	6.63	0.02
Row Crop + Hay	3	249.50	7.53	0.01
Trees	2	249.65	7.68	0.01
Row Crop + Grain Crop + Hay	4	250.25	8.28	0.01
Row Crop + Water + Trees	4	250.76	8.79	0.01
Water	2	251.47	9.50	0.00
Constant	1	251.48	9.51	0.00

^a Number of parameters.

^b Akaike's information criterion corrected for small sample size (Burnham and Anderson 2002).

^c Difference in AIC_c relative to the minimum AIC_c .

^d Akaike weight (Burnham and Anderson 2002).

Table 5. Parameter estimates (β), 95% confidence intervals, and significance tests from the top-ranked analysis of covariance model to determine the influence of habitat variables on home range size of breeding Swainson's hawks in south-central North Dakota and north-central South Dakota , 2013–2014.

Model ^a	β	95% CI	<i>t</i> -value	<i>P</i> -value
[Grass + Development]				
Intercept	171.43	32.09–310.77	1.23	0.24
Grass	3.43	1.68–5.18	1.95	0.07
Development	-19.04	-31.92 to -6.16	-1.48	0.16

^a Grass = percent grass within breeding Swainson's hawks home range (100% MCP).
Development = percent of farm sites and roads within breeding Swainson's hawks home range (100% MCP).

Table 6. Estimated selection ratios and confidence intervals for adult Swainson's hawks ($n = 19$) during the 2013 – 2014 breeding season in north-central South Dakota and south-central North Dakota, using design III (Manly et al. 2002).

Habitat	2013			2014		
	Ratio (w)	90% CI		Ratio (w)	90% CI	
		Lower	Upper		Lower	Upper
Row Crop	0.72	0.30	1.13	0.67	0.15	1.19
Grain Crop	1.41	0.07	2.75	1.97	0.00 ^a	4.32
Hay	1.40	0.71	2.11	0.71	0.09	1.33
Grass	0.36 ⁻	0.18	0.53	0.47 ⁻	0.35	0.60
Wetland	0.06 ⁻	0.00 ^a	0.17	1.29	0.00 ^a	3.78
Trees	115.23 ⁺	21.29	209.17	50.42	0.00 ^a	110.19
Development ^a	1.88	0.00 ^a	3.77	1.07	0.00 ^a	2.23

^a Negative lower limit changed to 0.000.

⁺ Indicates that the selection coefficient (w) was significantly different from 1 and the habitat was used more than expected from the availability of this habitat.

⁻ Indicates that the selection coefficient (w) was significantly different from 1 and the habitat was used less than expected from the availability of this habitat.

Table 7. Survival models for radio-tagged adult Swainson's hawks in south-central North Dakota and north-central South Dakota, 2013–2014.

Model	AIC_c^a	ΔAIC_c^b	w_i^c	K^d	Deviance
S_{Time}	9.96	0.00	0.81	1	7.94
S_{Year}	13.67	3.71	0.13	1	11.65
$S_{Constant}$	14.94	4.98	0.07	1	12.92

^a Akaike's information criterion corrected for small sample size (Burnham and Anderson 2002).

^b Difference in AIC_c relative to the minimum AIC_c .

^c Akaike weight (Burnham and Anderson 2002).

^d Number of parameters.

Figure 1. Swainson's hawk spatial ecology study area in south-central North Dakota and north-central South Dakota, USA, 2013–2014.

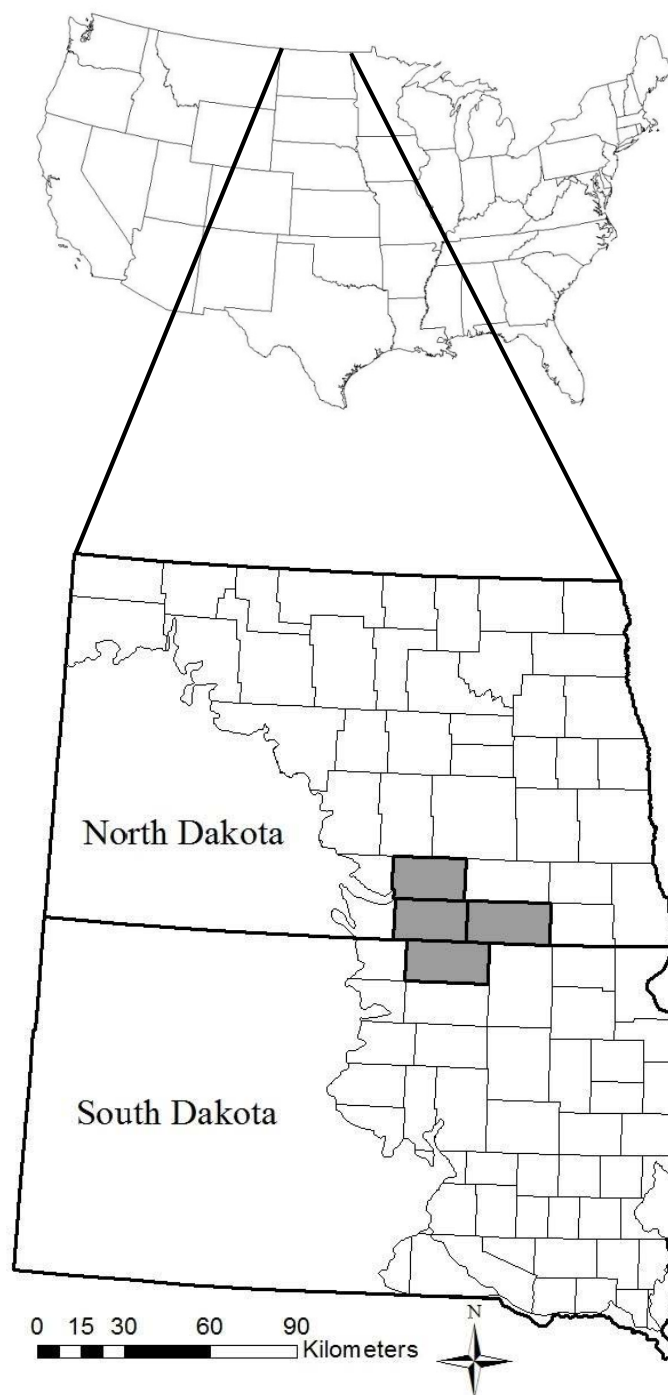
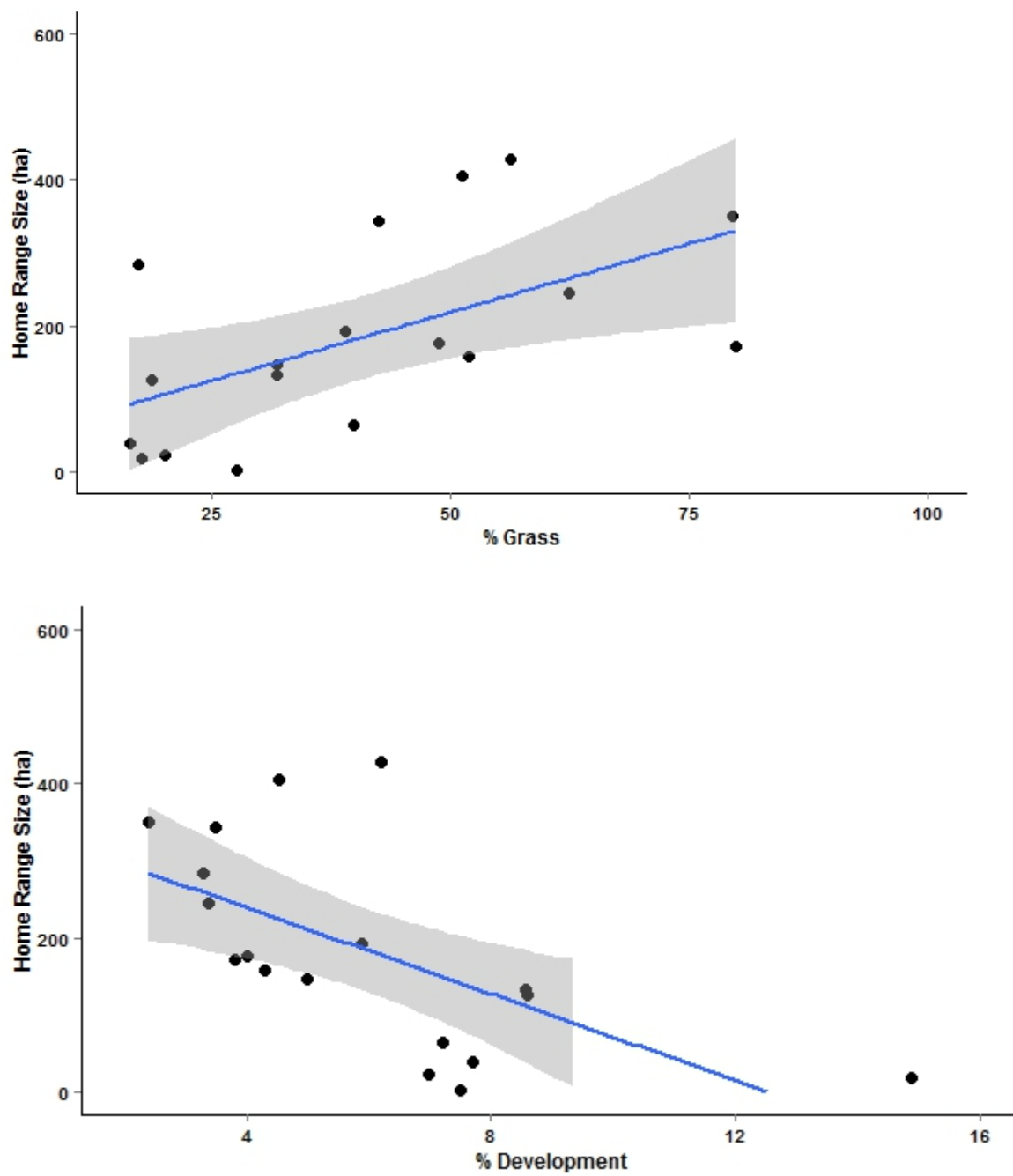


Figure 2. The influence of percent development and percent grass on home range sizes of breeding Swainson's hawks in south-central North Dakota and north-central South Dakota, 2013–2014.



**CHAPTER 3: DIET COMPOSITION AND PROVISIONING OF SWAINSON'S
HAWK NESTLINGS IN THE NORTHERN GREAT PLAINS**

*This chapter was prepared for submission to the Journal of Field Ornithology and was
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Grovenburg

Diet Composition and Provisioning of Swainson's Hawk Nestlings in the Northern Great
Plains

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ABSTRACT

The Swainson's hawk is an opportunistic, generalist predator that nests in areas of high grassland density. During the 2013–2014 breeding seasons, we monitored 18 Swainson's hawk nests using time-lapse video cameras to document diet composition and provisioning rates. We recorded 5091.4 total hr ($\bar{x} = 282.8 \pm 47.8$ hrs/nest) of daylight video footage and documented 2,221 prey deliveries, identifying 2017 (93.9%) of 2221 delivered prey items to species, genus, family, or class. Overall biomass consumed during the study was 189.2 ± 3.0 kg. The five most delivered prey items accounted for 74.7% of all deliveries and consisted of small mammals and reptiles. Small mammals accounted for 61.7% of total biomass, however reptiles (e.g., common garter snake [*Thamnophis sirtalis*]) accounted for a considerable proportion of biomass (19.2%). We documented a significant effect of brood size on the frequency of prey delivered to nests. Prey deliveries/nestling decreased as brood size increased ($F_{2,17} = 3.75$, $P = 0.04$); however, biomass did not differ ($F_{2,17} = 0.18$, $P = 0.84$) in relation to brood size. Provisioning rates during our study differed in biomass over 5-day interval periods during the nesting season (grams/nestling/day; $F_{6,70} = 2.12$, $P = 0.06$). We observed an increase in biomass delivered/nestling/day to nest sites at early age stages of nestling growth and delivery peaked at 25–30 days of age. This observed trend seemed to correlate with critical growth stages in Swainson's hawk nestling development. Overall, Swainson's hawks exhibited a generalist approach to foraging by providing a wide variety of prey species. Our results suggest that Swainson's hawks in our study were killing smaller prey more frequently than other Swainson's hawk populations studied in the Northern

Great Plains; primary prey and prey species selected varies spatial and temporally among Swainson's hawk populations.

Understanding diet composition is a critical component in animal ecology (Errington 1935) and more specifically is used to understand the impacts of predators on prey species (e.g., McAtee 1935). Historic research in relation to raptor diets has focused on the impacts on prey species of concern (e.g., livestock, game species; Fisher 1983); however, current research on raptor diets has shifted to the use of diet/prey selection to improve understanding of raptor community ecology (Green and Jaksic 1983, Marti et al. 2007). Diet analysis provides the necessary information to elucidate the dynamics of prey communities and its effect on raptor population structure (e.g., availability, distribution; Woffinden and Murphy 1989).

Literature specifically addressing the diets of nesting Swainson's hawks (*Buteo swainsoni*) within the last 25 years is limited in the Northern Great Plains Region (e.g., Schmutz et al. 2001, Murphy 2010). Swainson's hawks have commonly been categorized as an opportunistic generalist predator with a wide dietary breadth (Bednarz 1988); prey consists of birds, reptile, and amphibians, with the majority of diets comprised of small mammals (e.g., mice, voles). Diets of Swainson's hawks in northwest North Dakota consisted primarily of wetland-dependent species (Murphy 2010) whereas Swainson's hawks in Canada relied extensively on ground squirrels (38% – 60%; Schmutz et al. 2001). Moreover, alterations in diet composition are largely attributed to temporal fluctuations in prey populations (Schmutz 1987, Schmutz et al. 2001, Murphy 2010).

Techniques used to analyze diets of raptors have remained stagnant over the last 80 years (e.g., McAtee 1935). Traditional techniques such as indirect and direct assessment of diets at raptor nests have been preferred for assessing raptor diets;

however, both are inherently biased (e.g., Lewis et al. 2004). Indirect assessment (i.e., pellet analysis and prey remains) is a minimally invasive technique that provides both quantitative and qualitative information on raptor diets (Steenhof and Kochert 1988, Marti et al. 2007). The disadvantage of analyzing pellets and prey remains is that more conspicuous prey is overestimated whereas less conspicuous prey species may be grossly underestimated (Simmons et al. 1991). The adequacy of pellet analysis in evaluating raptor diets greatly depends on the feeding behavior of the species (Lewis et al. 2004). Feeding habits differ among raptors; Falconiformes generally tear prey into pieces as they consume them, which can lead to associated bias (Lewis et al. 2004). Bias also may exist with pellet analysis when trying to determine age structures of consumed prey due to lack of identifiable characteristics (i.e., adult versus juvenile; Bednarz 1988).

A secondary technique used to evaluate raptor diets is direct observation of prey deliveries at nest sites (e.g., Murphy 2010). This technique generally involves the presence of a researcher observing nests from a blind (Rogers et al. 2005). Direct observation allows researchers to visually observe delivered prey, which alleviates associated biases with conspicuous prey items as it relates to frequency and biomass (Collopy 1983, Lewis et al. 2004). However, observer presence may negatively influence nesting by disturbing raptors (Rogers et al. 2005). Additionally, direct observations are labor-intensive and present logistical constraints that limit sample size and thus, reduce the feasibility of this technique (Marti et al. 2007).

Advanced videography technology has created an alternative method to direct observations that offers additional advantages to analyzing raptor diets at nest sites. Use of time-lapse videography to observe raptor nest sites has become increasingly popular in

the last 15 years (e.g., Cutler and Swann 1999, Redpath et al. 2001, Giovanni et al. 2007). Nest mounted video cameras provide multiple benefits over other direct techniques such as decreased labor costs, minimizing disturbance to nest site, and creating a permanent record of nesting activity (Kristan et al. 1996, Lewis et al. 2004). Limitations in the use of video surveillance technology still currently exist primarily due to high equipment costs and the transporting and installing of bulky equipment (Kristan et al., 1996, Lewis et al., 2004). Despite these limitations, technological advances in video surveillance have allowed this method to be a more readily available tool for wildlife monitoring (Booms and Fuller 2003).

Provisioning rates can negatively affect growth rates and physiological condition of nestling raptors (Olendorff 1974). Larger broods require more frequently delivered prey as well as increased prey biomass to compensate for the demand of caloric requirements of nestlings during the nesting season (Wright et al. 1998). Studies evaluating provisioning rates of Peregrine Falcons (*Falco peregrinus*; Palmer et al. 2004), Northern Goshawks (*Accipiter gentilis*; Smithers et al. 2005), and Bald Eagles (*Haliaeetus leucocephalus*; Warnke et al. 2002) have postulated that adults compensate for dietary demands of larger broods during the nesting season (e.g., forage more frequently, larger prey). Similarly, Swainson's hawks and Ferruginous hawks (*Buteo regalis*) in the Southern Great Plains increased prey deliveries and biomass, but did not adjust provisioning rates with increasing brood sizes (Giovanni et al. 2007).

Understanding diets of Swainson's hawks is fundamental to the conservation and management of this species (Giovanni et al. 2007). Therefore, we initiated a study using time-lapse video monitoring as a primary method to quantify diets at Swainson's hawk

nests on the Northern Great Plains during the 2013–2014 breeding seasons. Our objectives were to quantify food habits associated with Swainson's hawk nests and evaluate daily provisioning rates in relation to frequency and biomass delivered to nest sites. We hypothesized that Swainson's hawks in our region would take a variety of prey species and not specialize on prey due to the wide array of available prey species in the Northern Great Plains (e.g., Murphy 2010). We also hypothesized that Swainson's hawk adults would compensate for brood size and growth of nestlings by increasing frequency and biomass of prey delivered to nest sites as caloric demands of nestlings increased.

METHODS

The 11,137 km² study area consisted of four counties located in south-central North Dakota and north-central South Dakota (Fig. 1). McPherson County, South Dakota and Dickey, McIntosh, and Logan counties, North Dakota, lie within the Northern and Northwestern Glaciated Plains level III ecoregion (Bryce et al. 1998). This moraine landscape contains numerous pothole wetlands scattered throughout the rolling terrain, which is typical of the Missouri Coteau Region (Lokemoen and Duebbert 1976, Bryce et al. 1998). Land use in the four counties consisted of cultivated land (62.5%), grassland (17.4%), and development (13.7%), with the remaining land constituting forested cover (3.6%) and wetlands (2.8%; United States Department of Agriculture 2012). Average high and low temperatures for the months of April through July ranged from 11.6° C to 29.3° C and –0.5° C to 14.4° C, respectively. Average annual precipitation was 45–53 cm and the majority of precipitation events occurred May to September (North Dakota State Climate Office 2010). Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern reedgrass

(*Calamagrostis stricta*), prairie cordgrass (*Spartina pectinata*) big bluestem (*Andropogon gerardi*), western wheatgrass (*Pascopyrum smithii*), porcupine grass (*Stipa spartea*), and little bluestem (*Schizachyrium scoparium*; Bryce et al. 1998). Tree species were primarily cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*; Lokemoen and Duebbert 1976).

We began searching for active nests on 1 May of each breeding season targeting all tree sites (e.g., shelterbelts, farmsteads, riparian areas) in the study area. We attempted to locate all nest structures before tree foliage obscured our ability to locate nests. If we located a nesting pair when tree growth obscured our view of the nest, we gained landowner permission and located nest sites by foot. We used vehicles to systematically drive all accessible roads in each county; roads that were not accessible by vehicle were traveled by foot. We used aerial surveys to survey remaining areas inaccessible by vehicle or foot. We considered nest sites active if there was evidence of nesting behavior (e.g., copulation, incubation; Gilmer and Stewart 1983). All active nest sites were recorded in handheld Global Positioning System (GPS) units and were then entered into ArcGIS 10.1 (ESRI, Inc., Redlands, CA). We documented prey deliveries at randomly selected Swainson's hawk nests each year; however, logistical constraints (e.g., permission, nest accessibility) required selection of nests that were more accessible for camera installation. Once permission was secured, we monitored nest sites from roads (distance ≤ 600 m) using binoculars and spotting scopes at least biweekly throughout each breeding season (1 May – 5 July). To avoid nest abandonment, we waited until nestlings were visible in nests (≥ 10 days old) to enter nest sites and used ladders or climbing equipment when installing nest cameras. We used Plotwatcher Pro HD (Day 6 Outdoors,

LLC) game cameras equipped with 32 gigabyte (gb) secure digital (SD) cards and eight AA batteries. We installed cameras using trail camera screw-in mounting brackets (HME Products) ≤ 1 m from nests at approximately 45° angles, which provided the best viewing angle to monitor diets throughout the breeding season. Cameras were programmed to initiate surveillance at sunrise and end at sunset each day (~05:30 to 22:00) and to record 1 frame/5 sec. This frame setting allowed recording of about 12–14 days of video footage on 32 GB SD cards, which minimized nest disturbance by reducing visits to nest sites to a maximum of four times during the nesting season.

We used GameFinder (Day 6 Outdoors, LLC) software to review all recorded nest footage; this software allowed us to watch video footage frame by frame for identification of prey deliveries. It also provided a zoom option that was beneficial when items were delivered opposite the camera. Data recorded from video footage included prey type delivered and the number of chicks present. We attempted to identify all prey items to the lowest taxonomic level using reference photos from multiple sources (Hoberg and Gause 1992, Fisher et al. 1999, Higgins et al. 2000, Poole 2005, Seabloom 2011). We classified prey that were not identifiable, due to immediate ingestion or obstructed camera view, as unknown prey. Closely related species that were difficult to differentiate were classed at the genus level (e.g., Vole sp., Mouse spp.). When we were not able to group prey into one of the aforementioned categories we labeled prey items to class (e.g., unknown Avian).

Biomass was estimated for prey species using mean weights of males and females for each species. All weight estimates were referenced from multiple sources; small mammals (Higgins et al. 2000, Seabloom 2011), avian (Dunning 1993), reptile (Hoberg

and Gause 1992, Kiesow 2006), and amphibian (Hoberg and Gause 1992, Fisher et al. 1999). Identification between adults and juveniles among species was difficult to determine so unless obvious juvenile characteristics were seen (e.g., feather sheaths in avian species, notable size difference in small mammals), we classed prey as adult (Giovanni et al. 2007). Prey items that returned to the nest partially consumed, once identified, were estimated to the amount of species that was available for consumption (e.g., one-third, two-thirds, half available). Prey items that could not be classified to species, genus, or family were assigned to a category of unknown taxonomic order (e.g., unknown passerine, unknown shorebird; Lewis et al. 2004). Biomass estimates for unknown passerines were assigned based on the most frequently identified passerine genus (*Tyrannus* spp.; Lewis et al. 2004). Mammals that were smaller than ground squirrel species (e.g., thirteen-lined ground squirrel [*Spermophilus tridecemlineatus*]) were classified as unknown small mammal and biomass estimates were assigned based on the most frequently delivered small mammal (e.g., *Microtus* spp.; Lewis et al. 2004). Unknown prey deliveries not identified due to immediate complete ingestion or blocked camera view were assigned biomass estimates of the least conspicuous, most frequently delivered prey species (e.g., *Microtus* spp.; Giovanni et al. 2007). For species that were classified to genus (e.g., *Peromyscus* spp., *Microtus* spp.), we assigned a mass value that was the average weight of all species in consideration. We were unable to determine whether the adults were actively feeding in unison with nestlings due to the time-lapse interval settings on our cameras so we assumed all prey was consumed by nestlings. Any prey species that was observed mostly consumed by adults (e.g., ≥ 0.75 of item

consumed) was excluded from the analysis. It was common in our analysis that, due to our time-lapse interval, half of prey items were consumed between successive photos.

We evaluated dietary provisioning rates and frequency as deliveries/day as well as deliveries/nestling/day at Swainson's hawk nests (Giovanni et al., 2007). Biomass was estimated for g/day, g/nestling/day, and g/delivery and provisioning rates were analyzed by nest and brood size. We also evaluated provisioning rates on a temporal scale throughout the nestling growth period (Giovanni et al. 2007). Nestlings were aged (Gossett and Makela 2005) during camera installation and were assigned to an established 5-day interval period (Giovanni et al. 2007). The time interval spanned from youngest observed nestling (~10 days old) and continued until fledging (~43 days old; Bechard et al. 2010). This established seven, 5-day age intervals that all nests were assigned based upon the age of the youngest nestling.

All statistical analysis was completed using program R (R Core Team 2014) with an alpha level of 0.05. We used a repeated-measures analysis of variance (ANOVA; Weinfurt 2000) to test for differences among provisioning rates at nest sites over 5-day nestling growth intervals. We used a one-way ANOVA to determine if brood size had an effect on frequency and biomass provisioning.

RESULTS

Over the course of the 2013–2014 breeding seasons, we analyzed diets of nesting Swainson's hawks at 18 nests and assumed nests were independent between years. Monitored nests contained $\bar{x} = 2.0 \pm 0.2$ nestlings/nest. We recorded 5091.4 total hr ($\bar{x} = 282.8 \pm 47.8$ hrs/nest) of daylight video footage and recorded 2221 prey deliveries ($\bar{x} =$

123.4 ± 21.3 deliveries/nest/season). Total biomass consumed at all nest sites ($N = 18$) was 189.2 ± 3.0 kg. Overall, mean grams/day was 555.9 ± 68.3 g and mean grams/nestling/day was 277.93 ± 44.1 g for all Swainson's hawk nests. Swainson's hawks delivered on average 6.4 ± 0.6 prey items/nest/day and 3.1 ± 0.3 prey items/nestling/day throughout the study. We identified 23 prey categories classified into species ($N = 16$), genus ($N = 5$), family ($N = 1$), and class ($N = 1$). We were able to accurately identify 2017 (93.9%) of 2221 delivered prey items to species, genus, family, or class (Table 1). We were unable to classify the remaining 6.1% of prey items delivered to nests and classified them as unknown due to various constraints (e.g., view of prey blocked, immediate ingestion).

The five most frequently delivered prey accounted for 74.7% of all prey delivered to nests. Most frequently delivered prey included *Microtus* spp. (26.2%), northern leopard frog (*Rana pipiens*; 15.3%), thirteen-lined ground squirrel; 12.3%), common garter snake (*Thamnophis sirtalis*; 10.8%), and *Peromyscus* spp. (9.0%; Table 1). Small mammals accounted for more than half of all prey delivered to nests (58.0%). In terms of biomass, small mammals accounted for 61.7% of total biomass at Swainson's hawk nests. Top prey items in terms of biomass included thirteen-lined ground squirrel (29.4%), common garter snake (19.2%), northern pocket gopher (*Thomomys talpoides*; 16.0%), *Microtus* spp. (8.9%), and Richardson's ground squirrel (*Spermophilus richardsonii*, 7.4%; Table 1). Deliveries/nestling/day differed ($F_{2,17} = 3.75$, $P = 0.04$; Table 2) among brood size and prey deliveries/nestling/day and decreased with increasing brood size.

Deliveries/nestling/day estimates remained relatively constant ($F_{6,70} = 1.81$, $P = 0.11$; Table 3) over the 5-day nestling interval growth period. Swainson's hawks did not differ in terms of deliveries/hr ($F_{6,70} = 1.12$, $P = 0.27$) or deliveries/nestling/hr ($F_{6,70} = 0.43$, $P = 0.68$; Table 3). Conversely, estimates of biomass (grams/nestling/day) increased throughout the nestling growth period and peaked at ~30 days old then decreased as nestlings matured to fledging age (Fig. 2). Test results indicated a significant difference ($F_{6,70} = 2.12$, $P = 0.06$) in grams/nestling/day over the 5-day interval growth period. However, grams/hr ($F_{6,70} = 0.89$, $P = 0.46$) and grams/nestling/hr ($F_{6,70} = 1.45$, $P = 0.21$; Table 3) did not differ among 5-day period intervals. Biomass estimates for broods of one, two, and three nestlings were not affected by brood size ($F_{2,17} = 0.18$, $P = 0.84$; Table 2).

DISCUSSION

Swainson's hawks have often been regarded as generalist foragers (e.g., Schmutz et al. 2001) and diet composition varies spatially across much of its range (Gilmer and Stewart 1984, Schmutz et al. 2001, Giovanni et al. 2007, Murphy 2010). We documented a wide diversity in prey species in Swainson's hawk diets similar to studies in south-central North Dakota (Gilmer and Stewart 1984), Saskatchewan and Alberta, Canada (Schmutz et al. 2001), north-western North Dakota (Murphy 2010), and the Southern Great Plains (Giovanni et al., 2007). Research conducted in north-western North Dakota indicated that nearly half of all prey items delivered were wetland-dependent species. Interestingly, Gilmer and Stewart (1984) did not document reptiles or amphibians as prey in south-central North Dakota with prey consisting primarily of small mammals (>85%); however, this study only analyzed diet from pellet and prey remains found at nest sites.

Swainson's hawk diets in our study were comprised primarily of small mammals, which accounted for the majority of frequency and biomass of prey species. Unlike other studies (e.g. Schmutz et al. 2001, Giovanni et al. 2007), we did not document Swainson's hawks taking prey ≥ 400 g (e.g., *Lepus* spp., *Sylvilagus* spp.). Because we did not sample available prey items around nest sites, our study period may have been associated with low densities of these larger prey species.

We documented a relatively high number of reptiles and amphibians in our study, in contrast to the results of Gilmer and Stewart (1984). These results were similar to studies in north-western North Dakota (Murphy 2010) and the southern Great Plains (Giovanni et al. 2007) that documented a relatively high frequency of reptiles and amphibians, contrary to studies in Saskatchewan and Alberta Canada (Houston and Schmutz 1995). However, unlike north-western North Dakota, we did not observe a significant contribution of wetland dependant species in Swainson's hawk diets. Wetland dependent species (e.g., Killdeer; *Charadrius vociferus*, *Anas* spp., northern leopard frogs) only contributed to 8% of overall biomass, while small mammals were the most important prey item we observed in terms of biomass and frequency. Decline in wetland-dependent prey items in our study may be representative of the hypothesis proposed by Murphy (2010) that suggested relationships between wetland-dependent prey species and Swainson's hawk diets may be a management concern for this species due to continuing loss of wetlands in the Northern Great Plains. We did not assess the relationship between wetland percentage around camera-monitored nest sites and diets of Swainson's hawks; long-term monitoring of diets in relation to landscape conversion may provide insight into this potential concern.

In the Southern Great Plains, Swainson's hawk diets contained a high frequency of herpetofauna and grasshoppers; however, small mammals accounted for the bulk of biomass (Giovanni et al., 2007). Interestingly, Giovanni et al. (2007) documented that grasshoppers accounted for the highest frequency of occurrence of any species. We did not document any grasshoppers as prey items during our study. The lack of grasshoppers observed during our study may be due to the limited availability of grasshoppers in this localized area; representative of the periodic boom and bust cycles of this insect (Edwards 1960). Observed ingestion of grasshoppers could have been missed because of inconspicuous nature of this prey item or due to the time interval on our time-lapse cameras, which may not have recorded immediate ingestion of this species.

Provisioning rates vary greatly among raptor species nesting throughout North America (Elliot et al. 1998, Palmer et al. 2004, Smithers et al. 2005, Giovanni et al. 2007). Brood size may be the biggest factor negatively affecting provisioning rates as larger broods require adults to provide more prey to meet the caloric needs of nestlings (Olendorff 1974). Research conducted on Peregrine Falcons in Alaska (Palmer et al. 2004) and Northern Goshawks in Minnesota (Smithers et al. 2005) suggest that adults may compensate for increasing brood sizes by increasing frequency of prey deliveries and providing larger prey. However, Swainson's hawks in the Southern Great Plains did not maintain consistent provisioning rates over growth periods for larger broods by providing larger prey (Giovanni et al. 2007). Swainson's hawks during our study exhibited provisioning rates similar to those documented in the Southern Great Plains (Giovanni et al. 2007). Our results indicated that deliveries/nestling/day decreased as brood size increased. This suggests that Swainson's hawks did not compensate for

increasing broods size as documented by Palmer et al. (2004) and Smithers et al. (2005) by increasing frequency of prey items. Swainson's hawk broods in our study consumed less grams/nestling/day relative to those in the Southern Great Plains (Giovanni et al. 2007).

Biomass estimates indicated there was not a significant variation in grams/nestling/day as brood size increased however, adult Swainson's hawks appeared to compensate for the lack of increased prey deliveries/nestling/day in larger broods by providing larger prey (Olendorff 1974, Giovanni et al. 2007). Our results also suggest that broods with a single nestling did not have a nutritional advantage over nests containing three nestlings as grams/nestling/day was similar per nestling in broods of two and three Swainson's hawk chicks. Decreased biomass that we observed in broods compared to those previously documented (Giovanni et al. 2007) suggest that Swainson's hawk low reproductive rates in our study (Inselman 2015) could be attributed to the loss of important large prey species (e.g., *Sylvilagus* spp., Richardson's ground squirrel). The loss of potentially important prey species may contribute to low reproductive rates, which were documented in Saskatchewan and Alberta, Canada in the 1980s and 1990's when the primary prey species (i.e., Richardson's ground squirrel) of Swainson's hawks declined (Houston and Schmutz 1995).

Dietary needs of nestling raptors vary greatly as nestlings grow to fledging age (Olendorff 1974). Olendorff (1974) indicated that food consumption of Swainson's hawks increased to an asymptote of maximum food intake at 28–35 days old. Deliveries/nestling/day and grams/nestling/day for Swainson's hawks in our study varied slightly throughout our 5-day intervals during the nestling growth period. Similar to

Olendorff (1974), we experienced a similar increase in deliveries and biomass from days 11–16 that eventually peaked during our 26–30 day growth interval. Increased biomass over this critical stage in nestling development (e.g., growth of all major flight feathers; Gossett and Makela 2005) indicated that adult Swainson's hawks may be increasing the amount of biomass for nestlings specifically during this period of development. The increased amount of biomass delivered to nest sites during this growth interval was correlated with alfalfa harvest and grain harvest, which could have made prey more available to foraging adults.

CONCLUSION

Swainson's hawks foraged primarily on small mammals, reptiles, and amphibians and the primary prey for Swainson's hawks during our study was voles. Their diets also contained a relatively high proportion of wetland-dependent species as has previously been observed in the Northern Great Plains (Murphy 2010). Swainson's hawks in our study consumed fewer grams/nestling/day than previously documented (Giovanni et al. 2007) and did not consume any large prey items (e.g., *Sylvilagus* spp.) or insects (e.g., grasshoppers). Deliveries/nestling/day and grams/nestling/day increased throughout the 5-day intervals during the nestling growth period until nestlings were about 35 days old; rates quickly decreased as nestlings reached fledging age. Our results suggest that prey species available to Swainson's hawks during the time of highest caloric demand (25–35 days old) may be an important factor for the management and conservation of this species. Also, the use of wetland-dependent species as prey may be a concern when assessing potential impacts of wetland loss on offspring diets of raptors in the Northern Great Plains.

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Table 1. Diet composition, frequency (%), and biomass (%) at Swainson's hawk nests ($N = 18$) in south-central North Dakota and north-central South Dakota, 2013–2014.

Prey	Swainson's Hawk Nests ($N = 18$)			
	N	%DF ^a	kg	%BM ^b
Mammals				
<i>Micotus</i> spp.	581	26.2	20.3	10.5
Thirteen-lined ground squirrel	275	12.4	55.0	29.4
<i>Peromyscus</i> spp.	199	9.0	4.9	2.6
Northern pocket gopher	149	6.7	29.8	16.0
Richardson's ground squirrel	46	2.1	13.8	7.3
Grasshopper mouse	17	0.8	0.7	0.4
Shrew spp.	15	0.7	0.2	<0.0
Franklins ground squirrel	6	0.3	2.4	1.2
Least weasel	3	0.1	0.1	<0.0
Kangaroo rat	1	<0.0	0.1	<0.0
Eastern mole	1	<0.0	0.1	<0.0
Domestic Cat	1	<0.0	0.3	<0.0
Subtotal	1294	58.3	127.7	67.4
Amphibian				
Northern leopard frog	339	15.3	12.8	6.8
Tiger Salamander	3	0.1	0.0	<0.0
Subtotal	342	15.4	12.8	6.8
Reptile				
Common garter snake	239	10.8	35.9	19.2
Green snake	8	0.4	0.8	0.4
Prairie Skink	2	0.1	0.2	<0.0
Subtotal	249	11.3	36.9	19.6
Avian				
<i>Tyrannus</i> spp.	74	3.3	0.7	0.4
Ring-necked pheasant	44	2.0	2.9	1.5
Shorebird spp.	34	1.5	1.7	0.9
Unknown avian	33	1.5	1.3	0.7
Juvenile duck	14	0.6	0.5	0.3
Subtotal	199	8.9	7.1	3.8
Unknown				
Subtotal	137	6.1	4.7	2.4
Totals	2221	100	189.2	100

^a Delivery frequency

^b Percent Biomass

Table 2. Provisioning rates at Swainson's hawk nests with broods of 1 ($N = 5$), 2 ($N = 8$), and 3 ($N = 5$) nestlings in south-central North Dakota and north-central South Dakota, 2013–2014.

Brood Size	Deliveries/nestling/day	Grams/nestling/day
1	4.4 ± 0.5	303.9 ± 53.5
2	3.1 ± 0.5	294.6 ± 19.4
3	3.5 ± 0.4	314.9 ± 12.3

Table 3. Provisioning rates over 5-day intervals during nestling growth at Swainson's hawk nests ($N = 18$) in south-central North Dakota and north-central South Dakota, 2013–2014.

	Age (days)						
	11–15	16–20	21–25	26–30	31–35	36–40	41–45
Deliveries/nestling/day	3.2 ± 0.8	3.2 ± 0.48	4.6 ± 0.48	3.9 ± 0.48	3.9 ± 0.40	3.5 ± 0.54	2.3 ± 0.57
Grams/nestling/day	257.8 ± 60.10	239.9 ± 60.21	330.9 ± 78.45	347.3 ± 43.23	343.6 ± 38.09	289.2 ± 26.59	190.6 ± 44.0
Deliveries/hr	0.49 ± 0.09	0.42 ± 0.18	0.56 ± 0.13	0.47 ± 0.11	0.48 ± 0.09	0.42 ± 0.12	0.30 ± 0.03
Deliveries/nestling/hr	0.21 ± 0.08	0.21 ± 0.12	0.30 ± 0.16	0.26 ± 0.10	0.26 ± 0.09	0.23 ± 0.09	0.15 ± 0.12
Grams/hr	39.71 ± 4.77	31.68 ± 2.94	41.25 ± 6.72	41.67 ± 7.12	41.58 ± 9.06	34.99 ± 4.81	25.16 ± 4.96
Grams/nestling/hr	17.02 ± 2.81	15.84 ± 8.88	21.84 ± 9.11	22.92 ± 10.09	22.68 ± 5.92	19.09 ± 2.52	12.58 ± 4.38

Figure 1. Diet composition and provisioning rates at Swainson's hawk nests study area in south-central North Dakota and north-central South Dakota, 2013–2014.

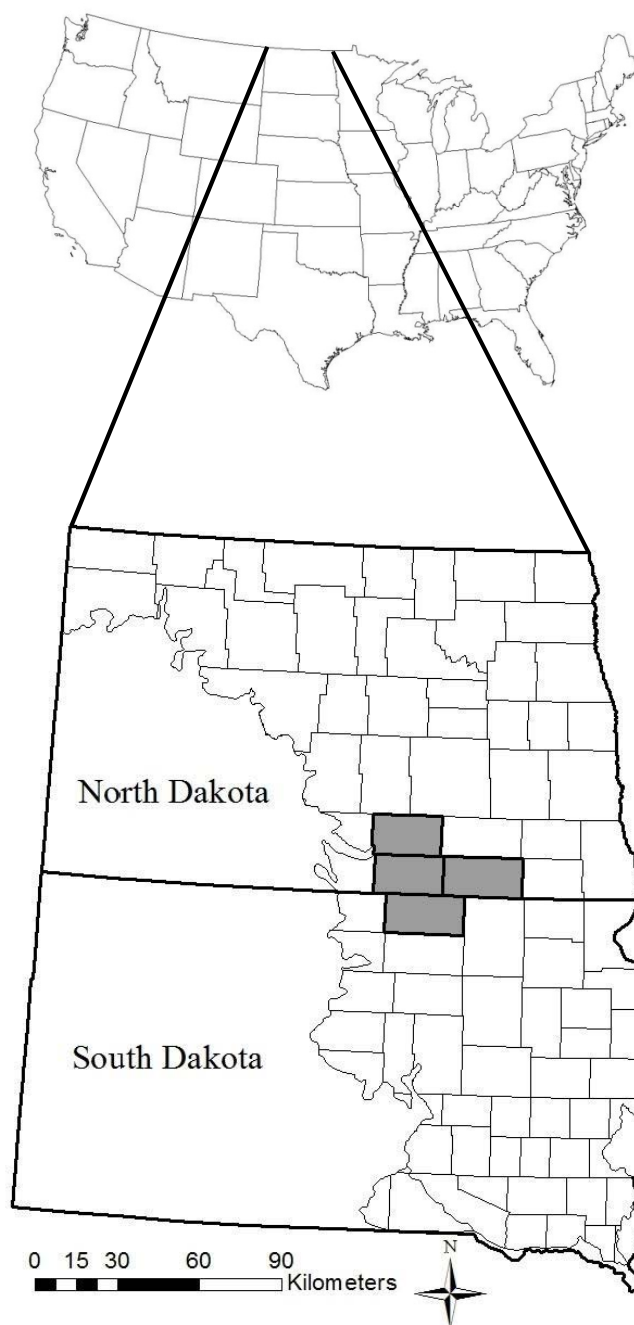


Figure 2. Provisioning rates (grams/nestling/day and deliveries/nestling/day) for 7, 5-day nestling age periods at Swainson's hawk nests ($N = 18$) in south-central North Dakota and north-central South Dakota, 2013–2014.

