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RAPTORS IN TEMPERATE GRASSLANDS: ECOLOGY OF FERRUGINOUS HAWK, GOLDEN EAGLE, AND NORTHERN HARRIER IN THE NORTHERN GREAT PLAINS

BY

SHUBHAM DATTA

A dissertation submitted in partial fulfillment of the requirements for the

Doctorate of Philosophy

Major in Wildlife and Fisheries Sciences

South Dakota State University

2016

RAPTORS IN TEMPERATE GRASSLANDS: ECOLOGY OF FERRUGINOUS HAWK, GOLDEN EAGLE, AND NORTHERN HARRIER IN THE NORTHERN GREAT PLAINS

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctorate of Philosophy in Wildlife and Fisheries Sciences degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidates are necessarily the conclusions of the major department.

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Dissertation Advisor

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RAPTORS IN TEMPERATE GRASSLANDS: ECOLOGY OF FERRUGINOUS HAWK, GOLDEN EAGLE AND NORTHERN HARRIER IN THE NORTHERN GREAT PLAINS

SHUBHAM DATTA

2016

Ferruginous hawks (*Buteo regalis*) are a grassland and shrubland obligate nesting raptor and prefer lightly grazed pasture or idle areas for nesting. Their population reportedly declines in number if more than 30% of an area is cultivated and they rarely nest in areas dominated by croplands. Golden eagles (*Aquila chrysaetos*) are long-lived raptors with high nest-site fidelity and relatively low reproductive success. Population trends of golden eagles in western United States are unclear although long-term monitoring of populations shows declines in occupancy and breeding performance. Northern harriers (*Circus cyaneus*) prefer relatively open grasslands and wetland areas of various natures. During the breeding season from 2013–2015, we investigated the influence of factors associated with the landscape on survival and nest-site selection of ferruginous hawks, golden eagles, and northern harriers in the northern Great Plains (north-central South Dakota, south-central North Dakota hereafter, Eastern Dakota [ED], and northwestern South Dakota hereafter, Western Dakota [WD]). Using ground and aerial surveys, we located and monitored active ferruginous hawk, golden eagle, and northern harrier nests (ferruginous hawk, n = 55; golden eagle. n = 35; northern harrier, n = 22). In ED, one pair of ferruginous hawk was found every 655 km^2. In a more suitable subset of 4420 km^2 in

ED, we found one pair per 340 km^2. In WD, we documented one breeding pair in 315 km^2. In ED, all ferruginous hawk nests were in trees, and apparent nest success was 62% in 2013, 94% in 2014, and 87% in 2015. In WD, apparent nest success was 62% in 2013, 43% in 2014 and 94% in 2015. Overall, 101 ferruginous hawk chicks fledged in ED; 2.4 fledglings/successful nest, and 100 chicks fledged in WD; 2.6 fledglings/successful nest. In WD golden eagle pairs were documented with one nest every 1740.4 km^2 for the duration of the study. Active nests of golden eagles were placed on two different substrates (i.e., steep cliff-side [n = 5] and trees [n = 30]) and apparent nest success was 62% in 2013, 94% in 2014, and 87% in 2015. Overall, 41 golden eagle chicks successfully fledged; 1.4 chicks/successful nest (SE = 0.09). Cottonwood (*Populus deltoides*) was the sole tree of choice for nesting golden eagles in WD (n = 30) followed by steep cliff-side (n = 5). No golden eagle nest was documented in ED. During breeding seasons in 2013 and 2014, one breeding pair of northern harrier was found every 370.6 km^2. Most northern harrier nests were in seasonal or permanent wetlands with cordgrass (*Spartina* spp; n = 12), bulrush (*Scirpus* spp.; n = 6), cattail (*Typha* spp.; n = 3), and residual corn (*Zea mays*; n = 1). Apparent nest success was 25% in 2013, and 70% in 2014. During the 2013 breeding season, 3 of 12 active nests fledged 7 chicks (2.3 chicks/successful nest). During 2014, 7 of 10 active nests fledged 22 chicks (3.1 chicks/successful nest); overall, 29 (2.9 chicks/successful nest) nestlings fledged in our study area. We used Program MARK to evaluate the influence of land cover on nest success. The top-ranked nest survival model for ferruginous hawks in ED was S_{Null} (w_i = 0.87) suggesting that none of the landscape predictor variables had any effect on survival and survival probability was constant between years; it also may suggest low sample size and an inability to detect an effect. Probability of nest survival during the study period in ED was 0.69 (95% CI = 0.61–0.83). In WD, the top-ranked nest survival model for ferruginous hawks was $S_{Substrate}$ suggesting nest substrate had most influence on nest survival in WD; the probability of ground nest survival during the study was 0.77 (95% CI = 0.64–0.83) and the probability of tree nest survival during the study was 0.43 (95% CI = 0.28–0.56). We used logistic regression analysis to evaluate the influence of landscape variables on nest site selection. In ED, percent grass and percent pasture/hay was the top-ranked model for predicting nest site selection of ferruginous hawks and indicated positive association of nest-site selection with grasslands and pasture. In WD, percent grass and development was the top-ranked model indicating positive influence of grasslands and development on nest-site selection. . Top-ranked nest survival model for golden eagle was S_{Null} ($w_i = 0.91$) suggesting that none of the predictor variables had any effect on survival and survival was constant between years. Probability of golden eagle nest survival during the study period was 0.76 (95% CI = 0.58–0.81). We used logistic regression analysis to evaluate the influence of landscape variables on nest-site selection of golden eagles. Development was the top-ranked model ($w_i = 0.72$) for predicting nest site selection of golden eagles and indicated negative association of nest-site selection with development. The model containing grass, pasture, and development ranked second and was competitive indicating positive association of active nests with higher percentages of grass and negative association with increase in development. The top-ranked nest survival model was S_{Year} ($w_i = 0.65$) suggesting survival was different between the 2013 and 2014 breeding seasons. $S_{\%Grass+\%Water+Year}$ model ($w_i = 0.23$; ≤ 4 ΔAIC_c away) also was competitive indicating positive relationship of nests with %grass

and % water in the landscape. Estimated nest survival for northern harriers in 2013 was 0.21 (95% CI = 0.22–0.55), and in 2014 was 0.49 (95% CI = 0.32–0.61). We used logistic regression analysis to evaluate the influence of landscape variables on nest-site selection. Grass, pasture, and water ranked as the top model for northern harrier (w_i = 0.87). Logistic odds-ratio estimates from the top-ranked model for northern harrier indicated the odds of nest-site selection were 1.48 (95% CI = 1.27–1.58) times greater for every percent increase in grasslands, and 1.2 (95% CI = 1.06–1.31) times greater for every percent increase in water; logistic odds ratio for percent pasture indicated no effect at the 900-m scale (1.06, 95% CI = 0.98–1.14).

Our results indicate major decline of nesting ferruginous hawks in agriculture dominated regions of the northern Great Plains where land-use change has modified open grassland and pastures into row crop agriculture in the last four decades. Our study also demonstrate close association of grassland, pastures and wetlands with nest-site selection of ferruginous hawks, golden eagles and northern harriers, and avoidance of ground based disturbance by all three raptor species. Our findings indicate a need to manage pasture, wetlands, and grasslands in areas suitable for nesting of ferruginous hawks, golden eagles, and northern harriers and control increased fragmentation to support all grassland nesting raptors in the northern Great Plains.

CHAPTER 1: Raptors in Temperate Grasslands: Ecology of Ferruginous Hawk (*Buteo regalis*) in the Northern Great Plains

This chapter was prepared for submission to PLOS ONE and was coauthored by

Will Inselman, Jonathan A. Jenks, Kent C. Jensen, Robert W. Klaver, and Troy W. Grovenburg

Raptors in Temperate Grasslands: Ecology of Ferruginous Hawk (*Buteo regalis*) in the Northern Great Plains

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Abstract

Ferruginous hawks are a grassland and shrubland obligate nesting raptor and prefer lightly grazed pasture or idle areas for nesting. Their population reportedly declines in number if more than 30% of an area is cultivated and they rarely nest in areas dominated by croplands. At the landscape level, ferruginous hawks may have vacated close to half of their reproductive range on the northern prairies. During the breeding season from 2013–2015, we investigated influence of factors associated with the landscape on survival and nest-site selection of ferruginous hawks in north-central South Dakota, south-central North Dakota (grouped as ED), and northwestern South Dakota (WD). Using ground and aerial surveys, we located and monitored active ferruginous hawk nests: a total of 51 in ED and 55 in WD for the duration of the study. In ED, one pair of hawks was found every 655 km^2. In a more suitable subset of 4420 km^2 in ED, we found one pair per 340 km^2. In WD, we documented one breeding pair in every 315 km^2. In ED, all ferruginous hawk nests were in trees, and apparent nest success was 62% in 2013, 94% in 2014, and 87% in 2015. In WD, apparent nest success was 62% in 2013, 43% in 2014 and 94% in 2015. Overall, 101 ferruginous hawk chicks fledged in ED; 2.4 fledglings/successful nest, and 100 chicks fledged in WD; 2.6 fledglings/successful nest. We used Program MARK to evaluate the influence of land cover on nest success. The top-ranked nest survival model in ED was S_{Null} (w_i = 0.87) suggesting that none of the landscape predictor variables had any effect on survival and survival probability was constant between years. Probability of nest survival during the study period in ED was 0.69 (95% CI = 0.61–0.83). In WD, the top-ranked model was $S_{Substrate}$ suggesting nest substrate had most influence on nest survival in WD; the probability of ground nest survival during the study was 0.77 (95% CI = 0.64–0.83) and the probability of tree nest survival during the study was 0.43 (95% CI = 0.28–0.56). We used logistic regression analysis to evaluate the influence of landscape variables on nest site selection. In ED, percent grass and percent pasture/hay was the top-ranked model for predicting nest-site selection of ferruginous hawks and indicated positive association of nest-site selection with grasslands, and pasture. In WD, percent grass and development was the top-ranked model indicating positive influence of grasslands and development on nest-site selection. Although inclusion of development in the top model in WD seemed counter intuitive, most ferruginous hawk nests were close to undeveloped roads and the birds possibly utilized the edge habitat for better foraging and lower risk of predation. Our results indicate a decline in the ferruginous hawk population in ED since the 1970s. Further, decline in grass and pasture may have negatively influenced ferruginous hawk populations in ED. In ED, tendency of ferruginous hawks to nest exclusively in trees may indicate attempts to maximize next success by eliminating ground-based disturbance. Our findings indicate a need to provide pasture and idle grasslands in areas suitable for ferruginous hawk nesting in ED as well as nesting structures in both ED and WD to facilitate recovery and persistence of this species at the eastern edge of its breeding range.

Introduction

Free-ranging animals are systematically distributed across spatial and temporal scales and thus, various characteristics of the occupied landscape can affect components of their survival and fitness [1]. Reproductive success in birds may be influenced by a multitude of factors including composition and configuration of the surrounding landscape [2–3], interference emanating from natural and anthropogenic sources [4–5], nest substrate and placement [6], environmental conditions [7], resource availability [8], and community interaction [9].

The ferruginous hawk (*Buteo regalis*) is a species of conservation concern [10–11], a Tier 1 Species of Conservation Priority in North Dakota [12], and a Species of Greatest Conservation Need in South Dakota [13]. Ferruginous hawks are a grassland and shrubland obligate nesting raptor [14] and prefer lightly grazed pasture or idle areas for nesting [15–18]. Breeding populations of ferruginous hawks have been stable within portions of its range [19–21] although breeding range, local abundance, and reproduction of several populations of ferruginous hawk have declined in the Great Plains [14, 22]. The contrast in population status is likely due to differences in intensity of agricultural activities, modes of land use, and trends in prey populations among areas [23]. At the landscape level, ferruginous hawks may have vacated close to half of their reproductive range on the northern prairies [19, 22, 24]. Ferruginous Hawks reportedly decline in number if more than 30% of an area is cultivated [19] and rarely nest in areas dominated by croplands [15, 19 25–27]. Although impacts of oil and gas development on breeding success of some bird species have been observed [28–30], its impact on ferruginous hawks are equivocal [31]. Sensitivity of ferruginous hawks to disturbance at nest sites [32–33] might have affected breeding success in areas, which have been fragmented due to oil and gas development [34–35] and agriculture [26]. However, human created landscape structures like roads [25–26] may provide increased abundance of prey by creating edge habitats [23, 36] and anthropogenic structures like power-line poles, nest platforms, and fences may provide additional forms of perches and nesting substrates [36–38]. Several studies have documented fine-scale habitat selection for nesting and foraging [e.g., 39–40]; however, few studies have investigated landscape-level attributes of nesting habitat for this species. Conversion of grasslands to row-crop agriculture has reduced the amount of preferred habitat available to ferruginous hawks, and has been implicated in the population decline of the species in some areas [19, 41]. Potentially wide-ranging effects on wildlife (i.e., raptors) may be occurring due to increased fragmentation and habitat loss [42], but these effects have not been quantified to date for raptors in the Prairie Pothole Region of North America.

We examined nest survival, reproductive parameters, and nest site selection at a landscape level of ferruginous hawks in two study sites in the short- and mixed-grass prairies of the northern Great Plains that represent the eastern edge of their breeding distribution in North America. With extensive conversion of grasslands into row crops in the eastern Dakotas in the past few decades and approximately 77% of land used for agriculture, we hypothesized that nest survival of ferruginous hawks would be influenced by extrinsic factors like percent cultivated land, percent development, and percent grass. We also predicted that ferruginous hawks would select for areas with higher percentages of grass and pasture over agriculture-dominated landscapes for nesting, and would avoid areas with higher percentages of development. With minimal modification of landscape in the western Dakotas, we hypothesized little change in overall abundance but expected to observe influence of development on nest survival as an impact of recent oil and gas development in the region. We predicted selection for higher percentages of grass and avoidance of development during nest selection in the western Dakotas.

Materials and Methods

Study Area

Counties in north-central South Dakota and south-central North Dakota were combined and referred to as hereafter eastern Dakota (ED), and Counties in north-western South Dakota hereafter western Dakota (WD) were grouped together based on modes of land-use i.e., primarily agricultural, and in contrast, livestock-grazing based consecutively.

The ED study area (Fig. 1) included McPherson County in South Dakota and McIntosh, Dickey, and Logan counties in North Dakota and encompassed approximately 11,137 km^2 in the Missouri Coteau Physiographic Region [45]. Elevation ranged from 579–685 m above mean sea level throughout the study area. Numerous lakes and prairie potholes (>100 basins/2.59 km^2) were present and most of them are intermittently wet and dry. 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%; [46]). 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 [47]. Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern reedgrass (*Calamgrostis stricta*), prairie cordgrass (*Spartina pectinata*) big bluestem (*Andropogon gerardi*), porcupine grass (*Stipa spartea*), and little bluestem (*Schizachyrium scoparium*; [45]). Tree species were primarily cottonwood (*Populus deltoides*), American elm (*Ulmus americana*), box-elder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*; [15, 48]). Land use in McPherson County in 1973 and 1974 was comprised of 31% native grasslands, 13% wetlands, 25% cropland, and 29% pasture/hay [15]. Gilmer and Stewart's (1983) study area in south-central North Dakota comprised 36.1% pasture, 21.6% hayland/alfalfa and 36.7% cultivated crops. However, cropland and pasture constituted 87.7% of available land cover in McPherson County two decades later [43] and approximately 77% of the ED study area is used for agriculture currently.

The WD study area encompassed approximately 20,293 km^2 and included Harding, Butte, and Perkins counties in north-western South Dakota. The area is semi-arid and has a mid-continental climate with long, cold winters and short, warm summers [49]. Approximately 83% of the WD study area was pastureland dominated by grasses including western wheatgrass (*Pascopyrum smithii*), prairie Junegrass (*Koeleria pyramidata*), buffalograss (*Buchloe dactyloides*), green needlegrass (*Nassella viridula*), and blue grama (*Bouteloua gracilis*). Silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*) were widely distributed throughout the county [50]. Croplands occupied about 16 percent of the WD study area. Elevated table lands were dominated by ponderosa pine (*Pinus ponderosa*) savannah, whereas green ash (*Fraxinus* *pennsylvanicus*), willow (*Salix* spp.) and Siberian elm (*Ulmus pumila*) predominated in riparian areas and ravines [17]. Most of the land area in WD was treeless, semiarid rolling plains [50]. Land elevation ranged between 817 and 1,224 m above mean sea level [50]. The WD study area had a continental climate characterized by cold winters and hot summers, averaging -7° C in winter and 20° C in summer with an annual precipitation average of 37 cm and average seasonal snowfall of 101 cm [50]. Most farm or ranch land was utilized for grazing cattle (*Bos taurus*) and some sheep (*Ovis aries*). In WD, oil and gas extraction started in 1953 in the south-eastern section of the Williston Basin (i.e., Cedar Creek Anticline) in Harding County, South Dakota. In 2015, oil and gas extraction in Harding County contributed to approximately 98% of South Dakota’s production and 160 active wells produced approximately 1.6 million barrels [44].

Nest Monitoring

During the 2013–2015 breeding seasons, we searched for active ferruginous hawk nests beginning 15 March in WD and 1 April in ED. To locate nests we systematically drove all accessible roads in each county and surveyed area inaccessible to vehicles on foot and by air. Nests also were located on foot using landowner’s knowledge of nests and using historic nest locations [66–67]. Locating nests was facilitated by the lack of foliage during early spring conditions. We considered nests to be occupied when evidence of nesting behavior (e.g., nest building, mating behavior) was observed. Because ferruginous hawks are believed to be sensitive to disturbance [51], we did not access nests until eggs hatched at which time considerable investment had been bestowed. Nests were considered active when evidence of prolonged incubation was confirmed. All active nest-site locations were recorded using a handheld Garmin Global Positioning System (GPS; Garmin Ltd.) unit and ArcGIS 10.1 was used to plot locations [52]. We monitored nests at least once every week from access roads or vantage points (distance $\leq$ 200 m) using binoculars and spotting scopes until eggs hatched. After confirming nestling presence in a nest, we observed nests ensuring minimal impact on the nest or the nest substrate using ladders or climbing equipment. At each nest, we recorded the number of nestlings and each nestling received a United States Fish and Wildlife Service lock-on band when $\geq$28 days of age. Several measurements (e.g., weight, hallux diameter) also were recorded for each nestling. Nest substrate was noted, height of nest from the ground was recorded using a clinometer and a rangefinder, nest tree species was identified for tree nests, a difficulty-to-access-nest score was assigned for each nest (i.e., easy or difficult), and nest slope and aspect also were recorded. Young were aged using the photographic guide of Moritsch (1985) and were considered successfully fledged when nestlings reached 90% (~40 days) of average fledging age (~45 days; [53]).

Our nest monitoring protocol followed established guidelines [54], all animal handling methods followed 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 (License # 14), North Dakota Game and Fish (License # GNF03312634), and the United States Fish and Wildlife Service (Permit # 21408). Individual landowners granted permission to access nests 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.

We calculated nesting densities of ferruginous hawks in ED and WD. To compare population abundance in ED with previous studies of Lokemoen and Duebbert (1976) and Gilmer and Stewart (1983), we also considered a sub-set of 4,420 km^2 area representing suitable habitat for ferruginous hawk nesting within a larger study area that contained 85% of all nests in the study area. To be able to compare nesting ferruginous hawk abundance between our study in WD and the Blair and Schitoskey (1982) study, we also calculated nesting densities using nests only in Harding County, South Dakota in a 6,935 km^2 area.

Statistical Analysis

Habitat Measurements

We used the Cropland Data Layer (CDL; [46]) to evaluate land cover components at nest sites and South Dakota Department of Environment and Natural Resources for oil and gas extraction location information [44]. We reclassified the CDL layers from 2013, 2014 and 2015 for the study area to represent the land cover variables that were biologically significant [55]; cultivated, pasture/hay, grassland, water, forested, and development. For logistic regression analysis, we generated random points using the Random Point Generator tool in ArcGIS 10.1 to simulate random nest sites. We clipped reclassified CDL layers to 1600-m buffers around each random and nest site using Geospatial Modeling Environment [56] and calculated land cover percentages for extrinsic variables using ArcGIS 10.1. We selected the 1600-m (ca. 8 km^2) buffer after Smith and Murphy

(1973) and Lokemoen and Duebbert (1976), which represented an estimated home range size for breeding ferruginous hawks in the northern Great Plains. To associate nest survival with landscape features, we assessed distances of actual and simulated random nests from roads, farms, and water bodies using ArcGIS 10.1. All statistical tests were conducted using Program R [57] with an experiment-wide error rate of 0.05.

Nest Survival Analysis

From published literature and based on field observations, we determined 12 predictors, which included land cover variables, nest characteristics (e.g., nest substrate, nest accessibility), and distance from landscape features as potential factors influencing nest survival (Table 1; Table 2). We used Pearson's correlation for evidence of multicollinearity and excluded covariates from the same model if $r \geq |0.7|$. Nests were considered successful when at least one young fledged; we used Program MARK [58] with the logit-link function to run nest survival models to evaluate effects of predictor variables. We created 13 and 15 biologically significant models for ED and WD, respectively, and used Akaike's Information Criterion (AIC_c) corrected for small sample size to select models that best described the data [59]. We used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤4 ΔAIC_c from the top model as competitive models [60]. Covariates of competing models were verified so that the β-estimates did not have 95% confidence intervals that encompassed zero [61–63]. Because there is no goodness-of-fit test for nest survival models available currently, model robustness was assessed by artificially inflating ĉ (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; [62, 64]).

Nest-Site Selection

To determine effects of landscape on nest-site selection, we used logistic regression and Akaike's Information Criterion (AIC). We generated an equal number of pseudo-absent points as total number of active nests identified from 2013–2015 in ED and WD (51 random nest sites in ED and 56 random nest sites in WD). Using our predictor variables we created 10 *a priori* models from field observations and published literature (Table 5; [17, 15]) to estimate the influence of those variables on nest site selection (Table 1). We used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤4 ΔAIC_c from the top model as competitive models [60]. Receiver operating characteristic (ROC) values were used to test predictive capacities of significant models. We followed guidelines [65] 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 on nest-site selection in the top-ranked model.

Results

In ED, we located 51 active ferruginous hawk nests (20 in 2013, 18 in 2014, and 13 in 2015) and in WD, we located 56 active ferruginous hawk nests (24 in 2013, 14 in 2014, and 18 in 2015). In ED, mean date when first pairs were observed was 10 April and in WD mean date of first observed pairs was 18 March. In ED, apparent nest success was 62% in 2013, 94% in 2014, and 87% in 2015. In ED, during the 2013 breeding season, 12 of 20 active nests fledged 27 chicks (2.3 chicks/successful nest). During 2014, 17of 18 active nests fledged 45 chicks (2.7 chicks/successful nest), and in 2015, 13 of 15 active nests fledged successfully producing 29 fledglings (2.2 chicks/successful nest); overall, 2.4 chicks/successful nest (*n* = 101) were fledged in ED. In WD, apparent nest success was 62% in 2013, 43% in 2014 and 94% in 2015. In WD, during the 2013 breeding season, 15 of 24 active nests fledged 38 chicks (2.5 chicks/successful nest), during 2014, six of 14 active nests fledged 11 chicks (1.8 chicks/successful nest), and in 2015, 17 of 18 active nests fledged successfully producing 51 fledglings (2.8 chicks/successful nest); overall, 2.6 chicks/successful nest (*n* = 100) were fledged.

No nest abandonment occurred post-hatching. Wind and hail contributed 83% of nest-loss in ED while predation contributed approximately 10%; remaining causes of nest loss were unknown. In ED, premature-fledging via falling out of nests was the primary cause of fledgling death (32%; *n* = 6), followed by West Nile virus (WNv) and *E. coli* (26%; *n* = 5), malnutrition (5%; *n* = 1), and unknown but suspected WNv infection (26%; *n* = 5). In WD, nest abandonment early in the season was observed on 12 occasions. Primary cause of fledgling death was premature fledgings via falling out of nests (65%; *n* = 11) followed by predation (18%; *n* = 3), and unknown (18%; *n* = 3).

Percent cultivated and percent grassland were negatively correlated ($r = –0.78$) in ED. Therefore, nest survival models in ED did not include both variables. The top-ranked nest survival model in ED was S_{Null} ($w_i = 0.87$) suggesting that none of the predictor variables had any effect on survival and survival was constant among years (Table 3). Probability of nest survival during the study period in ED was 0.69 (95% CI = 0.61–0.83). Remaining models were ≥4 ΔAIC_c from the top model and were not competitive. In WD, the top-ranked model was $S_{Substrate}$ ($w_i = 0.91$) suggesting nest substrate had most influence on nest survival (Table 4). The 95% confidence intervals of the β estimate for substrate (0.23, 95% CI = 0.08–0.76) did not encompass zero; the probability of ground nest survival during the study was 0.77 (95% CI = 0.64–0.83) and the probability of tree nest survival during the study 0.43 (95% CI = 0.28–0.56). Remaining models were ≥4 ΔAIC_c from the top model and therefore, were not competitive. Interpretation of our top model ($S_{Substrate}$) remained the same when adjusting ĉ from 1.0 to 3.0 to test for over dispersion; when ĉ = 2.0 (moderate dispersion; $QAIC_c$ wt = 0.61) and through ĉ = 3.0 (extreme dispersion; $QAIC_c$ wt = 0.48).

In ED, all ferruginous hawk nests were in trees. Cottonwood was the most popular tree nest (54%) followed by American elm (37%); box-elder (*Acer negundo*) and Russian olive (*Elaeagnus angustifolia*) accounted for the remainder (9%) of trees. Average nest height was 5.8 m (SE = 0.61) and highest recorded nest was 18.6 m (eastern cottonwood) and the lowest recorded nest height was 1.8 m (American elm). In WD, 59% of nests were ground nests most on badland knobs, and 41% were tree nests that were exclusively in cottonwood trees. Average tree-nest height in WD was 9.2 m (SE = 2.27); highest recorded tree-nest was 17 m and lowest tree-nest was at 2.5 m.

In ED, percent grass and percent pasture/hay was the top-ranked model (w_i = 0.82) for predicting nest site selection of ferruginous hawks; predictive capability of the model was excellent (ROC = 0.89; Table 5). Logistic odds-ratio estimates from the top-ranked model for ferruginous hawks in ED indicated the odds of nest site selection were 1.23 (95% CI = 1.12–1.46) times greater for every percent increase in grasslands, and 1.09 (95% CI = 1.02–1.19) times greater for every percent increase in pasture. All 95% confidence intervals for parameter estimates for percent grassland (β = 0.41, SE = 0.16) and percent pasture/hay (β = 0.19, SE = 0.08) across models did not overlap zero, indicating significant influence on ferruginous hawk nest site selection.

In WD, percent grass and development was the top-ranked model (w_i = 0.88) for predicting nest-site selection of ferruginous hawks; predictive capability of the model was excellent (ROC = 0.94; Table 6). Logistic odds-ratio estimates from the top-ranked model for ferruginous hawks indicated the odds of nest-site selection were 1.35 (95% CI = 1.23–1.44) times greater for every percent increase in grasslands and 1.21 (95% CI = 1.13–1.39) times greater for every percent increase in development. All 95% confidence intervals for parameter estimates for percent grass (β = 0.22, SE = 0.13) and development (β = 0.09, SE = 0.02) across models did not overlap zero, indicating significant influence on ferruginous hawk nest-site selection.

Discussion

Our study area in ED (11,137 km^2) and WD (20,293 km^2) had administrative boundaries (i.e., county limits) rather than any biologically relevant limits. Although we comprehensively surveyed seven counties (3 in WD and 4 in ED), parts of those counties were only marginally favorable or unfavorable for nesting ferruginous hawk due to land use [24]. In ED, a major part of our study area was within the more intensively cultivated Drift Plain (Dickey County, ND and eastern McPherson County, SD); however, historically, parts of our ED study area (i.e. Logan County, ND) lay within one of the highest density breeding grounds of ferruginous hawks [24] on the Missouri Coteau. In 1973 and 1974, Lokemoen and Duebbert (1976) observed the raptor community in a 269 km^2 area in McPherson County, South Dakota, which is within our ED study site. Their study documented ferruginous hawk populations, among other raptor species, and land use characteristics of the study area. In the 1970s, the raptor community consisted mainly of ferruginous hawks (31 of 48 total raptor pairs). Other species were red-tailed hawks (*Buteo jamaicensis*), Swainson’s hawks (*Buteo swainsoni*), northern harriers (*Circus cyaneus*), great horned owls (*Bubo virginianus*), and burrowing owls (*Speotyto cunicularia*). Gilmer and Stewart (1983) surveyed the ferruginous hawk population in a 1,259-km^2 study area in south-central North Dakota from 1977 to 1979 and reported that about 95% of the area around ground nests was grassland. Blair and Schitoskey (1982) documented breeding ecology and food habits of ferruginous hawks at 18 active nests in Harding County in northwestern South Dakota during 1976–1977, which was within our WD study site. Subsequent aerial surveys of Butte, Harding, and Perkins counties during 2005 and 2011, observed 19 and 14 active nests, respectively [66–67].

During our study period (2013–2015), ferruginous hawk nesting density in our ED study area was considerably lower compared to one pair in every 79 km^2 [after 24] in 1977–1979, and one pair every 17.4 km^2 [after 15] in 1973–1974, indicating a decline in breeding ferruginous hawk populations in that area. Compared to other studies [15, 24, 68–72], densities of breeding ferruginous hawks in our ED study area also was considerably lower. Nesting density of breeding ferruginous hawks in our WD study area was comparable to the Blair and Schitoskey (1982) study, which was conducted in the same area (Harding County, South Dakota). Blair and Schitoskey documented one breeding pair per 292 km^2 and 412 km^2 during 1976 and 1977, respectively.

In ED, apparent nest survival ([62%–94%] [otherwise nesting success; 24, 15]) was comparable to studies conducted in the same area by Gilmer and Stewart (64%–75.9%;

1983) and Lokemoen and Duebbert (59%; 1976) as well as other studies (e.g. [65%; 70], [70%; 71], [92%; 69]). Although the apparent nest survival and nest survival probability from program MARK were comparable, nesting densities during our study were considerably lower than most studies. Total fledgling productivity therefore, was severely impacted although clutch size and fledglings produced/successful nest was comparable to most studies [15, 24, 68–72]. Ferruginous hawks in the northern Great Plains nest in low-densities and high nest survival and fledging rates are therefore crucial for population viability. Our study indicated that nesting densities of ferruginous hawks in ED have declined severely in the past four decades. Although survival rates are similar, decline in nesting density may have potential impacts on the breeding population of ferruginous hawks at the eastern limits of their range.

Ferruginous hawks nest on a variety of substrates (e.g., ground, haystack, and tree) and are known for their versatility in nest placement [73]. All ferruginous hawk nests in ED during 2013–2015 were tree nests. Previous studies [24, 15] conducted in the area found multiple nesting substrates. Lokemoen and Duebbert (1976) documented 44% nests on the ground, 44% on trees, and 7% on haystacks. Gilmer and Stewart (1983) reported 17% nests on ground, 56% on trees, 7% on haystacks, and 18% on powerline towers. According to their study, the tree nests had the lowest success rate (i.e., 65.3%) although they contributed to the majority of productivity due to higher proportion of nests. Tree nests seem more vulnerable to natural elements (e.g., wind, hail), which also were the main identified cause for nest loss during our study in ED. In WD, apparent nest survival (72% and 82%; [17]), and fledging productivity also were comparable between studies. Our nest survival model indicated that tree nests had a lower survival than ground nests.

Blair and Schitoskey (1982) reported that all ferruginous hawk nests were ground nests during 1976–1977. Ferruginous hawks although versatile in nest placement are possibly being compelled to nest in trees (more widespread in the agricultural ED than in minimally modified WD) while coping with increased anthropogenic disturbance (e.g., conversion of grassland to row crop, expansion of energy extraction activities, human settlement) in the northern Great Plains.

In ED, during 2013–2015 we found evidence of West Nile virus (WNv) and *E. coli* infection and subsequent death of fledged nestlings in at least two nests [74] in 2013, and suspected WNv to be the cause for fledgling deaths at the same nests in 2014; although cause-specific mortality was not confirmed due to rapid decomposition of carcasses. In 2015, both impacted nests fledged successfully and fledglings appeared healthy and survived at least 15 days post fledging at which time we concluded our nest monitoring. Although diseases like WNv may act as additional stressors on productivity, population level impacts are still unclear [74]. Although speculative, successful fledging and subsequent survival of previously WNv exposed nests in 2015 also may indicate effective immune response. Cause-specific mortality during our study also indicates that high-wind conditions in ED and WD may negatively influence tree-nests.

Percent grass, and percent pasture/hay most influenced nest-site selection of ferruginous hawks in ED. Ferruginous hawks are grassland obligate nesting raptors [14] and their nests have been associated with a high percentage of grasslands [15, 17, 19, 24]. Ferruginous hawks decline in number if more than 30% of an area is cultivated [19] and rarely nest in areas dominated by croplands [15, 19, 24, 26]. Grasslands in the ED study site have declined from ca. 60% to ca. 20% in the last four decades. Most of this general decline in grassland and pasture may be attributed to conversion of pasture and grassland to row crop agriculture [43, 75]. Grassland and pasture possibly provide good foraging habitat under relatively low ground based disturbance and ferruginous hawks, known for their sensitivity to disturbance [54], avoid areas with higher levels of disturbance (e.g., cropland and farming operations). The increase in cropland and farming activity is likely a source of disturbance at ferruginous hawk nest sites and loss of grassland and pasture are directly and negatively correlated with this increased land conversion; the decline in nesting ferruginous hawks in ED also may be explained by this phenomenon.

In WD, nest site selection was associated with percent grass and development with positive association to both variables. Although percent grass possibly ensured good foraging habitat, positive association with development appears counter-intuitive. Most ferruginous hawk nests were close to roads, which may ensure low predator activity e.g., coyotes (*Canis latrans*), red fox (*Vulpes vulpes*) [76], and also provide edge habitats. Edge habitats also are associated with greater prey abundance [23, 36] and anthropogenic structures like power-line poles and fences may provide additional perches. Most nests in WD were near relatively idle undeveloped roads (e.g., dirt roads, graded gravel roads) and ferruginous hawks were frequently observed perched on fences along these roads and foraging in hayed road ditches. Northeastern regions of WD were used for small grain farming and south western WD lacked land surface features frequently used by ferruginous hawks in the region [17]. A majority of ferruginous hawk nests in WD in 1976–1977 as well as in 2013–2015 were concentrated in a strip of 25 km wide landscape with the greatest concentration of buttes and lightly vegetated hills [17]. Oil and gas extraction did not seem to influence ferruginous hawk nesting. Ferruginous hawks selected nest sites based on habitat characteristics at the local-level preferring nest sites with a high percent of grass [15, 53, 77]. Our results indicate that ferruginous hawks selected for grass and pasture dominated regions in ED away from ground-based disturbance, and selected for grasslands in WD while exploiting edge habitats for efficient foraging.

Conclusion

Our ferruginous hawk reproductive ecology study revisited former studies conducted from 1970–1980 in the northern Great Plains. Our study was conducted in two areas with distinct modes of land-use (i.e., agricultural and ranch-based). Significant changes have occurred in both study areas in the last four decades. Conversion of grassland and pasture to row crop agriculture in south-central North Dakota and north-central South Dakota have increased the loss of nesting habitat for ferruginous hawks and breeding populations have declined; however, nest survival and productivity have remained similar to previous studies in the area. In WD, nesting substrate explained some of the variation in nest survival although survival remained constant during our study and was similar to the earlier studies. Ferruginous hawks selected for nest sites with higher percentages of grass and pastures in eastern and western study sites, while in relatively less modified WD they also utilized areas with greater edge for benefits associated with foraging and prey avoidance. Oil and gas extraction seemed to have no influence on ferruginous hawk nesting. This project documented the response of ferruginous hawks during a time of rapid expansion in agriculture and oil and gas extraction. Our results show decline in the ferruginous hawk population in a landscape modified extensively from grassland prairies to row crop agriculture in the northern Great Plains. It also indicates a definite adaptive nesting behavioral change where tree nesting has become an alternative strategy to avoid ground-based disturbance. We suggest that specific need-based research and management (e.g., strategic placement of artificial nesting structures, returning less productive land strategically to grassland or pasture, and long-term monitoring of populations in breeding and wintering grounds) would aid in recovery of the species at the eastern limits of its breeding range.

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Figure 1. Ferruginous hawk reproductive ecology study area in North Dakota and South Dakota, USA.

Ferruginous hawk (*Buteo regalis*) study area in Logan, McIntosh, and Dickey counties (light grey), in south-central North Dakota, McPherson County (dark grey) in north-central South Dakota, and Harding, Butte, and Perkins counties (dark grey) in north-western South Dakota, USA, 2013–2015.

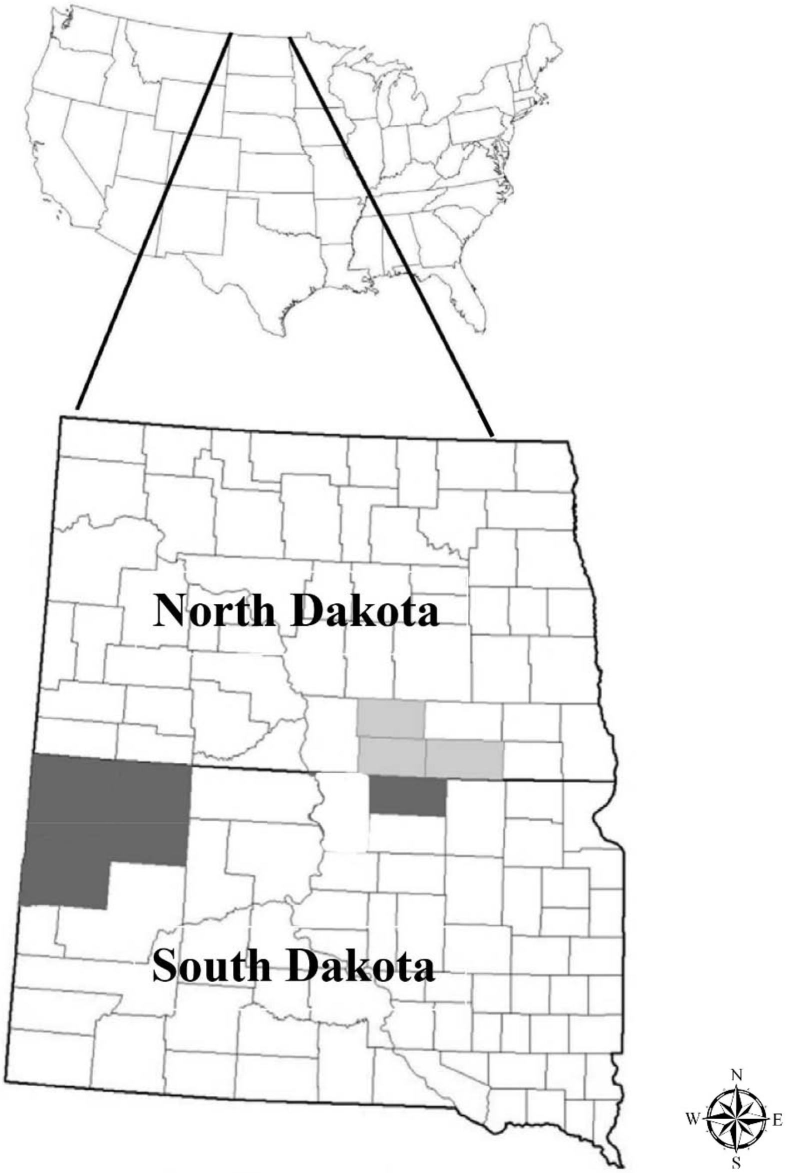

Table 1. Predictor variables within 1600-m buffers of active and random nest sites used to model the influence of landscape on ferruginous hawk nest survival and nest-site selection in the northern Great Plains, USA, 2013–2015.

Variable Name	**Definition**
Cultivated	Total area under row and grain crop (%)
Grass	Total grass cover (%)
Pasture/hay	Total pasture and alfalfa/grass hay cover (%)
Water	Total wetland cover (%)
Forest	Total tree cover (%)
Development	Total farm sites (%)
Distance to homestead*	Distance to nearest homestead (m)
Distance to road*	Distance to nearest road (m)
Distance to oil well*	Distance to nearest oil well (m)
Year*	Year of observation
Nest substrate*	Ground vs. tree nest
Nest accessibility*	Easy vs. difficult

* Excluded from nest site selection analysis

Table 2. Mean and standard error (SE) for land cover and distance to landscape features for ferruginous hawk nests in northern Great Plains, USA, 2013–2015.

Variable Name	Eastern Dakota (ED) (N = 55)		Western Dakota (WD) (n = 51)	
	$\bar{x}$	SE	$\bar{x}$	SE
Cultivated (%)	19.23	4.17	4.84	2.33
Grass (%)	51.63	6.29	62.46	7.42
Pasture/Hay (%)	14.37	2.40	24.58	8.29
Water (%)	6.18	1.96	3.11	1.84
Forest (%)	6.33	1.17	2.73	0.64
Development (%)	2.23	0.71	3.13	0.15
Distance to homestead (m)	1265.21	228.91	1412.63	304.66
Distance to road (m)	163.48	33.10	1046.47	254.13
Distance to oil well (m)	-*	-	1338.52	386.43

*****No oil and gas wells in ED

Table 3. Nest survival models of ferruginous hawk during the 2013–2015 breeding season in south-central North Dakota and north-central South Dakota (ED), USA.

Model	AIC_c[a]	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
S_{Null}	521.35	0.00	0.87	1	515.41
$S_{\text{\%Grass+\%Pasture/hay}}$	526.78	5.43	0.11	3	517.15
$S_{\text{\%Grass+\%Pasture/hay+\%Forest}}$	527.47	6.12	0.01	4	517.79
$S_{\text{\%Grass+\%Pasture/hay+Year}}$	528.27	6.92	0.01	4	518.05
$S_{\text{\%Grass+\%Development}}$	529.03	7.68	0.00	3	516.22
$S_{\text{\%Development}}$	530.32	8.97	0.00	2	516.84
$S_{\text{Saturated}}$	532.57	11.22	0.00	12	519.03
S_{Year}	534.43	13.08	0.00	1	519.91
$S_{\text{\%Water+\%Grass}}$	535.75	14.40	0.00	3	520.71
$S_{\text{\%Water+\%Grass+\%Forest}}$	537.18	15.83	0.00	4	521.55
$S_{\text{\%Development+\%Forest}}$	538.56	17.21	0.00	3	523.01
$S_{\text{\%Forest+\%Grass+\%Development+Year}}$	539.69	18.34	0.00	5	523.97
$S_{\text{\%Cultivated}}$	541.05	19.70	0.00	2	524.56

[a] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).
[b] Difference in AICc relative to min. AIC.
[c] Akaike wt (Burnham and Anderson 2002).
[d] Number of parameters.

Table 4. Nest survival models of ferruginous hawks during the 2013–2015 breeding season in north-western South Dakota (WD), USA.

Model	AIC_c[a]	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
$S_{\text{Substrate}}$	633.19	0.00	0.91	2	627.91
$S_{\text{Substrate+Year}}$	639.09	5.90	0.07	3	628.58
$S_{\text{\%Grass+DistancetoRoad}}$	639.95	6.76	0.02	3	629.89
S_{Null}	641.04	7.85	0.00	1	631.33
$S_{\text{DistancetoHomestead+\%Grass+\%Pasture/Hay}}$	642.74	9.55	0.00	4	632.42
$S_{\text{\%Cultivated+Substrate}}$	644.11	10.92	0.00	3	632.94
$S_{\text{Year+\%Development+\%Grass+\%Pasture/Hay}}$	646.06	12.87	0.00	5	634.02
$S_{\text{Saturated}}$	648.23	15.04	0.00	13	636.43
$S_{\text{\%Forest+\%Development}}$	650.01	16.82	0.00	3	639.10
$S_{\text{Year+\%Water+\%Cultivated}}$	651.81	18.62	0.00	4	640.81
$S_{\text{Substrate+\%Development+Year+\%Grass}}$	653.35	20.16	0.00	5	641.75
S_{Year}	655.69	22.50	0.00	2	643.02
$S_{\text{\%Water+\%Cultivated}}$	657.15	23.96	0.00	3	644.35
$S_{\text{\%Development+Substrate+\%Water+\%Cultivated}}$	658.17	24.98	0.00	5	645.41
$S_{\text{\%Forest+\%Development}}$	659.43	26.24	0.00	3	647.13

[a] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).
[b] Difference in AICc relative to min. AIC.
[c] Akaike wt (Burnham and Anderson 2002).
[d] Number of parameters.

Table 5. Akaike's Infromation Criterion (AIC) model selection of logistic regression models for nest-site selection of ferruginous hawk in south-central North Dakota and north-central South Dakota (ED), USA, 2013–2015.

Model Covariates	K	AIC	ΔAIC	w_i	ROC[d]
Grass + Pasture/hay	3	221.96	0.00	0.82	0.89
Grass + Forest + Development	4	227.41	5.45	0.15	0.83
Cultivated + Forest	3	228.03	6.07	0.03	0.84
Water + Development + Pasture/hay	4	230.94	8.98	0.00	0.77
Cultivated + Water	3	238.34	16.38	0.00	0.79
Development	2	241.54	19.58	0.00	0.81
Forest	2	243.29	21.33	0.00	0.70
Null	1	245.05	23.09	0.00	0.77
Grass + Development	3	247.91	25.95	0.00	0.69
Grass + Pasture/hay + Development + Water + Forest	6	248.57	26.61	0.00	0.73

[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)

Table 6. Akaike's Infromation Criterion (AIC) model selection of logistic regression models for nest-site selection of ferruginous hawk in north-western South Dakota (WD), USA, 2013–2015.

Model Covariates	K	AIC	ΔAIC	w_i	ROC[d]
Grass + Development	3	395.84	0.00	0.88	0.94
Grass + Pasture/hay + Development	4	401.52	5.16	0.11	0.88
Null	1	403.76	7.92	0.01	0.81
Grass + Pasture/hay + Cultivated	4	406.61	10.77	0.00	0.74
Water + Forest	3	409.64	13.80	0.00	0.84
Development + Forest + Grass + Pasture/hay	5	414.54	18.16	0.00	0.76
Grass	2	417.49	21.65	0.00	0.80
Pasture/hay + Forest	3	420.01	24.17	0.00	0.79
Water	2	421.95	26.11	0.00	0.76
Grass + Forest	3	423.17	27.33	0.00	0.78

[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: Raptors in Temperate Grasslands: Ecology of Golden Eagle (*Aquilla chrysaetos*) and Nesting Decline at the Eastern Fringe of its Year-Round Range in North America

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Raptors in Temperate Grasslands: Ecology of Golden Eagle (*Aquilla chrysaetos*) and Nesting Decline at the Eastern Fringe of its Year-Round Range in North America

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Abstract

Golden eagles (*Aquila chrysaetos*) are long-lived raptors with high nest-site fidelity and relatively low reproductive success. Population trends of golden eagles in western United States are unclear although long-term monitoring of populations shows declines in occupancy and breeding performance. The year round resident population in north western South Dakota (NWSD) faces an increase in existing threats like energy development, climate change, and changes in land use. During the breeding season from 2013–2015, we investigated influence of factors associated with the landscape on survival and nest-site selection of golden eagles in NWSD. Using ground-based surveys, aerial surveys, and historic nest locations, we located and monitored active golden eagle nests in NWSD: a total of 35, i.e., one nest every 1,740.4 km^2 for the duration of the study. Active nests were placed on two different substrates (i.e., steep cliff-side [n = 5] and trees [n = 30]) and apparent nest success was 62% in 2013, 94% in 2014, and 87% in 2015. Overall 41 chicks successfully fledged; 1.4 chicks/successful nest (SE = 0.09). Cottonwood (*Populus deltoides*) was the sole tree of choice for nesting golden eagles in NWSD (n = 30) followed by steep cliff-side (n = 5). We used Program MARK to evaluate the influence of land cover on nest success. Top-ranked nest survival model was S_{Null} (w_i = 0.91) suggesting that none of the predictor variables had any effect on survival and survival was constant between years. Probability of nest survival during the study period was 0.76 (95% CI = 0.58–0.81). We used logistic regression analysis to evaluate the influence of landscape variables on nest-site selection. Development was the top-ranked model (w_i = 0.72) for predicting nest site selection of golden eagles and indicated

negative association of nest-site selection with development. A model containing grass, pasture, and development ranked second and was competitive indicating positive association of active nests with higher percentages of grass and negative association with increase in development. Our results indicate a decline in the golden eagle population in NWSD during the last decade. Developments in NWSD like human settlements, roads, oil and gas extraction, and agriculture may have fragmented golden eagle habitat in NWSD. Lagomorph population cycles also have major influence on golden eagle reproductive rates and may have influenced nesting in NWSD. Manifold decrease in nesting abundance in NWSD since 2005 also may indicate increased disturbance and degraded habitat in the area. Our findings indicate a need to implement strategic development, and provide pasture and idle grasslands in areas suitable for golden eagle nesting in NWSD. Assessing year round survival rates of golden eagles, estimating trends in prey abundance in relation to golden eagle nesting, and documenting cause-specific mortality will be a crucial next step when managing golden eagle populations in NWSD to facilitate recovery and persistence of this species at the eastern edge of its year-round range.

Introduction

Ecological requirement of a species are often in conflict with human interests. Quantifying habitat preferences and evaluating influence of intrinsic and extrinsic factors on animal survival is therefore essential to improve habitat management and conservation strategies in human dominated landscapes [1–2]. Reproductive success in birds may be influenced by a multitude of factors including composition and configuration of the surrounding landscape, interference emanating from natural and anthropogenic sources, nest substrate and placement, environmental conditions, resource availability, and community interactions [3–9].

Golden eagles (*Aquila chrysaetos*) are long-lived raptors with high nest-site fidelity and relatively low reproductive success [10–13]. In north western South Dakota (hereafter NWSD), golden eagles occupy open areas, nesting on sandstone and limestone cliffs, rocky outcrops, mud buttes, creek banks, and in trees [14–16]. The golden eagle is a Species of Conservation Concern in the United States Fish and Wildlife Service (USFWS) Mountain-Prairie Region [17] and although population trends in western United States are unclear [18], long-term monitoring of populations shows declines in occupancy and breeding performance [19–20]. The year round resident population in NWSD face an increase in existing threats like energy development [21–22], climate change [23–24] and changes in land use [19,13]. North western South Dakota is characterized by intensely grazed monotypic pastureland and conversion of native grasslands to areas with less structural and plant species diversity such as small-grain agriculture may lead to further fragmentation of habitat. This loss in diversity is not only a direct impact on habitat, but also may reduce suitable nesting sites and negatively alter the available prey base. The golden eagle is a wide-ranging species; as a consequence, identifying changes in habitat and their effect on breeding success of golden eagles across its range in the western United States may be difficult. Smaller scale studies will therefore provide much needed information on factors influencing breeding success locally, i.e., in NWSD, which may be integrated with information from other areas for a comprehensive understanding of golden eagle ecology [18].

In NWSD, 52 of 121 golden eagle nests were classified as active in 2005 [25]. During 2011, only 26 of 121 nests were active with an additional 5 new active nests discovered [26]. To investigate factors influencing this decline in golden eagle nesting we examined nest survival, reproductive parameters, and nest-site selection at a landscape level in NWSD. With some conversion of grasslands into row crops and grain crops in the past few decades and expansion of oil and gas extraction in NWSD [36] we hypothesized that nest survival of golden eagles would be influenced by extrinsic factors like percent cultivated, percent development, and percent grass. We also predicted that golden eagle would select for areas with higher percentages of grass and pasture over agriculture dominated landscapes for nesting, and would avoid areas of higher percentages of development. With decline in occupied territories of golden eagles we expected to observe influence of development like human settlements, roads, energy extraction, and agriculture on nest survival as an impact of land-use change and recent oil and gas development in NWSD.

Materials and Methods

Study Area

At the eastern limit of year-round range of golden eagle in the western United States, our study area encompassed approximately 20,293 km^2 and included Harding, Butte, and Perkins counties in north-western South Dakota (Figure 1). The area is semi-arid and has a mid-continental climate with long, cold winters and short, warm summers [27]. Approximately 83% of the study area was pastureland dominated by grasses including western wheatgrass (*Pascopyrum smithii*), prairie Junegrass (*Koeleria pyramidata*), buffalograss (*Buchloe dactyloides*), green needlegrass (*Nassella viridula*), and blue grama (*Bouteloua gracilis*). Silver sagebrush (*Artemisia cana*) and big sagebrush (*Artemisia tridentata*) are widely distributed throughout the county [28–29]. Croplands occupy about 16 percent of the study area. Elevated table lands are dominated by ponderosa pine (*Pinus ponderosa*) savannah, whereas green ash (*Fraxinus pennsylvanicus*), willow (*Salix* spp.) and Siberian elm (*Ulmus pumila*) dominate in riparian areas and ravines [30]. Most of the land area was treeless, semiarid rolling plains [28]. Land elevation ranged between 817 and 1,224 m above mean sea level [28]. The study area has a continental climate characterized by cold winters and hot summers, averaging -7° C in winter and 20° C in summer with an annual precipitation average of 37 cm and average seasonal snowfall of 101 cm [28–29]. Most farm or ranch land was utilized for grazing cattle (*Bos taurus*) and some sheep (*Ovis aries*).

Nest Monitoring

During the 2013–2015 breeding seasons, we searched for active golden eagle nests beginning 15 March each year. To locate nests we systematically drove all accessible roads in each county and surveyed area inaccessible to vehicles on foot and by air. Nests also were located on foot using landowner's knowledge of nests and using historic nest locations. Locating nests was facilitated by the lack of foliage during early spring conditions. We also revisited 126 previously documented golden eagle nests as provided by the South Dakota Department of Game Fish and Parks [(SDGFP); [25–26]) in Harding, Perkins and Butte counties to confirm their present status and calculated nesting densities of golden eagles in NWSD. We considered nests to be occupied when evidence of nesting behavior (e.g., nest building, mating behavior) was observed. We did not access nests until eggs hatched at which time we assumed considerable investment had been administered for pairs so that they would not abandon nests. Nests were considered active when evidence of prolonged incubation was confirmed. All active nest-site locations were recorded using a handheld Garmin Global Positioning System (GPS; Garmin Ltd.) unit and ArcGIS 10.1 was used to plot locations [31]. We monitored nests at least once every week from access roads or vantage points (distance ≤ 200 m) using binoculars and a spotting scope until eggs hatched. After confirming nestling presence in a nest, we entered nests ensuring minimal impact on the nest or the nest substrate (i.e., tree branch supporting nest, surface around ground nests) using ladders or climbing equipment. At each nest we recorded the number of nestlings and recorded general health conditions. Nest substrate was noted, height of nest from the ground was recorded using clinometers and a rangefinder, nest tree species was identified for tree nests, a difficulty-to-access-nest score was assigned for each nest (i.e., easy or difficult), and nest slope and aspect also were recorded. Young were aged using the photographic guide by

Hardy (2006; [32]) and were considered successfully fledged when nestlings reached 90% (~63 days) of average fledging age (~70 days; [10, 33]).

Our nest monitoring protocol for this study followed established guidelines approved by The Ornithological Council [34] 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 SDGFP (License # 14) and the United States Fish and Wildlife Service (USFWS; Permit # 21408). Individual landowners granted permission to access nests for data collection. All data collected on public lands were conducted with permission from SDGFP and the USFWS. No federally endangered or threatened species were involved in this study.

Statistical Analysis

Habitat Measurements

We used the Cropland Data Layer (CDL; [35]) to evaluate land cover components at nest sites and South Dakota Department of Environment and Natural Resources for oil and gas extraction location information [36]. We reclassified the CDL layers from 2013, 2014, and 2015 for the study area to represent the land cover variables that were biologically significant suggested by published literature [10]; cultivated, pasture/hay, grassland, water, forested, and development. For nest-site selection analysis, we generated random points using the Random Point Generator tool in ArcGIS 10.1 to simulate random nest sites. We clipped reclassified CDL layers to 3000-m buffers around each random and nest site using Geospatial Modeling Environment (Beyer 2012) and calculated land cover percentages for extrinsic variables using ArcGIS 10.1. We selected the 3000-m (ca. 28 km^2) buffer after Smith and Murphy (1973; [37]) and Kochert et al. (2002; [10]), which represented an estimated home range size for breeding golden eagles in the western United States and the northern Great Plains. To associate nest survival with landscape features we assessed distances of actual and simulated random nests from roads, farms, oil wells and water bodies using ArcGIS 10.1. All statistical tests were conducted using Program R [38] with an experiment-wide error rate of 0.05.

Nest Survival Analysis

From published literature and based on field observations, we selected 12 predictor variables, which included land cover metrics, nest characteristics (e.g., nest substrate, nest accessibility), and distance from landscape features as potential factors influencing nest survival (Table 1; Table 2). We used Pearson's correlation for evidence of multicollinerity and excluded covariates from the same model if $r \geq |0.7|$. Nests were considered successful when at least one young fledged; we used Program MARK [39] with the logit-link function to run nest survival models to evaluate effects of predictor variables. We created 12 biologically significant models using field observations and used Akaike's Information Criterion (AIC_c) corrected for small sample size to select models that best described the data [40]. We used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤4 ΔAIC_c different from the top model as competitive models [41]. Covariates of competing models were verified so that the β-estimates did not have 95% confidence intervals that encompassed zero [42–44].

Nest Site Selection

Nest Site Selection

To determine effects of landscape on nest-site selection, we used logistic regression and Akaike's Information Criterion (AIC). We generated an equal number of pseudo-absent points within our study area as total number of active nests identified from 2013–2015 in NWSD (35 random nest sites). Using our predictor variables, we created 11 *a priori* models from field observations and published literature (Table 4; [10, 19, 37]) to estimate the influence of those variables on nest-site selection (Table 1). We used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤4 $\Delta \mathrm{AIC}_c$ different from the top model as competitive models [41]. Receiver operating characteristic (ROC) values were used to test predictive capacities of significant models. We considered acceptable discrimination for ROC values between 0.7 and 0.8 and excellent discrimination between 0.8 and 1 [45]. We used an Odds-ratio test to evaluate the effect of variables on nest-site selection in the top-ranked model.

Results

We revisited 126 previously documented golden eagle occupied territories to confirm status during breeding seasons and also searched for any new nests independent of all previous information from 2013–2015. Of those 126 territories, the nest was absent in 59 locations and from 2013–2015 we found 4 new occupied territories, two of which had active nests in one or more of the breeding seasons during our study. We documented 35 active golden eagle nests from 2013–2015 (8 in 2013, 18 in 2014, and 9 in 2015), one nest every 1,740.4 km^2 for the entire duration of the study. Active nests were placed on two different substrates (i.e. steep cliff-side [$n = 5$] and trees [$n = 30$]). Mean egg-laying date was 18 March ± 11 days and no attempts of renesting were documented during the study. Apparent nest success was 100% in 2013, 67% in 2014, and 88% in 2015. During the 2013 breeding season, 8 active nests fledged 12 chicks (1.5 chicks/successful nest), 12 of 18 active nests fledged 16 chicks (1.3 chicks/successful nest) during 2014, and 8 of 9 active nests fledged successfully producing 13 fledglings (1.6 chicks/successful nest) in 2015; overall 41 chicks successfully fledged (1.4 chicks/successful nest; SE = 0.09). No nest abandonment occurred post-hatching. All nest failures were attributed to nest abandonment early in the season. In three such cases after continued incubation had ceased, birds were found occupying the territory for up to 13 days before the territory became unoccupied by at least one golden eagle. All fledglings from a current year survived at least until 1 August. A total of five carcasses of fledglings were found in the following years during surveys, in close vicinity to three different occupied nests that were active in the previous breeding season; causes of death remained undetermined.

Top-ranked nest survival model was S_{Null} ($w_i = 0.91$) suggesting that none of the predictor variables had any effect on survival and survival was constant between years (Table 3). Probability of nest survival during the study period was 0.76 (95% CI = 0.58–0.81). $S_{\%Grass+\%Development}$ was the second-ranked model and was 6.78 ΔAIC_c away from the top model, which therefore did not fit the criteria of a competitive model (i.e. ≤ 4 ΔAIC_c different).

Cottonwood was the sole tree of choice for nesting golden eagles in NWSD ($n = 30$) followed by steep cliff-side ($n = 5$). Average tree-nest height was 15.8 m (SE = 2.9); highest recorded nest was 18.2 m and the lowest recorded nest height was 10.9 m. All cliff nests were above 30 m and were placed on steep sides of limestone cliffs.

Development was the top-ranked model (w_i = 0.72) for predicting nest-site selection of golden eagles; predictive capability of the model was excellent (ROC = 0.92; Table 4). Logistic odds-ratio estimates from the top-ranked model indicated the odds of nest site selection were 0.87 (95% CI = 0.85–0.94) times less for every percent increase in development. The model containing grass, pasture, and development ranked second and was competitive (i.e., <4 ΔAIC_c away) with the top-ranked model. Logistic odds-ratio estimates from the second-ranked model indicated the odds of nest site selection were 1.10 (95% CI = 1.35–1.04) times greater for every percent increase in grass, 1.06 (0.88–1.19) times greater for every percent increase in pasture, and 0.91 (95% CI = 0.82–0.96) times less for every percent increase in development. All 95% confidence intervals for parameter estimates for development (β = –0.008, SE = 0.023) and grass (β = 0.66, SE = 0.28) across models did not overlap zero, indicating significant influence on golden eagle nest site selection. Although pasture/hay was included in the competitive model, logistic odds ratio (1.06, 95% CI = 0.88–1.19) did not differ from one, indicating no effect on nest-site selection.

Discussion

Our results suggest a decline in nesting golden eagle numbers in NWSD. Although we observed many territories occupied by golden eagles early on in the season, only a small portion of those territories became active during the breeding season. Pairs of golden eagles occupying a territory often refrain from laying eggs some years particularly when prey is scarce [10]. The intensely grazed monotypic pastureland, characteristic of NWSD may have fragmented golden eagle nesting habitat and negatively impacted available prey base. Continued conversion of native grasslands to areas with less structural and plant species diversity such as cropland agriculture [46–47] also may have enhanced further fragmentation of habitat. Lagomorphs, like jackrabbits (*Lepus spp.*) and rabbits (*Sylvilagus spp.*), population cycles also have major influence on golden eagle reproductive rates [9–10, 48–49] and may have influenced nesting in NWSD. Although golden eagles are well known to re-nest [10] when eggs fail to hatch, no renesting was observed during our study, which also may indicate low prey availability. Manifold decrease in nesting abundance (amount of area/nesting pair) in NWSD since 2005 (approximately one pair every 384 km^2 in 2005; [25–26]) also may indicate increased disturbance and degraded habitat in the area. Nesting abundance of golden eagles in NWSD is among the lowest in the western United States when compared to 28 km^2/pair in Denali National Park, AK, [49], 60 km^2/pair in Wyoming [50], 100–119 km^2/pair in Utah [51–52], 66 km^2/pair in south-western Idaho [53], 65–192 km^2/pair in Montana [54], and 252 km^2/pair in Nevada [55]. Although golden eagle nesting abundance in Hudson Bay, Canada was lower than in the western United States (i.e., 961 km^2/pair [56]), it was still greater than the abundance we documented in NWSD.

In south western Idaho, apparent nesting success was 61% in 1969, 70% in 1970, and 62% in 1971 [57], which also compared favorably with a stable population in eastern Scotland [58]. Nesting success ranged from 63 to 91% during a 6-year study in Montana [54]. Although apparent nesting success in NWSD was similar to these previous studies, breeding populations and nesting abundance in NWSD was lower. Lockie and Ratcliffe (1964; [59]) reported a 29% nesting success in a declining population in western Scotland; although our study in NWSD indicated a decline in golden eagle nesting numbers, it estimated a reproductive success comparable to other stable populations in the western United States. Long term (≥10 years) annual reproductive success (number of young reared to nest leaving/pair [10]) in Montana and Wyoming (0.78; [60]), in south-west Idaho (0.79; [61]), in Utah (0.82; [62]), in Oregon (1.08; [63]), in Alaska (0.66; [49]), and in Scotland (0.80; [64]) also were comparable to our study, although total productivity in NWSD was much lower pertaining to the low density nesting.

Golden eagles nested in low densities within the eastern year-round limit of the northern Great Plains. A high nest survival and fledging rate is therefore crucial for their population viability. Our study indicates that nesting densities of golden eagles have declined severely in the past decade. Although survival rates are similar, decline in nesting density may have severe potential impact on the breeding population of golden eagles at the eastern limits of their year-round range. Continued round the year monitoring of golden eagle populations as well as information on population level influences of factors like diseases (e.g., WNv; [65]; lead poisoning [10]), and food availability on fledgling survival over winter is therefore crucial and recommended to keep track of the population status in NWSD. In conjunction, long-term and comprehensive prey-base assessment also will inform wildlife managers of prey cycles and their relationship to golden eagle and other raptor nesting and will aid in habitat management decisions.

Golden eagles are versatile in nest placement (e.g. cliff-side, tree; [10]). Although the majority (69%) of historic nests in NWSD were on cliff-sides [25]; (assuming no inherent difference in detection probability between cliff-nests and tree nests), only 14% of active nests during 2013–2015 were found on cliffs. Heat stress is a major source of mortality in golden eagles [10, 66–67]. Cliff nests are exposed more to heat stress and with rise in global temperatures [68–69], avoidance of cliff nests by golden eagles may possibly be an adaptation in NWSD. Most cliff nests in NWSD were in public use areas (e.g., United States Forest Service, Custer National Forest), which also may have served as a source of ground based, anthropogenic disturbance. Fires are relatively common in these public use areas and mine related activities (i.e., Uranium mine clean up, Erionite hazards [70]) also may have affected golden eagle nesting. In contrast, most active tree nests were on privately-owned land with minimal ground based disturbance.

Our nest survival models failed to identify any extrinsic or intrinsic factors that influenced nest survival and survival was consistent between breeding seasons. Fledgling mortality from previous breeding seasons was documented; although cause-specific mortality was not determined. Although diseases like WNv were reported in raptors from the northern Great Plains [65] no conclusive evidence was collected during this study.

Percent development and percent grass had most influence on nest-site selection. Across the western United States, golden eagles prefer open habitats with native vegetation and avoid urban, agricultural, and forested areas [71–74]. Golden eagles are common in grazed areas and in patches of inaccessible mountainous country with primarily livestock ranches [75]. Development like human settlements, roads, energy development, and agriculture in NWSD had a negative impact on nest-site selection and golden eagles selected areas away from development. Grass was positively associated with nest-site selection and possibly provided good foraging areas away from disturbance. As a top consumer in the ecosystem, golden eagles have a relatively small predation pressure, but food resources, human disturbance, and adverse climate may have impacted the fecundity of golden eagles [49, 76–78]. Our results indicate selection of grass dominated regions and avoidance of developed areas for nest site selection by golden eagles in NWSD.

Conclusion

Our golden eagle reproductive ecology study revisited areas in NWSD where former aerial surveys documented nesting golden eagles in 2005 and 2011. Golden eagle nesting has declined approximately 75% in the past decade in NWSD. Our results show avoidance of developed areas by golden eagles and a reduction in use of cliff nests. Although nest survival probabilities from our study were comparable between other studies in the western United States, nesting abundance in NWSD was considerably lower, which implies lower productivity. Overall decline in golden eagle nesting may be attributed to increased disturbance and low prey availability and although a speculation, possibly due to rise in average temperatures, which may potentially increase heat stress in nestlings. Extrinsic and intrinsic factors did not influence nest survival in our study, but to specifically identify factors influencing nest survival in golden eagles is difficult, especially on a broad geographic scale [18]. Assessing year round survival rates of golden eagles and documenting cause-specific mortality will be a crucial next step when managing golden eagle populations in NWSD. Assessing prey abundance and documenting trends in prey fluctuations with respect to golden eagle nesting densities also will be an imperative for species management and taking actions for their effective conservation. We suggest that objective research and management (e.g., year-round survival assessment, prey-base monitoring, targeted control of disturbance, and long-term monitoring of the population) would aid in recovery of the species at the eastern limit of its year-round range.

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Figure 1. Golden eagle reproductive ecology study area in north-western South Dakota, USA.

Golden eagle (*Aquilla chrysaetos*) study area in Harding, Perkins and Butte counties (dark grey) in north-western South Dakota, USA, 2013–2015.

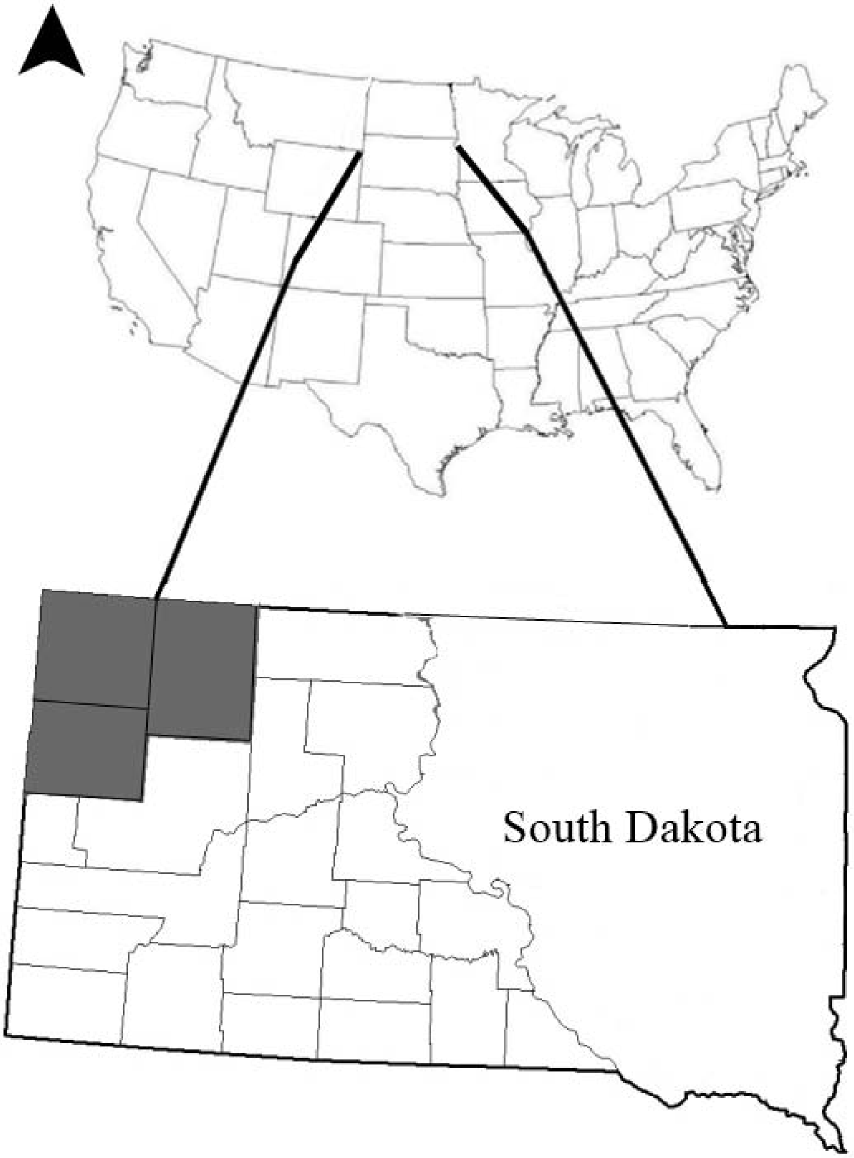

Table 1. Predictor variables within 3000-m buffers of active and random nest sites used to model the influence of landscape on golden eagle nest survival and nest-site selection in north western South Dakota, USA, 2013–2015.

Variable Name	**Definition**
Cultivated	Total area under row and grain crop (%)
Grass	Total grass cover (%)
Pasture/hay	Total pasture and alfalfa/grass hay cover (%)
Water	Total wetland cover (%)
Forest	Total tree cover (%)
Development	Total farm sites (%)
Distance to homestead*	Distance to nearest homestead (m)
Distance to road*	Distance to nearest road (m)
Distance to oil well*	Distance to nearest oil well (m)
Year*	Year of observation
Nest substrate*	Cliff vs. tree nest
Nest accessibility*	Easy vs. difficult

* Excluded from nest site selection analysis

Table 2. Mean and standard error (SE) for land cover and distance to landscape features for golden eagle nests in northern western South Dakota, USA, 2013–2015.

Variable Name	North western South Dakota (NWSD) (n = 35)	
	$\bar{x}$	SE
Cultivated (%)	3.18	2.05
Grass (%)	61.14	11.72
Pasture/Hay (%)	27.44	9.38
Water (%)	4.36	2.24
Forest (%)	2.73	0.89
Development (%)	1.13	0.35
Distance to homestead (m)	1908.31	422.54
Distance to road (m)	1261.17	186.36
Distance to oil well (m)	2105.29	569.84

Table 3. Nest survival models of golden eagle during the 2013–2015 breeding season in north western South Dakota, USA.

Model	AIC_c[a]	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
S_{Null}	765.43	0.00	0.91	1	753.11
$S_{\text{\%Grass+\%Development}}$	772.22	6.78	0.06	3	752.89
$S_{\text{\%Grass+\%Pasture/hay+\%Development}}$	773.85	8.42	0.03	4	755.63
$S_{\text{\%Development+\%Forest}}$	775.10	9.67	0.01	3	756.05
$S_{\text{\%Cultivated+\%Development}}$	776.66	11.23	0.00	3	753.54
$S_{\text{\%Cultivated+\%Forest+Year}}$	777.17	11.74	0.00	4	753.38
S_{Year}	779.29	13.86	0.00	2	759.81
$S_{\text{Saturated}}$	781.24	15.81	0.00	13	761.06
$S_{\text{\%Water+\%Grass+\%Development}}$	783.75	18.32	0.00	4	758.21
$S_{\text{Year+\%Development}}$	784.87	19.44	0.00	3	757.32
$S_{\text{\%Forest+\%Grass+\%Development+Year}}$	786.42	20.99	0.00	5	756.25
$S_{\text{\%Cultivated+\%Development+Year}}$	788.14	22.71	0.00	4	755.76
$S_{\text{\%Development}}$	789.95	24.52	0.00	2	754.55

[a] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).
[b] Difference in AICc relative to min. AIC.
[c] Akaike wt (Burnham and Anderson 2002).
[d] Number of parameters.

Table 6. Akaike's Infromation Criterion (AIC) model selection of logistic regression models for nest-site selection of golden eagle in north western South Dakota, USA, 2013–2015.

Model Covariates	*K*	AIC	ΔAIC	w_i	ROC[d]
Development	2	487.77	0.00	0.72	0.92
Grass + Pasture + Development	4	489.89	2.12	0.23	0.88
Cultivated + Forest	3	491.73	3.96	0.04	0.87
Development + Forest	3	493.72	5.95	0.01	0.74
Forest	2	495.08	7.31	0.00	0.81
Development + Cultivated	3	498.18	10.41	0.00	0.79
Null	1	502.93	15.16	0.00	0.66
Water + Pasture/hay + Cultivated + Development	5	504.49	16.72	0.00	0.71
Water + Development	3	508.19	20.42	0.00	0.73
Grass + Forest	3	511.58	23.81	0.00	0.77

[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 3: RAPTORS IN TEMPERATE GRASSLANDS: AGRARIAN LAND-USE AND BREEDING NORTHERN HARRIERS (*Circus cyaneus*) IN THE PRAIRIE POTHOLE REGION OF THE NORTHERN GREAT PLAINS

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CHAPTER 3: RAPTORS IN TEMPERATE GRASSLANDS: AGRARIAN LAND-USE AND BREEDING NORTHERN HARRIERS (*Circus cyaneus*) IN THE PRAIRIE POTHOLE REGION OF THE NORTHERN GREAT PLAINS

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ABSTRACT

Northern harriers (*Circus cyaneus*) prefer relatively open grasslands and various types of wetlands. Although cropland and fallow fields are used for nesting, most nests across studies in the northern prairies were found in undisturbed wetlands or grasslands dominated by thick vegetation. During the breeding season from 2013–2014, we investigated influence of factors associated with an agrarian landscape on survival and nest-site selection of northern harriers in south central North Dakota. Using ground-based surveys, we located and monitored active northern harrier nests: a total of 22 for the duration of the study. During our study, one breeding pair of northern harriers was found every 370.6 km^2. Most northern harrier nests were in seasonal or permanent wetlands with cordgrass (*Spartina* spp; n = 12), bulrush (*Scirpus* spp.; n = 6), cattail (*Typha* spp.; n = 3), and residual corn (*Zea mays*; n = 1). Apparent nest success was 25% in 2013, and 70% in 2014. During the 2013 breeding season, 3 of 12 active nests fledged 7 chicks (2.3 chicks/successful nest). During 2014, 7 of 10 active nests fledged 22 chicks (3.1 chicks/successful nest); overall, 29 (2.9 chicks/successful nest) nestlings fledged in our study area. We used Program MARK to evaluate the influence of land cover on nest success. The top-ranked nest survival model was S_{Year} ($w_i = 0.65$) suggesting survival was different between the 2013 and 2014 breeding seasons. $S_{\%Grass+\%Water+Year}$ model (w_i = 0.23; ≤4 ΔAIC_c away) also was competitive indicating a positive relationship of nests with %grass and % water in the landscape. Estimated nest survival for northern harriers in 2013 was 0.21 (95% CI = 0.22–0.55), and in 2014 was 0.49 (95% CI = 0.32–0.61). We used logistic regression analysis to evaluate the influence of landscape variables on nest site selection. Grass, pasture, and water ranked as the top model for northern harriers (w_i

= 0.87). Logistic odds-ratio estimates from the top-ranked model for northern harrier indicated the odds of nest site selection were 1.48 (95% CI = 1.27–1.58) times greater for every percent increase in grasslands, and 1.2 (95% CI = 1.06–1.31) times greater for every percent increase in water; logistic odds ratio for percent pasture indicated no effect at 900-m scale (1.06, 95% CI = 0.98–1.14). Our results indicate that northern harrier in south-central North Dakota nests at low densities. Further, wetland decline, and extensive conversion of grass and pasture into croplands may have negatively influenced northern harrier populations in our study area. Increased ground-based disturbance (e.g. agricultural activities) also may have influenced nesting of northern harrier in south-central North Dakota. Our findings indicate a need to manage pasture and grasslands in areas suitable for northern harrier nesting and control the loss of wetlands in the prairie pothole region to support northern harrier and all grassland nesting species and to facilitate recovery and persistence of this species at the southern edge of its breeding range.

Northern harriers (*Circus cyaneus*) prefer relatively open grasslands and wetland areas of various natures (Apfelbaum and Seelbach 1983, Bildstein 1988 Herkert et al. 1999). They nest in open wetlands, including marshy meadows; wet, lightly grazed pastures, old fields, freshwater and brackish marshes, and tundra (Smith et al. 2011). In the northern Great Plains, northern harriers prefer relatively open habitats characterized by tall, dense vegetation, and abundant residual vegetation (Duebbert and Lokemoen 1977, Hamerstrom and Kopeny 1981, Apfelbaum and Seelbach 1983, Kantrud and Higgins 1992). They also are known to use native or tame vegetation in wet or dry grasslands, fresh to alkali wetlands, lightly grazed pastures, croplands, fallow fields, old fields, and brushy areas (Stewart and Kantrud 1965, Stewart 1975, Linner 1980, Evans 1982, Apfelbaum and Seelbach 1983, Faanes 1983, Kantrud and Higgins 1992, Dhol et al. 1994, Prescott et al. 1995, MacWhirter and Bildstein 1996, Prescott 1997). Although cropland and fallow fields are used for nesting, most nests are found in undisturbed wetlands or grasslands dominated by thick vegetation (Duebbert and Lokemoen 1977, Apfelbaum and Seelbach 1983, Kantrud and Higgins 1992). Nest success of northern harriers was found to be lower in cropland and fallow fields than in undisturbed grasslands (Kibbe 1975). Ground nests of northern harriers are well-concealed by tall, dense vegetation, including living and residual grasses and forbs, or low shrubs, and are located in undisturbed areas with much residual cover (Hecht 1951, Duebbert and Lokemoen 1977, Hamerstrom and Kopeny 1981, Kantrud and Higgins 1992, Herkert et al. 1999). In the northern Great Plains, few nests were found in croplands or in areas where litter cover was <12% of total cover; areas with >40% residual cover were commonly used (Kantrud and Higgins 1992).

Free-ranging animals are systematically distributed across spatial and temporal scales and thus, various characteristics of the occupied landscape can affect components of their survival and fitness (Danchin et al. 1998, unpublished Datta et al. 2016). Reproductive success in birds may be influenced by a multitude of factors including composition and configuration of the surrounding landscape (Rodewald 2002, Inselman et al. 2015), interference emanating from natural and anthropogenic sources (Rota et al. 2014, Beale and Monaghan 2004), nest substrate and placement (Roth and Marzluff 1989), environmental conditions (Drietz et al. 2012), resource availability (Steenhoff et al 1997), and community interaction (Chalfoun et al. 2002).

Northern harriers, although fairly common throughout the United States (US Department of Agriculture 2003), is a Species of Conservation Priority in North Dakota (Level II; Hagen et al., 2005). Northern harriers are fairly common in North Dakota, but populations are unstable due to loss of grassland and wetland habitat (Hagen et al. 2005) and density of northern harriers is sensitive to habitat patch size (Ribic et al. 2009). Northern harriers have been documented to avoid breeding if woody cover exceeds 30% in northern Great Plains grasslands, and loss or increased fragmentation of available habitat may impact breeding success of the species (Winter et al. 2006). Northern harriers also have been identified as species of national management concern by the U.S. Fish and Wildlife Service because of its dependence on rare and vulnerable habitats (U.S. Fish and Wildlife Service 1995). Because of the rarity of this species in the northern Great Plains and the United States' Midwest, little is known about their response to grassland management in the region, especially from the southern portion of their breeding ranges where populations are most sparse.

We examined nest survival, reproductive parameters, and nest-site selection of northern harrier at the landscape level in the short- and mixed-grass prairies and Prairie Pothole Region of the northern Great Plains that represents the southern edge of their breeding distribution in North America. With extensive conversion of grasslands into row crops in the Prairie Pothole Region in the past few decades and approximately 60% of land used for agriculture, we hypothesized that nest survival of northern harrier would be influenced by extrinsic factors like percent cultivated land, percent development, and percent grass. We also predicted that northern harrier would select for areas with higher percentages of wetlands, grass, and pasture, over agriculture dominated landscapes for nesting, and would avoid areas with higher percentages of development.

MATERIALS AND METHODS

Study Area– Our study was conducted between 2013 and 2014, in McIntosh, Dickey, and Logan counties in North Dakota (Fig. 1). It encompassed approximately 8,153 km^2 in the Missouri Coteau Physiographic Region (Bryce et al. 1998). Elevation ranged from 579–685 m above mean sea level, throughout the study area. Numerous lakes and prairie potholes (>100 basins/2.59 km^2) were present and most of them were intermittently wet and dry. Land use in the three counties consisted of cultivated land (58.5%), grassland (17.4%), and development (13.7%), with the remaining land constituting forested cover (3.6%) and wetlands (6.8%; USDA 2015). 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 from May to September (North Dakota State Climate Office 2012). Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern reedgrass (*Calamgrostis 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*; Duebbert and Lokemoen 1977, Johnson and Larson 2007). In 1983, south-central North Dakota comprised 36.1% pasture, 21.6% hayland/alfalfa, and 36.7% cultivated crops (Gilmer and Stewart 1983). However, approximately 60% of the study area currently is used for agriculture currently.

Nest Monitoring– During the 2013–2014 breeding seasons, we searched for active northern harrier nests beginning 1 April. To locate nests, we systematically drove all accessible roads in each county and surveyed area inaccessible to vehicles on foot. We spotted northern harriers in flight and often spotted mid-air food exchanges between male and female northern harrier, which facilitated determining paired northern harriers in territories. We considered territories to be occupied when evidence of nesting behavior (e.g., carrying nesting material, mating behavior, food provisioning) was observed. Once paired birds were confirmed in an area we continued monitoring occupied territories until signs of nest presence were confirmed. We marked nest sites using a GPS, and searched to locate nests after prey deliveries to nests were consistent and confirmed (i.e., suggesting nestling presence, or presence of incubating female). Nests were considered active when evidence of prolonged incubation and food provisioning was confirmed. All active nest site locations were recorded using a handheld Garmin Global Positioning System (GPS; Garmin Ltd.) unit and ArcGIS 10.1 was used to plot locations (ESRI

2011). We monitored nests at least once every week from access roads or vantage points (distance ≤ 200 m) to determine continued territory occupancy. After confirming possible nestling presence in a nest, we accessed nests ensuring minimal impact on the nest. We accessed nests ≤ 3 times during the breeding season and spent ≤ 15 minutes at each nest to collect nesting information, install cameras at the nest, or change memory cards of installed cameras. At each nest, we recorded the number of eggs, or nestlings, nest substrate, micro-habitat characteristics (e.g., nesting vegetation species, vegetation height). Young were considered successfully fledged when installed cameras suggested no nestling presence at the nest, and food delivery at nests by adults ceased. We calculated nesting densities of breeding northern harriers within our study area, i.e., 8,153 km^2 and represented abundance as pairs/km^2.

Our nest monitoring protocol followed established guidelines (Fyfe and Olendorff 1976), all animal handling methods followed guidelines approved by The Ornithological Council (Oring 1999), 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 North Dakota Game and Fish (License # GNF03312634), and the United States Fish and Wildlife Service (Permit # 21408). Individual landowners granted permission to access nests for data collection. All data collected on public land was conducted with permission from 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; USDA 2015) to evaluate land cover components at nest sites. We reclassified the CDL layers from 2013 and 2014 for the study area to represent the land cover variables that were biologically significant (McConnell et al. 2008); cultivated, pasture/hay, grassland, water, forested, and development. For logistic regression analysis, we generated random points using the Random Point Generator tool in ArcGIS 10.1 to simulate random nest sites. We clipped reclassified CDL layers to 900-m buffers around each random and nest site using Geospatial Modeling Environment (Beyer 2012) and calculated land cover percentages for extrinsic variables using ArcGIS 10.1. We selected the 900-m (ca. 2.6 km$^{2;}$ after Smith and Murphy 1973, Rees 1976, Toland 1985, Martin 1987, Serrentino 1987) buffer, which represented the estimated median home range size for breeding northern harrier from eight studies (Smith et al. 2011) in the United States and Canada. To associate nest survival with landscape features, we assessed distances of actual and simulated random nests from roads, farms, and water bodies using ArcGIS 10.1. All statistical tests were conducted using Program R (R Development Core Team 2009) with an experiment-wide error rate of 0.05.

Nest Survival Analysis– From published literature and based on field observations, we determined nine predictors, which included land cover variables, nest characteristics (e.g., nest substrate), and distance from landscape features as potential factors influencing nest survival (Table 1; Table 2). We used Pearson's correlation for evidence of multicollinerity and excluded covariates from the same model if $r \geq |0.7|$. Nests were considered successful when at least one young fledged; we used Program MARK (White and Burnham 1999) with the logit-link function to run nest survival models to evaluate effects of predictor variables. We created 12 biologically significant models (Table 3) and 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 used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤ 4 ΔAIC_c from the top model as competitive models (Neter et al. 1996). Covariates of competing models were verified so that the β-estimates did not have 95% confidence intervals that encompassed zero (Neter et al. 1996, Barber-Meyer et al 2008, Grovenburg et al. 2012). Because there is no goodness-of-fit test for nest survival models currently available, model robustness was assessed 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; (Devries et al. 2003, Barber-Meyer et al 2008).

Nest Site Selection– To determine effects of landscape on nest-site selection, we used logistic regression and Akaike's Information Criterion (AIC). We generated an equal number of pseudo-absent points as total number of active nests identified from 2013–2014 (22 random nest sites). Using our predictor variables we created 10 *a priori* models from field observations and published literature (Table 4; Duebbert and Lokemeon 1977) to estimate the influence of those variables on nest-site selection (Table 1). We used Akaike weights (w_i) as an indication for support for our models and considered models that were ≤ 4 ΔAIC_c from the top model as competitive models (Richards 2005). Receiver operating characteristic (ROC) values were used to test predictive capacities of significant models. We followed guidelines (Hosmer et al. 2013) 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 on nest-site selection in the top-ranked model.

RESULTS

During breeding seasons of 2013 and 2014, we located 22 active northern harrier nests (12 in 2013, and 10 in 2014), i.e., one breeding pair in 370.6 km^2. Mean date when first pairs were observed was 10 April ±4 days. Apparent nest success was 25% in 2013, and 70% in 2014. During the 2013 breeding season, 3 of 12 active nests fledged 7 chicks (2.3 chicks/successful nest). During 2014, 7 of 10 active nests fledged 22 chicks (3.1 chicks/successful nest); overall, 2.9 chicks/successful nest (*n* = 29) fledged nestlings in our study area. Primary reason for nest failures were predation (2013 – *n* = 3; 2014 – *n* = 1) and nest abandonment (2013 – *n* = 3; 2014 – *n* = 2). No nest abandonment occurred post-hatching. Primary cause of fledgling death was predation (53%; *n* = 8) followed by starvation (20%; *n* = 3), and unknown (27%; *n* = 4).

Percent cultivated and percent grassland were negatively correlated ($r = –0.71$) in our study area. Therefore, nest survival models did not include both variables. The top-ranked nest survival model was S_{Year} ($w_i = 0.65$) suggesting survival differed between 2013 and 2014 (Table 3). The 95% confidence intervals of the β estimate for the S_{Year} model (0.92, 95% CI = 0.64–1.96) did not encompass zero, indicating a significant effect of year. We also considered the $S_{\%Grass+\%Water+Year}$ model ($w_i = 0.23$) as competitive. This model was 1.5 ΔAICc from the top-ranked model and the 95% confidence intervals of the β estimates for %Grass (0.23, 95% CI = 0.06–0.39), %Water (0.21, 95% CI = 0.002–0.280), and Year (0.54, 95% CI = 0.03–0.81) did not encompass zero and indicated positive association to both %Grass and %Water. Estimated nest survival for northern harriers in 2013 was 0.27 (95% CI = 0.22–0.55), and in 2014 it was 0.49 (95% CI = 0.32–0.61). Remaining models were ≥4 ΔAIC_c from the top model and were not competitive. Interpretation of our top model (S_{Year}) remained the same when adjusting ĉ from 1.0 to 3.0 to test for over dispersion; when ĉ = 2.0 (moderate dispersion; QAIC_c wt = 0.73) and through ĉ = 3.0 (extreme dispersion; QAIC_c wt = 0.39).

Most northern harrier nests were in seasonal or permanent wetlands with cordgrass (*Spartina* spp; *n* = 12), bulrush (*Scirpus* spp.; *n* = 6), cattail (*Typha* spp.; *n* = 3), and residual corn (*Zea Mays*; *n* = 1). Land-use around most nests was idle pastures or grasslands. Average height of vegetation surrounding a nest in a 315 m^2 i.e. 10 m radius was 1.79 m (SE = 0.61) and tallest recorded vegetation was 1.86 m (*Typha* spp.)

Grass, pasture, and water ranked as the top model for northern harrier nest-site selection (w_i = 0.87). Logistic odds-ratio estimates from the top-ranked model for northern harrier indicated the odds of nest site selection were 1.48 (95% CI = 1.27–1.58) times greater for every percent increase in grasslands, and 1.2 (95% CI = 1.06–1.31) times greater for every percent increase in water; logistic odds ratio for percent pasture indicated no effect at the 900-m scale (1.06, 95% CI = 0.98–1.14).

DISCUSSION

Breeding grassland bird populations are closely associated with plant communities that provide nesting and foraging habitats for successful reproduction (Lack 1933, Beecher 1942, Weller and Spatcher 1965). Northern harriers in the northern Great Plains had used lightly to moderately grazed grasslands (Kantrud and Kologiski 1982, Bock et al. 1993) but avoided heavily grazed habitats (Stewart 1975, Berkey et al. 1993, Bock et al. 1993). In congruence with our study, previous studies also have indicated that northern harriers traditionally nest in tall, coarse wet-meadow or marsh vegetation such as cordgrass (*Spartina* spp.), white-top grass (*Scolochloa festucacea*) , cattail (*Typha* spp.) , bulrush (*Scirpus* spp.), or common reed (*Phragmites communis*; Duebbert and Lokemoen 1977). Our study indicated that grass cover and wetlands influenced northern harrier nest selection in south-central North Dakota. In the aspen parklands of Alberta, northern harriers were most abundant in deferred grazed (grazed after 15 July) mixed-grass, but were absent from continuously grazed mixed-grass and deferred or continuously grazed tame pasture (Prescott et al. 1995). This indicates that management of grazing in pastures may facilitate northern harrier nesting and might support their nest survival.

Nest success of northern harriers across studies conducted in the short-and-mixed-grass prairies of the United States and Canada range widely (18%–79%; Breckenridge 1935, Hammond and Henry 1949, Craighead and Craighead 1956, Sealy 1967, Hamerstrom 1969, Follen 1975, Duebbert and Lokemoen 1977, Thompson-Hanson 1984, Hamerstrom et al. 1985, Toland 1986, Simmons et al. 1986, 1987, Sutherland 1987, Serrentino 1987, Kantrud and Higgins 1992). More recently, nesting success on reclaimed mine grasslands was only 23.8% (10 of 42 nests; Vukovich and Ritchison 2006). Nest survival from our study was low when compared to previous studies and northern harriers nested at low densities in our study area. Because northern harriers in the northern Great Plains nest in low-densities, high nest survival and fledging rates are crucial for their population viability in the region. Although survival rates in our study area were similar to previous studies, low nesting density in south-central North Dakota may have potential impacts on the breeding population of northern harriers at the southern limits of their breeding range.

Annual reproductive success (mean number of offspring fledged/pair) from previous studies of all nests and of successful nests averaged 1.8 and 3.1, respectively (Smith et al. 2011), which also was comparable to our results. Ground moisture and vegetation had a significant effect on nest success (proportion of clutches yielding ≥1 fledgling), as shown by previous studies, whereas visibility played no role (Smith et al. 2011). Wet sites were significantly more successful than dry sites because of reduced predation (Simmons and Smith 1985, Thompson-Hanson 1984). Although our study had a small sample size, most nests in our study area were associated with wetlands.

In New Brunswick, Canada, and the northern Great Plains, predation and nest abandonment were responsible for most egg loss, and starvation was responsible for most nestling loss (Simmons et al. 1986a, Sutherland 1987, Kantrud and Higgins 1992). In North Dakota (Sutherland 1987) and New Brunswick (Simmons et al. 1986), about 10% of clutches were abandoned by both parents. Elsewhere in New Brunswick, abandonment accounted for 29% of 31 nest failures (Simmons et al. 1986a), which also was comparable to our study.

As a ground nesting raptor, northern harriers can utilize various types of open grasslands, but is sensitive to disturbance (e.g., agriculture, over-grazing; Smith et al. 2011) and vulnerable to increased predation from mesopredators (Smith et al. 2011). In more fragmented south-central North Dakota, northern harriers are coping with increased anthropogenic disturbance (e.g., conversion of grassland to row crop, expansion of energy extraction activities, human settlement) and possibly a subsequent increase in mesopredator population (Crooks and Soule 1999).

Percent grass, and percent water most influenced nest site selection of northern harriers in our study area. As a grassland obligate nesting raptor their nests have been associated with a high percentage of grasslands (Kantrud and Higgins 1992, Smith et al. 2011). Grasslands in our study site have declined from ca. 60% to ca. 20% in the last four decades (Duebbert and Lokemoen 1977, Gilmer and Stewart 1983). Most of this general decline in grassland and pasture may be attributed to conversion of pasture and grassland to row crop agriculture (Fargione et al. 2009, Wright and Wimberly 2013). Grassland and pasture possibly provide good foraging habitat under relatively low ground based disturbance and northern harriers, possibly avoid areas with higher levels of disturbance (e.g., cropland and farming operations; Smith et al 2011). The increase in cropland and farming activity and resultant decline in wetlands is likely a source of disturbance at northern harrier nest sites and loss of grassland and pasture are directly and negatively correlated with this increased land conversion; the low density nesting of northern harriers also may be attributed to this general habitat loss in the region.

CONCLUSION

Significant changes in land-use have occurred in our study area over the last few decades. Increased conversion of grassland and pastures to row crop agriculture in south-central North Dakota may have impacted nesting habitat for northern harrier; however, nest survival and productivity have remained similar to previous studies in the prairies of North America and Canada. Northern harriers selected for nest sites with higher percentages of grass and wetlands in our study area. This study documented the response of northern harriers during a time of rapid expansion in agriculture. Our results show association of northern harriers to grasslands and wetlands in a landscape modified extensively from grassland prairies to row crop agriculture in the northern Great Plains. We suggest that specific need-based research (e.g., prey interaction, epidemiology) and management (e.g., returning less productive land strategically to grassland or pasture, returning wetlands from low productive agriculture, and long-term monitoring of populations in breeding and wintering grounds) would aid recovery of the species at the southern limits of its breeding range.

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Figure 1. Reproductive ecology of Northern harrier (*Circus cyaneus*) in south-central North Dakota, USA.

Northern harrier (*Circus cyaneus*) study area in Logan, McIntosh, and Dickey counties (light grey) in south-central North Dakota, USA, 2013–2014.

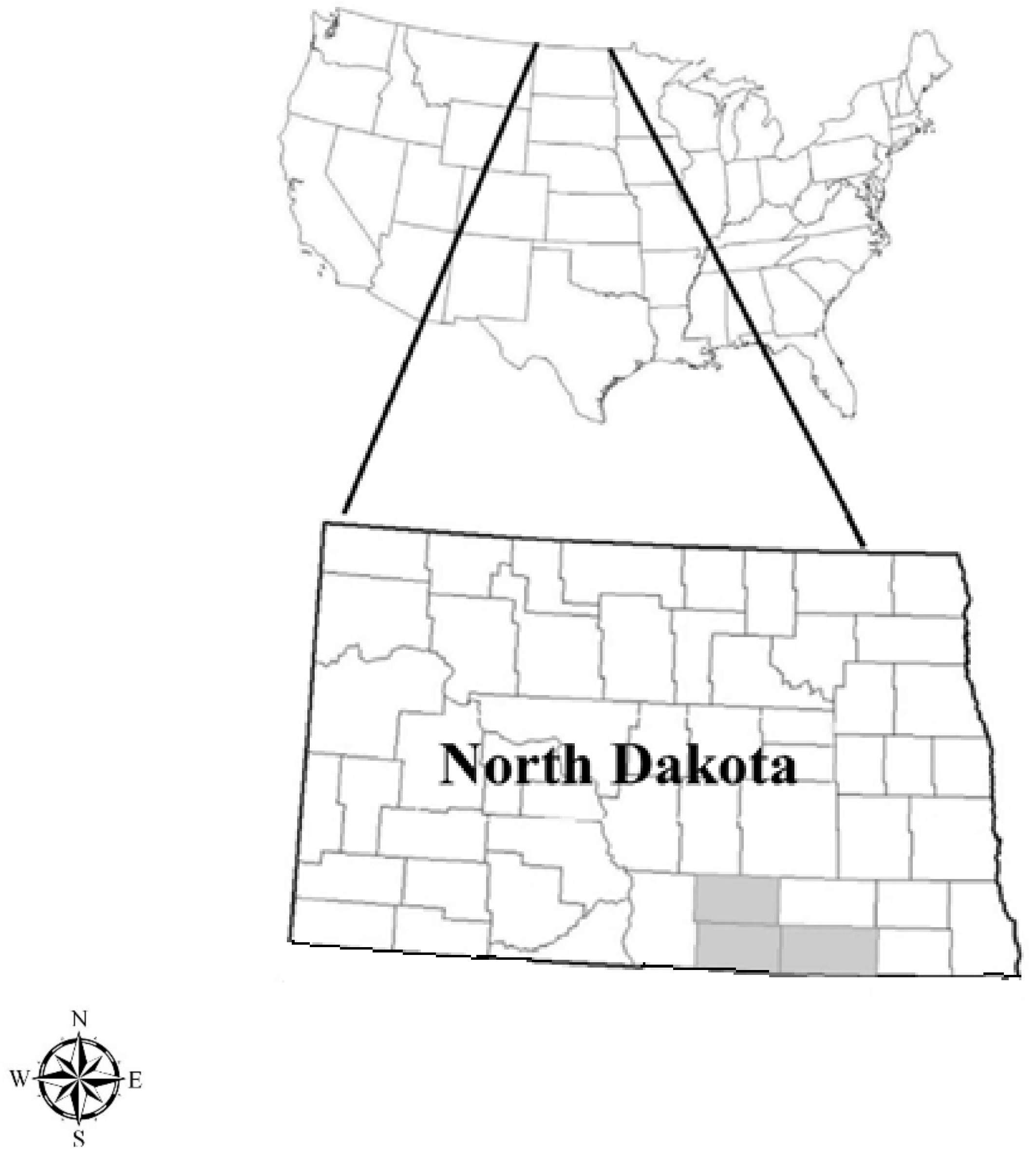

Table 1. Predictor variables within 900-m buffers of active and random nest sites used to model the influence of landscape on northern harrier nest survival and nest-site selection in the northern Great Plains, USA, 2013–2015.

Variable Name	**Definition**
Cultivated	Total area under row and grain crop (%)
Grass	Total grass cover (%)
Pasture/hay	Total pasture and alfalfa/grass hay cover (%)
Water	Total wetland cover (%)
Forest	Total tree cover (%)
Development	Total farm sites (%)
Distance to homestead*	Distance to nearest homestead (m)
Distance to road*	Distance to nearest road (m)
Year*	Year of observation

* Excluded from nest site selection analysis

Table 2. Mean and standard error (SE) for land cover and distance to landscape features for northern harrier nests in northern Great Plains, USA, 2013–2014.

Variable Name	South-central North Dakota (N = 22)	
	$\bar{x}$	SE
Cultivated (%)	21.19	5.51
Grass (%)	48.91	7.62
Pasture/Hay (%)	12.71	4.56
Water (%)	11.18	4.11
Forest (%)	3.78	1.17
Development (%)	2.23	0.71
Distance to homestead (m)	871.45	178.13
Distance to road (m)	521.11	41.81

Table 3. Nest survival models of Northern harrier during the 2013–2014 breeding season in south-central North Dakota, USA.

Model	AIC_c[a]	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
S_{Year}	298.48	0.00	**0.65**	2	296.64
$S_{\text{\%Grass +\%Water +Year}}$	299.99	1.51	0.23	4	295.58
$S_{\text{\%Grass+\%Water +DistancetoRoad}}$	302.92	4.43	0.09	4	296.09
S_{Null}	303.23	4.75	0.02	1	295.03
$S_{\text{\%Development+\%Cultivated}}$	304.54	6.07	0.01	3	297.31
$S_{\text{\%Development}}$	306.94	8.46	0.00	2	295.44
$S_{\text{\%Grass+\%Water}}$	307.97	9.49	0.00	3	296.46
$S_{\text{\%Water}}$	310.46	11.98	0.00	2	296.13
$S_{\text{\%Development+Year}}$	312.01	13.53	0.00	3	293.66
$S_{\text{Year+\%Water+\%Cultivated}}$	314.89	16.41	0.00	4	294.41
$S_{\text{\%Development+Year+\%Grass+\%Water}}$	315.22	16.74	0.00	5	297.24
$S_{\text{Saturated}}$	318.09	19.61	0.00	10	295.62

[a] Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002).
[b] Difference in AICc relative to min. AIC.
[c] Akaike wt (Burnham and Anderson 2002).
[d] Number of parameters.

Table 4. Akaike's Infromation Criterion (AIC) model selection of logistic regression models for nest-site selection of northern harriers in south-central North Dakota, USA, 2013–2014.

Model Covariates	*K*	AIC	ΔAIC	w_i	ROC[d]
Grass + Pasture + Water	4	323.94	0.00	0.87	0.95
Grass + Pasture	3	326.28	2.34	0.11	0.90
Pasture + Water	3	327.85	3.91	0.02	0.84
Water + Grass	3	330.07	6.13	0.00	0.75
Grass + Development + Water	4	333.41	8.66	0.00	0.82
Water	2	334.09	10.15	0.00	0.81
Grass	2	337.08	13.14	0.00	0.72
Null	1	339.05	15.11	0.00	0.74
Grass + Development	3	344.51	20.57	0.00	0.70
Grass + Pasture/hay + Development + Water + Forest	6	346.74	22.80	0.00	0.72

[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 4: DIET COMPOSITION AND PROVISIONING OF FERRUGINOUS HAWK NESTLINGS IN AGRICULTURAL AND GRAZING-BASED LANDSCAPES IN THE NORTHERN GREAT PLAINS

This chapter was prepared for submission to the Journal of Field Ornithology and was coauthored by Jonathan A. Jenks, Kent C. Jensen, Will Inselman, Robert W. Klaver, and Troy W. Grovenburg

CHAPTER 4: DIET COMPOSITION AND PROVISIONING OF FERRUGINOUS HAWK NESTLINGS IN AGRICULTURAL AND GRAZING-BASED LANDSCAPES IN THE NORTHERN GREAT PLAINS

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ABSTRACT

Ferruginous Hawk is a highly stenophagous species, feeding on a limited variety of prey. As grassland obligate species it prefers open areas for foraging and its choice of prey varies by location and availability of major prey. We collected diet composition and prey delivery data at 15 Ferruginous Hawk nests in primarily agriculture-based north-central South Dakota and south-central North Dakota, hereafter eastern Dakota (ED), and 14 Ferruginous Hawk nests in primarily grazing-based north-western South Dakota, hereafter western Dakota (WD), during 2013–2015 breeding seasons. Using time-lapse photography we recorded 6,872 hrs ($\bar{x}$ = 237 ± 39 hrs/nest) of daylight video footage (3,423 hrs in ED [$\bar{x}$ = 228 ± 31 hrs/nest]; 3,449 hrs in WD [$\bar{x}$ = 246 ± 34 hrs/nest]) and documented 3,187 prey deliveries. Of the prey species delivered, rodents dominated Ferruginous Hawk diets, comprising 77.3% in ED and 70.7% in WD. Rodents also accounted for 88.7% and 46.8% of the biomass is ED and WD respectively; lagomorphs constituted about 39.5% of prey biomass in WD. Deliveries/nestling/day differed (P = 0.02) among brood sizes in ED, and similarly in WD (P = 0.03); prey deliveries/nestling/day decreased with increasing brood size in both study areas. Ferruginous hawks did not differ in terms of deliveries/hr (P = 0.31) in ED or in WD (P = 0.36); deliveries/nestling/hr also remained constant in ED (P = 0.81) and WD (P = 0.72). Estimates of biomass i.e. grams/nestling/day also remained constant throughout the nestling growth period in both ED and WD. In ED grams/hr (P = 0.38) and grams/nestling/hr (P = 0.13) did not differ among 5-day period intervals and likewise, in WD (grams/hr [P = 0.29] and grams/nestling/hr [P = 0.17]). We did observe an increase in biomass delivered/nestling/day to nest sites at early age stages of nestling growth and

delivery peaked at 22–26 days of age; although the observation seems biologically significant there was no statistical support to it (*P* = 0.12). Ferruginous Hawks in ED had a lower measure of diet richness per nest (6.6 ± 0.4) than Ferruginous hawks in WD (8.2 ± 0.6; *P* = 0.041), but diet breadth did not differ between ED (*FT* = 0.69) and WD (*P* = 0.28). Overall, Ferruginous hawks used only a few major species for nestling provisioning. Our results suggest that Ferruginous Hawks in the northern Great Plains are dependent primarily upon grassland prey species. Management of prey-base for Ferruginous hawk should therefore be a primary concern when making decisions for conservation and management of this grassland obligate raptor.

Study of food habits in animals is fundamental when considering management of a species and its population (Errington 1935). Among altricial birds, provisioning (i.e., prey deliveries/nest/day and biomass delivered/nest/day) for nestlings is an important and crucial aspect (Lack 1947, Saether 1994) and may provide insights pertaining to reproductive performance and fitness of a species (Martin 1987, Boutin 1990). Composition and availability of prey in the context of habitat and prey community structure can affect raptor ecology and population trends (Newton 1979, Woffinden and Murphy 1989, Cully 1991, Olsen 1995). Understanding feeding behavior in raptor nestlings and quantifying components of food consumed by raptors is therefore a crucial element in analyzing the trophic interactions and dynamics of prey-predator relations both regionally and across ranges of predator species (Marti 1987, Giovanni et al. 2007).

Techniques to analyze raptor diet may be direct or indirect (Marti et al. 2007); although both contain inherent biases (Lewis et al. 2004). Analysis of pellets and prey remains is the most widespread indirect method to assess raptor diet (Steenhof and Kochert 1985, Marti et al. 2007) and may provide qualitative and quantitative information. While being minimally invasive, results from pellets and prey remains tend to overestimate large conspicuous prey species and remains of smaller species frequently escape detection (Simmons et al. 1991). Inadequacy of pellet analysis also may be associated with feeding behavior and digestibility of prey parts, which may lead to additional biases (Lewis 2004, Marti et al. 2007). Bias in age structure (adult vs. juvenile) and biomass of prey also may emanate from analysis of prey remains if unidentifiable (Lewis 2004, Marti et al. 2007, Bednarz 1988). Direct observation of prey deliveries at nests also may be used to evaluate raptor diet (Murphy 2010), where prey deliveries are observed from a blind (Rogers et al. 2005). Additionally, direct observations are labor-intensive and present logistical constraints that also may limit sample size (Marti et al. 2007) and therefore fail to encompass variation.

To eliminate the human intervention component from direct observation studies, advances in video surveillance systems provide a suitable alternative. The use of video surveillance using time-lapse recording at nest sites has become increasingly popular in the past two decades (Cutler and Swann 1999, Redpath et al. 2001, Giovanni et al. 2007, Ribic et al. 2012). Video surveillance at nest sites is less labor intensive, minimizes researcher-related disturbance, and limits human error by virtue of providing opportunities for expert verification (Kristan et al. 1996, Lewis et al. 2004). Despite a high investment cost associated with acquiring equipment and installation (Kristan et al., 1996, Lewis et al., 2004), technological advances in video surveillance and affordability of equipment will continue to drive this method to become a more suitable option for wildlife monitoring (Booms and Fuller 2003, Ribic et al. 2012)

Ferruginous hawk are highly stenophagous species, feeding on a limited variety of prey (Bechard and Schmutz 1995). As a grassland obligate species, it prefers open areas for foraging and its choice of prey varies by location and availability of major prey (Olendorff 1993). Their choice of main prey west of the continental divide is Lagomorphs, e.g., jackrabbits (*Lepus* spp.) or cottontail (*Sylvilagus* spp.) rabbits; larger rodents, e.g., ground squirrels and prairie dogs (Family *Scuiridae*), and pocket gophers (Family *Geomyidae*) are dominant food items in eastern populations (Olendorff 1993). Provisioning strategies adopted by parent bird impacts growth and physiologic conditions of nestlings (Olendorf 1974, Smout et al. 2013). Higher caloric demands during growth phase of altricial nestlings require adequate prey biomass and frequent delivery of prey during the nesting season (Wright et al. 1998). Nesting raptors reportedly adopt provisioning strategies (e.g. frequent foraging, selecting larger prey, to sustain greater dietary demands; Palmer et al. 2004, Smithers et al. 2005, Warnke et al. 2002); although larger broods were provisioned more frequently, available biomass/nestling was often lower than for smaller broods (Giovanni et al. 2007).

Previous studies in the northern Great Plains have analyzed diet of ferruginous hawk from pellets and prey remains (Lokemoen and Duebbert 1976, Blair 1978, Gilmer and Stewart 1983). The information furnished by prior studies in the northern Great Plains has been rendered outdated by major land-use changes (Fargione et al. 2009, Wright and Wimberly 2013) in the past four decades. The primary objective of our study was to quantify diet of ferruginous hawk during the breeding season through direct observation techniques utilizing video surveillance. Our specific objectives were to 1) identify prey species consumed by ferruginous hawk nestlings during the breeding season, 2) quantify prey delivery frequency and biomass of delivered prey, 3) evaluate diet breadth of ferruginous hawks in agriculture-dominated and grazing-dominated landscapes, and 4) evaluate effects of brood size and nestling age on prey provisioning. We hypothesized that Ferruginous hawks in the northern Great Plains will have *Squiridae* prey dominated diets (Olendorf 1993, Bechard and Schmutz 1995), which will differ in composition and breadth between the two land-use types. We also hypothesized that Ferruginous hawk parents will provision accounting for brood size and growth stage of nestlings by increasing frequency and biomass of prey delivered to nestlings.

METHODS

Study area–McPherson County in north-central South Dakota and McIntosh, Dickey, and Logan counties in south-central North Dakota were combined as and hereafter eastern Dakota (ED), and Harding, Perkins, and Butte counties in north-western South Dakota hereafter western Dakota (WD) were grouped together based on modes of land-use i.e. primarily agricultural, and in contrast, livestock-grazing based consecutively.

The ED study area (Fig. 1) included McPherson County in South Dakota and McIntosh, Dickey, and Logan counties in North Dakota and encompassed approximately 11,137 km^2 in the Missouri Coteau Physiographic Region (Bryce et al. 1998). Elevation ranged from 579–685 m throughout the study area. Numerous lakes and prairie potholes (>100 basins/2.59 km^2) were present and most of them are intermittently wet and dry. 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 2015). 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 (North Dakota State Climate Office 2012). Dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), northern reedgrass (*Calamgrostis 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, Johnson and Larson 2007). Land use in McPherson County in 1973 and 1974 was comprised of 31% native grasslands, 13% wetlands, 25% cropland, and 29% pasture/hay (Lokemoen and Duebbert 1976). In the 1980s south-central North Dakota was comprised of 36.1% pasture, 21.6% hayland/alfalfa and 36.7% cultivated crops (Gilmer and Stewart 1983). However, cropland and pasture constituted 87.7% of available land cover in McPherson County two decades later (Smith et al. 2002) and approximately 77% of the ED study area is currently used for agriculture.

The WD study area encompassed approximately 20,293 km^2 and included Harding, Butte, and Perkins counties in north western South Dakota. The area is semi-arid and has a mid-continental climate with long, cold winters and short, warm summers (Spuhler et al. 1971). Approximately 83% of the WD study area was pastureland dominated by grasses including western wheatgrass (*Pascopyrum smithii*), prairie Junegrass (*Koeleria pyramidata*), buffalograss (*Buchloe dactyloides*), green needlegrass (*Nassella viridula*), and blue grama (*Bouteloua gracilis*). Silver sagebrush (*Aretmisia cana*) and big sagebrush (*Artemisia tridentata*) were widely distributed throughout the county (Johnson 1988). Croplands occupied about 16 percent of the WD study area. Elevated table lands were dominated by ponderosa pine (*Pinus ponderosa*) savannah, whereas green ash (*Fraxinus pennsylvanicus*), willow (*Salix* spp.) and Siberian elm (*Ulmus pumila*) predominated in riparian areas and ravines (Blair 1978). Most of the land area in WD was treeless, semiarid rolling plains (Johnson 1988). Land elevation ranged between 817 and 1,224 m above mean sea level (Johnson 1988). The WD study area has a continental climate characterized by cold winters and hot summers, averaging -7° C in winter and 20° C in summer with an annual precipitation average of 37 cm and average seasonal snowfall of 101 cm (Johnson 1988). Most farm or ranch land was utilized for grazing cattle (*Bos taurus*) and some sheep (*Ovis aries*).

Nest Selection and monitoring.–During the 2013–2015 breeding seasons, we searched for active ferruginous hawk nests beginning 15 March in WD and 1 April in ED. To locate nests we systematically drove all accessible roads in each county and surveyed area inaccessible to vehicles on foot and by air. Nests also were located on foot using landowner's knowledge of nests and using historic nest locations (Knowles 2005, Baker 2011). Locating nests was facilitated by the lack of foliage during the early spring conditions. We considered nests to be occupied when evidence of nesting behavior (e.g., nest building, mating behavior) was observed. Because ferruginous hawks are believed to be sensitive to disturbance (Olendorff1993), we did not access nests until eggs hatched at which time considerable investment had been bestowed on nesting. Nests were considered active when evidence of prolonged incubation was confirmed. All active nest site locations were recorded using a handheld Garmin Global Positioning System (GPS; Garmin Ltd.) unit and ArcGIS 10.1 was used to plot locations (ESRI 2011). We randomly selected nests for video monitoring only constrained in some cases by unavailability of private property access or inaccessible and unsafe nest substrates. We monitored nests at least once every week from access roads or vantage points (distance ≤ 200 m) using binoculars and spotting scopes until eggs hatched. After confirming nestling presence in a nest, we observed nests ensuring minimal impact on the nest or the nest substrate using ladders or climbing equipment. For video-recording, we used Plotwatcher Pro HD (PW; Day 6 Outdoors, LLC) game cameras equipped with 32 gigabyte (gb) secure digital (SD) memory storage, and the camera was powered by eight 1.5 volts AA batteries. We installed PWs using trail camera screw-in mounting brackets (HME Products) ≤1 m from nests at an about 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 hrs to 22:00 hrs) and to record 1 frame/5 sec. This allowed recording for about 14–16 days before replacement of SD cards. We made ≤3 visits at each nest during video monitoring period (i.e., between day 7 [±3 days] post-hatching until day 45 [±5 days] when nestlings fledged), which minimized nest disturbance.

We used GameFinder (Day 6 Outdoors, LLC) software to review all video recordings, which allowed frame by frame inspection for identification of prey species, nestling numbers, and prey deliveries. We attempted to identify all prey items to the lowest taxonomic level using reference photos (Hoberg and Gause 1992, Fischer et al. 1999, Higgins et al. 2000, Seabloom 2011). We classified all unidentifiable prey as unknown prey. Ferruginous hawks had a unique tendency to smear the lens viewfinder, which posed challenges in identifying prey. Closely related species that could not be differentiated were grouped at the genus level (e.g., vole, mouse). All other prey were categorized according to their taxonomic class (e.g., unknown Avian).

Age and Mass Estimates–We used mean weights of male and female prey species to estimate biomass. Weight estimates were referenced using Higgins et al. (2000), and Seabloom (2011) for small mammals, Dunning (1993) for avian species, and Hoberg and Gause (1992) and Kiesow (2006) for reptiles. Unless juvenile characteristics were obvious (e.g., feather sheaths in avian species, notable size difference in small mammals), we classed prey as an adult (Giovanni et al. 2007). Weights of partially consumed prey species brought to nests, were estimated based on portion that was available for consumption (e.g., one-third, two-thirds). Prey items that were not classified to taxonomic family were assigned a 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 (*Sturnella* spp.; Lewis et al. 2004). Unidentified mammals that were smaller than a ground squirrel 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 small mammal prey species (e.g., *Microtus* spp.; Giovanni et al. 2007). Species that were classified to genus (e.g., *Peromyscus* spp., *Microtus* spp.), were assigned a mass value that was the average weight of all species in consideration. We assumed all prey was consumed by nestlings unless confirmed otherwise. Any prey primarily 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.

Provisioning analyses–Frequency of prey delivery and provisioning was expressed as deliveries/day and to address effects of brood size, deliveries/nestling/day at Ferruginous hawk nests (after Giovanni et al. 2007). Biomass delivered was calculated as g/day, g/nestling/day, and g/delivery and provisioning rates were analyzed by nest and brood size. We evaluated provisioning rates temporally at five day intervals to address association of provisioning with nestling growth (after Giovanni et al. 2007); young were aged using the photographic guide of Moritsch (1985) during camera installation. The time interval spanned from youngest observed nestling (~7 days old) and continued until fledging (~50 days old; Bechard and Schmutz 1995). This established nine, five-day intervals that all nests were assigned based upon the age of the youngest nestling.

Statistical analyses–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 effect of brood size on frequency and biomass provisioning. We examined differences in provisioning rates on the basis of deliveries/day and g/day between study areas with a *t*-test for independent samples by group (i.e. group1 – ED, and group 2 – WD) and also using one-way ANOVA. We compared diet richness and diet breadth between ED and WD study areas. We used Smith's Measure of Niche Breadth (*FT*) (Smith 1982) to calculate dietary breadth. We reported comparative data as means and standard errors.

RESULTS

During breeding seasons from 2013–2015 we collected and analyzed diets of nesting Ferruginous hawk nestlings at 29 nests (n = 15 in ED and n = 14 in WD). We video-monitored two Ferruginous hawk nests in 2013 (1 in ED, 1 in WD), 14 nests in 2014 (7 in ED, 7 in WD), and 13 nests in 2015 (6 in ED and 7 in WD). We assumed nests were independent between years. Monitored nests contained $\bar{x}$ = 3.5 ± 0.14 nestlings/nest (n = 49 in ED; n = 53 in WD). We recorded 6,872 hrs ($\bar{x}$ = 237 ± 39 hrs/nest) of daylight video footage (3,423 hrs in ED [$\bar{x}$ = 228 ± 31 hrs/nest]; 3,449 hrs in WD [$\bar{x}$ = 246 ± 34 hrs/nest]) and documented 3,187 prey deliveries (*n* = 1,432 in ED and *n* = 1,755 in WD). We identified 2,294 prey items (72%) of all prey deliveries. Of the prey species delivered, rodents dominated Ferruginous hawk diets comprising 77.3% in ED and 70.7% in WD. Rodents also accounted for 88.7% and 46.8% of the biomass is ED and WD respectively; lagomorphs constituted about 39.5% of prey biomass in WD.

Total biomass consumed at all nest sites in ED (*n* = 15) was 624.3 ± 6.1 kg; total biomass consumed at all nest sites in WD (*n* = 14) was 743.4 ± 6.1 kg. In ED, overall, mean grams/day was 1,387 ± 74.8 g and mean grams/nestling/day was 283 ± 51.7 g for all Ferruginous hawk nests. In WD, overall, mean grams/day was 1,632 ± 79.5 g and mean grams/nestling/day was 307.9 ± 48.8 g. Overall, Ferruginous hawks provided 6.2 ± 1.1 deliveries/nest/day and 2.6 ± 0.2 deliveries/nestling/day throughout the study in ED; in WD, ferruginous hawks provided 5.9 ± 1.2 deliveries/nest/day, and 2.2 ± 0.3 deliveries/nestling/day. We identified 16 prey categories classified by species (*n* = 11), genus (*n* = 3), family (*n* = 1), and class (*n* = 1). We were able to accurately identify 2,294 (72%) of 3,187 delivered prey items to species, genus, family, or class (Table 1). We classified the remaining 28% of prey items delivered to nests as unknown due to various constraints (e.g., view of prey blocked, immediate ingestion).

The five most frequently delivered prey in ED accounted for 89.9% of all prey delivered to nests (Table 1). Most frequently delivered prey in ED included Richardson’s ground squirrel (28%), unknown mammal (21.8%), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*; 17.8%), *Microtus* spp. (11.9%), and Franklin’s ground squirrel (*Poliocitellus franklinii*; 10.8%). In WD, the five most frequently delivered prey accounted for 73.6% of all prey delivered to nests by ferruginous hawks. Most frequently delivered prey in WD included northern pocket gopher (*Thomomys talpoides*; 31.3), *Microtus* spp. (17.9%), Passerines (13.4%), meadow voles (*Microtus pennsylvanicus*; 5.5%), and unknown mammals (5.5%). Richardson's ground squirrel, Franklin's ground squirrel, and thirteen-lined ground squirrel contributed about 65% of the biomass provisioned in ED by Ferruginous hawks. In WD, rodents contributed about 70.7% of the prey species delivered but only constituted 46.8% of the biomass; although lagomorphs contributed only about 5.5% of delivered prey, they constituted 39.5% of the biomass delivered.

Ferruginous hawks in ED had a lower measure of diet richness per nest (6.6 ± 0.4) compared to ferruginous hawks in WD (8.2 ± 0.6; $t_{27} = 2.1$, $P = 0.041$), but diet breadth did not differ between ED ($FT = 0.69$) and WD ($FT = 0.72$; $t_{27} = 0.59$, $P = 0.28$). Ferruginous hawks in ED made 6.2 ± 1.1 prey deliveries/nest/day, which was similar to prey deliveries/nest/day (5.9 ± 1.2; $t_{27} = 3.41$, $P = 0.61$) in WD. Deliveries/nestling/day also did not differ ($P = 0.32$) between ED (2.6 ± 0.2) and WD (2.2 ± 0.3; $t_{27} = 0.48$).

Deliveries/nestling/day differed ($F_{3,\,14} = 1.97$, $P = 0.02$; Table 2) among brood sizes in ED and in WD ($F_{3,\,13} = 2.17$, $P = 0.03$; Table 2); prey deliveries/nestling/day decreased with increasing brood size in both study areas. Deliveries/nestling/day estimates remained relatively constant in ED ($F_{8,\,48} = 2.46$, $P = 0.10$; Table 3) and in WD ($F_{8,\,52} = 2.88$, $P = 0.21$) over the 5-day nestling interval growth period.

Ferruginous hawks did not differ in terms of deliveries/hr ($F_{8,\,48} = 1.49$, $P = 0.31$) in ED or in WD ($F_{8,\,52} = 1.77$, $P = 0.36$); deliveries/nestling/hr also remained constant in ED ($F_{8,\,48} = 0.64$, $P = 0.81$; Table 3) and WD ($F_{8,\,52} = 0.69$, $P = 0.72$). Estimates of biomass, i.e., grams/nestling/day, also remained constant throughout the nestling growth period in both ED and WD. In ED, grams/hr ($F_{8,\,48} = 0.73$, $P = 0.38$) and grams/nestling/hr ($F_{8,\,48} = 1.03$, $P = 0.13$; Table 3) did not differ among 5-day period intervals and likewise, in WD (grams/hr [$F_{8,\,52} = 0.68$, $P = 0.29$] and grams/nestling/hr [$F_{8,\,52} = 0.97$, $P = 0.17$]). Biomass estimates for broods with two, three, four, and five nestlings did not differ between ED ($F_{3,14} = 0.34$, $P = 0.85$; Table 2) or WD ($F_{3,13} = 0.41$, $P = 0.78$).

DISCUSSION

Ferruginous hawks are considered highly stenophagous (feeding on limited number of food items; Bechard and Schmutz 1995) and the dominant portion of their diet consists of members of the order Lagomorphs or Sciurids. Diet composition of Ferruginous hawks does not vary across much of its range; the choice of main prey varies only spatially – west of continental divide, jackrabbits (*Lepus* spp.) or cottontail rabbits (*Sylvilagus* spp.); east, ground squirrels (Olendorff 1993). We documented dominance of relatively larger mammalian prey (94%), and only a small percentage of avian prey (5.8%) in Ferruginous hawk diet biomass during our study. This is consistent with at least 20 past studies within ferruginous hawk range (mammalian prey – 95.4%; avian prey – 3.8%; adapted from Olendorff 1993, Bechard and Schmutz 1995) and also consistent with studies conducted in the northern Great Plains (Lokemoen and Duebbert 1976, Schmutz et al. 1980, Blair and Schitoskey 1982, Gilmer and Stewart 1983, Restani 1991). Breeding Ferruginous hawks preyed primarily upon black-tailed jackrabbits (*Lepus californicus*) in Utah (Woffinden and Murphy 1977), northern pocket gophers (*Thomomys talpoides*) and ground squirrels in Idaho (Wakeley 1978, Steenhof and

Kochert 1985), Richardson's ground squirrels in North Dakota (Gilmer and Stewart 1983), Wyoming (MacLaren et al. 1988), and Alberta (Schmutz et al.1980), and *Spermophilus* spp. ground squirrels in Montana (Restani 1991). Dietary component analysis of Ferruginous hawks from pellets and prey remains was conducted by Gilmer and Stewart (1983) in south central North-Dakota and by Lokemoen and Duebbert (1976) in north central South Dakota, which equated as eastern Dakota (ED). Both studies found Richardson's ground squirrel as the main prey both in terms of frequency (60.4 and 96 consecutively) and biomass (65.9 and 68 consecutively). In both studies, diet was supplemented by lagomorph biomass ($\bar{x}$ = 20.5% ± 1.5). Indirect methods of diet analysis (i.e., analysis of pellets and remains) are known to bias results toward species whose remains are more detectable (e.g., large bones, thick skin, bright feathers) (Collopy 1983, Simmons et al. 1991, Bielefeldt et al. 1992). The finer resolution of our study in ED also documented dominance of ground squirrel in both frequency (57%) and biomass (65.3%) indicating the importance of ground squirrels during the ferruginous hawk breeding season in an agriculture dominated landscape. Lagomorphs (1%) and pocket gophers (5.4%) constituted less than six percent of the frequency and contributed towards only 9.3% of the total biomass when compared to results of Gilmer and Stewart (1983; biomass – 19%) and Lokemoen and Duebbert (1976; biomass – 22%). Land-use in ED has shifted from row crop agriculture (approximately 77% cropped) and Ferruginous hawk numbers have declined over the past four decades (unpublished Datta et al. 2016). Our finding may indicate a decline in availability of Lagomorphs in ED, which could be a function of the change in landscape pattern (e.g., edge interactions, heterogeneity of landscape; Calvete et al. 2004) due to change in land use, or could be a low point in lagomorph abundance cycle.

In north western South Dakota, regarded in this study as western Dakota (WD), Balir and Schitoskey (1982) studied Ferruginous hawk diets from pellets and prey remains and found occurrence of mammals in 70% of their samples. Thirteen-lined ground squirrel (44%), white-tailed jackrabbit (10%), northern pocket gopher (8%), and eastern cottontail (2%) were among the leading prey species found during their study (1976–1977). They also documented avian prey (Western meadowlark–24%; total 27%) as a major source of prey base, which probably did not contribute to major share of biomass (no biomass reported in Blair and Schitoskey 1982). Our results in WD document similar occurrences of mammalian (81.6%) and avian prey (17.5%), but a diminished lagomorph presence (5.5% vs. 12%). This may indicate a possible decline in available lagomorph population in WD. Our study also documented a wider use of rodent prey that contributed considerably ($\geq 5\%$) towards total biomass consumed during the breeding season (Table 1).

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 greatest 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, prey size, deliveries/day, g/day, and g/nestling/day did not vary significantly for Ferruginous Hawk nests in agriculture dominated ED and grazing-based WD; these results also did not vary with different brood sizes in our study area. A low sample size also may have been the reason for not detecting any statistical relationship between provisioning rates and brood sizes at an alpha level of 0.05. Nestling provisioning rates in g/nestling/day, however, decreased with increasing brood size. Thus, Ferruginous Hawks delivered more g/day with increasing brood size but did not maintain a constant nestling provisioning rate. Ferruginous hawk broods in our study consumed less grams/nestling/day relative to those in the Southern Great Plains (Giovanni et al. 2007). As caloric requirement may vary during nestling growth period, provisioning rates also must match this variation. Olendorff (1974) documented higher nestling provisioning rates in captive Ferruginous hawks at post-hatch week 4 (days 22–28). Our results approximate these findings as Ferruginous Hawks delivered the most g/nestling/hr during post-hatch days 22–26, although results were not statistically significant (*P* = 0.12). Diet richness was higher in WD suggesting Ferruginous Hawk selected for a wider prey base in a more heterogeneous landscape vs. in a more monotypic agriculture dominated landscape as in ED.

CONCLUSION

Our results show that Ferruginous hawks were dependent primarily upon ground squirrels in ED and pocket gophers, prairie dogs and lagomorphs in WD. These species should be considered while making management decisions for breeding Ferruginous hawks in the northern Great Plains. Primary prey declines limit Ferruginous hawk breeding efforts and numerous studies have shown that Ferruginous Hawks tend to have lower reproductive success and emigrate following primary prey population declines

(Smith et al. 1981, Schmutz and Hungle 1989, Woffinden and Murphy 1989, Cully 1991). Unregulated removal of grassland prey species e.g. black-tailed prairie dogs throughout their range (Kotliar et al. 1999), improper management of grasslands and continued conversion of heterogeneous landscapes into monotypic cropland may impact Ferruginous hawk breeding in the northern Great Plains.

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Figure 1. Ferruginous hawk diet and provisioning study area in North Dakota and South Dakota, USA.

Ferruginous hawk (*Buteo regalis*) study area in Logan, McIntosh, and Dickey counties (light grey), in south-central North Dakota, McPherson County (dark grey) in north-central South Dakota, and Harding, Butte, and Perkins counties (dark grey) in north-western South Dakota, USA, 2013–2015.

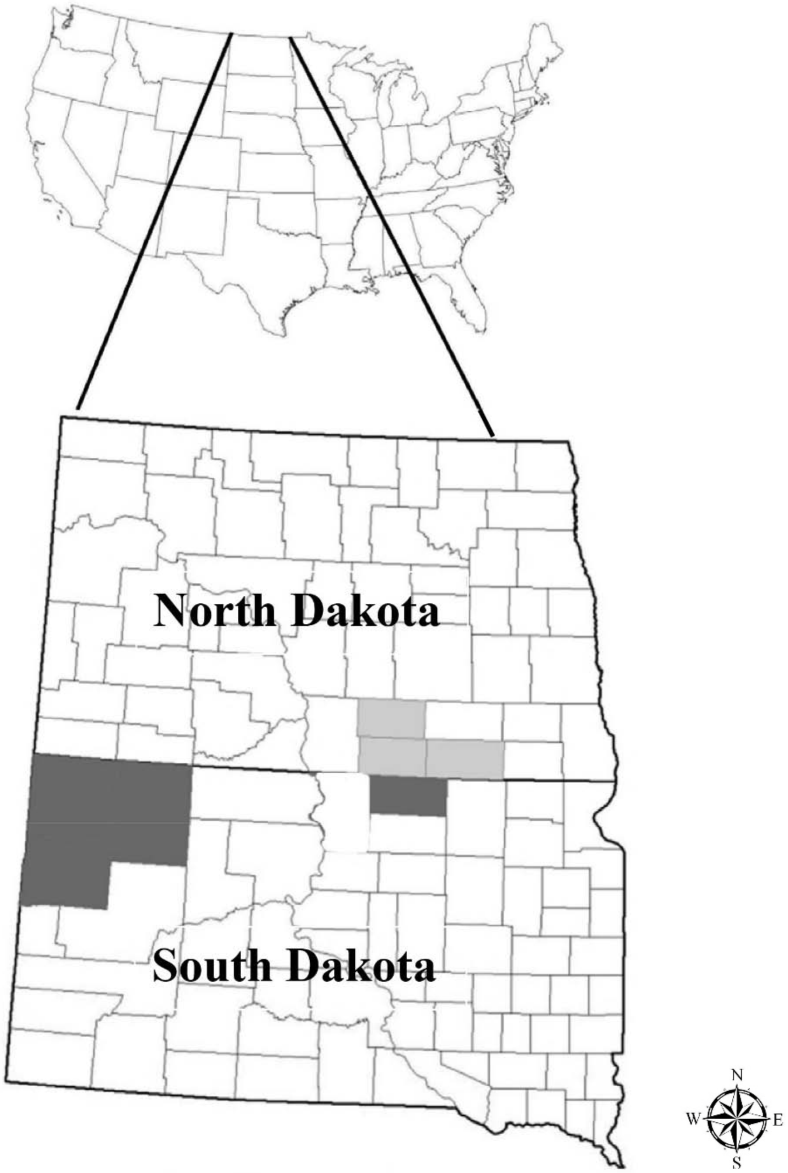

Table 1. Diet composition, frequency (%), and biomass (%) at Ferruginous hawk nests (N = 18) in south-central North Dakota and north-central South Dakota, 2013–2014.

		Ferruginous Hawk ED (*n* = 15)			Ferruginous Hawk WD (*n* = 14)		
Class	Prey	*n*	%DF[a]	%BM[b]	*n*	%DF[a]	%BM[b]
Mammals							
	Richardson's ground squirrel	404	28.1	33.7	31	1.6	1.6
	Thirteen-lined ground squirrel	256	17.9	14.3	81	4.5	3.3
	Unknown small mammal	254	17.8	21.4	96	5.5	4
	Micotus spp.	170	11.9	1.7	318	17.9	2.4
	Franklins ground squirrel	155	10.8	17.3	-	-	-
	Northern pocket gopher	77	5.4	4.3	554	31.4	23
	Meadow vole	23	1.6	0.3	96	5.5	0.9
	Deer mouse	15	1.1	0.1	35	2	.09
	Eastern cottontail	15	1.1	5	64	3.6	14.9
	Sorex spp.	8	0.5	<0.0	43	2.5	0.12
	White-tailed jackrabbit	-	-	-	35	2	24.8
	Black-tailed prairie dog	-	-	-	61	3.5	13.1
	Prairie vole	-	-	-	34	2	0.5
	Long-tailed weasel	-	-	-	3	0.17	0.01
	Subtotal	**1377**	**96.2**	**98.1**	**1448**	**82.17**	**88.72**
Reptile							
	Common garter snake	8	0.5	0.3	-	-	-
	Subtotal	**8**	**0.5**	**0.3**			
Avian							
	Passerine	24	1.7	0.7	239	13.7	5.7
	Unknown avian	23	1.6	0.7	43	2.6	1.0
	Juvenile *Anas* spp.	-	-	-	25	1.5	4.5
	Subtotal	**47**	**3.3**	**1.4**	**307**	**17.8**	**11.2**
	Total	**1432**	**100**	**99.9**	**1755**	**99.97**	**99.92**

[a] Delivery frequency

[b] Percent Biomass

Table 2. Mean (± SE) deliveries/nestling/day (d/n/d) and grams/nestling/day (g/n/d) at Ferruginous hawk nests in northern Great Plains. In south-central North Dakota and north-central South Dakota (ED) broods of 2 (*n* = 1), 3 (*n* = 10), 4 (*N* = 3), and 5 (*N* = 1), and in north western South Dakota (WD) broods of 2 (*n* = 1), 3 (*n* = 5), 4 (*N* = 7), and 5 (*N* = 1) nestlings in, 2013–2014.

	Ferruginous hawk (ED)		Ferruginous hawk (WD)	
Brood Size	d/n/d	g/n/d	d/n/d	g/n/d
2	2.9 ± 0.2	348.8 ± 62.1	3.1 ± 0.4	351 ± 58.2
3	2.6 ± 0.5	323.9 ± 53.5	2.7 ± 0.4	330 ± 55.1
4	2.5 ± 0.5	326.6 ± 28.4	2.4 ± 06	323 ± 21.4
5	2 ± 0.4	304.9 ± 29.8	2.1 ± 04	308 ± 33.1

Table 3. Provisioning rates over 5-day intervals during nestling growth at Ferruginous hawk nests (N = 29; ED – n = 15, WD – n = 14) in the northern Great Plains, USA 2013–2015.

	Age in days								
	7 – 11	12 – 16	17 – 21	22 – 26	27 – 31	32 – 36	37 – 41	42 – 46	47 – 51
Prey deliveries/hr									
FEHA ER	0.31 ± 0.04	0.31 ± 0.04	0.32 ± 0.06	0.38 ± 0.03	0.36 ± 0.04	0.30 ± 0.02	0.32 ± 0.04	0.33 ± 0.01	0.29 ± 0.02
FEHA WR	0.3 ± 0.05	0.33 ± 0.03	0.31 ± 0.05	0.36 ± 0.02	0.35 ± 0.03	0.35 ± 0.02	0.30 ± 0.04	0.29 ± 0.01	0.3 ± 0.02
Deliveries/nestling/hr									
FEHA ER	0.14 ± 0.01	0.16 ± 0.01	0.16 ± 0.02	0.19 ± 0.01	0.2 ± 0.01	0.17 ± 0.01	0.18 ± 0.01	0.15 ± 0.01	0.12 ± 0.01
FEHA WR	0.13 ± 0.01	0.12 ± 0.01	0.17 ± 0.02	0.22 ± 0.01	0.18 ± 0.01	0.19 ± 0.01	0.17 ± 0.01	0.12 ± 0.01	0.12 ± 0.01
Grams/hr									
FEHA ER	91 ± 20	91 ± 11	112 ± 23	119 ± 8	114 ± 27	99 ± 18	102 ± 32	100 ± 12	92 ± 39
FEHA WR	102 ± 31	98 ± 22	120 ± 35	122 ± 8	120 ± 17	107 ± 24	107 ± 32	92 ± 28	88 ± 36
Grams/nestling/hr									
FEHA ER	18 ± 3	24 ± 2	23 ± 5	29 ± 3	26 ± 7	22 ± 4	17 ± 6	17 ± 3	15 ± 10
FEHA WR	16 ± 4	21 ± 4	21 ± 5	31 ± 3	28 ± 3	20 ± 5	21 ± 2	18 ± 7	16 ± 12