

GAMEBIRD MANAGEMENT IN SOUTHWESTERN NORTH DAKOTA

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ABSTRACT

Grassland biodiversity is threatened by habitat loss associated with human expansion. In response, land managers need to collect wildlife data more efficiently and implement management practices that promote wildlife habitat. To assess methods and land use practices for managing game birds in the Northwestern Great Plains, we quantified the behavioral response of sharp-tailed grouse (*Tympanucus phasianellus*) to small unmanned aerial systems (sUAS) exposure and measured production of upland nesting ducks on former Conservation Reserve Program land. We found survey altitudes ≥ 121 m above ground level and moderate wind speeds reduced behavior response of grouse. For waterfowl production, we found that nest survival increased with nest age, vegetation height, and relative humidity. Future sUAS application for grouse surveys should explore altitudes ≥ 121 m above ground level. In terms of duck production, we suggest land managers use practices that increase vegetation structure.

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LIST OF ABBREVIATIONS

sUAS	Small Unmanned Aerial Systems
AGL	Above Ground Level
CRP	Conservation Reserve Program
HREC	Hettinger Research Extension Center
VOR	Visual Obstruction Reading
DSR	Daily Survival Rates

CHAPTER 1. USE OF SMALL UNMANNED AERIAL SYSTEMS FOR SHARP-TAILED GROUSE LEK SURVEYS

Introduction

Wildlife surveys are important to the management and conservation of animal populations globally. Annual surveys can provide indices of local populations (Autenreith 1982) or can help identify trends across larger landscapes (Sauer et al. 2013). Wildlife agencies often use methods such as point counts on foot or roadside counts from automobiles to conduct surveys (Ralph et al. 1995, Rabe et al. 2002). Rugged and roadless terrain makes ground surveys unfeasible in many areas, making aerial surveys the only means for assessing wildlife populations. Aerial surveys can provide more precise population information than ground based surveys (Schroeder et al. 1992), but a major problem with manned, aerial surveys is the associated risk to observers. Survey protocols may require flying aircrafts at reduced speeds and at low altitudes to collect data (Certain and Bretagnolle 2008, Laake et al. 2008), putting pilots and observers at risk of injury or death (Wiegmann and Taneja 2003). Recent technological advances and changes to Federal Aviation Administration rules associated with small unmanned aerial systems (hereafter, sUAS [FAA § 107]) have made them a possible alternative for wildlife managers, yet little is known about their efficacy for surveying many wildlife species.

Small unmanned aerial systems may provide a safer, cheaper, and more reliable means for collecting survey data on wildlife. However, before their implementation, methodologies need to be explored and the responses from wildlife determined. Because wildlife surveys often occur during important life history stages (e.g., nesting, lekking), it is important that any survey method be evaluated to minimize negative impacts to the species. Wildlife researchers have begun to evaluate the use of sUAS during aerial surveys, but greater information on species-

specific behavior in response to sUAS is still needed (Christie et al. 2016). Previous research demonstrates that some wildlife exhibit both behavioral and physiological responses to sUAS flights (Ditmer et al. 2015, Weissensteiner et al. 2015, Brisson-Curadeau et al. 2017, Weimerskirch et al. 2018), which can be both detrimental to the wildlife of interest and inhibit accurate data collection. Therefore, before protocols can be developed to best implement this new technology, greater investigation into individual species response to sUAS exposure is necessary.

Prairie grouse (*Tympanuchus spp.*) are distributed throughout the central and western United States and are of high conservation concern (Johnsgard 2002). Wildlife professionals commonly use aerial surveys with manned aircraft to monitor grouse and develop population indices by counting males each spring on centralized display areas known as leks. These surveys commonly provide more accurate data than ground-based road surveys alone (McRoberts et al. 2011). However, because of the dangers (Sasse 2003) and costs (McRoberts et al. 2011) associated with manned, aerial surveys, sUAS may present a realistic alternative. However, for sUAS to be effective, they need to collect accurate counts of individual grouse through imagery. Research using sUAS on greater sage-grouse (*Centrocercus urophasianus*) suggests still imagery are of sufficiently high resolution to detect individual males on leks (Hanson et al. 2014, Forbey et al. 2017). Prairie grouse (*Tympanuchus spp.*) are smaller than sage-grouse and often are found in denser vegetation. For these reasons, observers using manned, aerial surveys find flushed prairie grouse easier to count while quantifying populations (Lehmann and Mauermann 1963, Schroeder et al. 1992). Conversely, if sUAS trigger the flushed behavioral response it could inhibit the ability to capture prairie grouse in sUAS imagery (Gillette et al. 2013), and thus render the images useless for population estimation.

In addition to specific behavioral responses to sUAS, there are still much logistical uncertainty about the use of sUAS for wildlife surveys (e.g., altitude, weather conditions). Given the gap in sUAS knowledge and the major need for safer survey methods in remote landscapes, we designed a study to evaluate the potential use of sUAS to survey sharp-tailed grouse [*Tympanucus phasianellus* (hereafter, grouse)] on leks in remote areas of South Dakota. Our study objectives were to 1) assess behavioral responses of lekking grouse to sUAS exposure, and 2) discuss labor, technical requirements, and logistical challenges associated with sUAS wildlife surveys. By addressing these objectives, we will provide guidance for future applications of sUAS in grouse lek surveys.

Methods

Study Area

We conducted aerial surveys using sUAS during the spring of 2018 and 2019 in the Grand River National Grassland in Perkins County, South Dakota. This area is located within the semiarid, unglaciated portion of the Missouri Plateau. The Grand River National Grassland (GRNG; N 45°45'0"; W 102°30'11.52") was 626.4 km², and dominated by mixed grass prairie and hardwood river bottoms. Topographic features of the GRNG include gently rolling hills, steep grassy buttes, and broad river plains.

Small Unmanned Aerial System

We used DJI's Phantom 4 quadcopter [hereafter, quadcopter; (DJI, Shenzhen, China, Fig. 1)], which weighs 1.38 kg with camera on board. This platform has a plastic shell body and a diagonal wingspan of 35 cm. This quadcopters propulsion comes from four motors mounted on the tip of each wing, allowing speeds up to 72 km/hr. Power comes from a 5870 mAh battery,

which allows approximately 30 minutes of flight and is fitted with a 20 megapixel 3-axis-stabalizing gimbal camera.



Figure 1. Quadcopter small unmanned aerial systems (sUAS) by DJI with controls.

Small Unmanned Aerial System Flights

We carried out aerial lek surveys between dawn and 09:30 hours MST in correspondence to typical ground surveys of leks (Autenreith 1982). To avoid disturbance during pre-takeoff, we launched the sUAS at a minimum distance of 200 m from leks (Vas et al. 2015, Rümmler et al. 2016). To investigate behavior response by grouse at extreme flight-height gradients we flew the sUAS at 30 m and 121 m above ground, levels [hereafter, AGL]. Flights were designed to cover the entire lek and its proximity using linear flight paths. A visual observer accompanied the remote pilot during all controlled flights, as specified by the FAA § 107-31. The visual observer also took notes on labor and technical requirements to provide a general understanding of the logistics that accompany surveys.

Prior to takeoff, a third observer stationed at a concealed vantage point near the lek, counted grouse and noted behavior before, during, and after each sUAS survey using a spotting scope. Lek observers arrived at concealed vantage points 20 min prior to each survey.

Monitoring grouse prior to sUAS exposure allowed us to get a baseline on their behavior. We

“scored” sUAS response behavior into four categories: no response, acknowledgement, flush, and total disruption. Behavior for no response included continuing to display, preening, and foraging. Acknowledgement meant the birds stopped displaying and turned attention toward the sUAS or sought cover. We defined a flush score when at least one, but not all birds flushed from the lek. Total disruption signified a lek entirely abandoned (i.e., all birds flushed) after sUAS exposure. Following surveys, the lek observer stayed in position for 15 min to document post exposure behavior of grouse.

Statistical Analysis

To assess response behavior, we categorized scores by *No Flush* (i.e., no response and acknowledgement) or *Flush* [(i.e., flush and total disruption) (Rümmeler et al. 2016, Weimerskirch et al. 2018)]. We examined univariate, binomial generalized linear mixed models (GLMM) with a link function (Bates et al. 2014), using package lme4 in R statistical environment (R Core Team 2014, Bates et al. 2015). Univariate models were based on a priori variables of interest and categorized into three predetermined groups. The best models from each group were used to create a best model set on the basis of Akaike’s information criterion (AIC) corrected for small sample sizes [AIC_c (Burnham and Anderson 2002)].

We first assessed variables for multicollinearity using Pearson’s correlation, retaining one variable from any highly correlated variable pairs ($r > 0.7$; Coppedge et al. 2008). We then created three model groups based on weather, study design, and biological variables. This resulted in six weather, three study design, and three biological models. Variability in climatic conditions and lek tenacity was assessed by comparing both linear and quadratic trends of temperature, wind speed, and survey date. All covariates including a quadratic trend also included a linear term. We nested lek identification as a random effect within all univariate

models, null model (intercept only), and combination models for each step to account for repeated measures. We ran univariate models for all variables within the three groups and ranked them based on their AIC_c values and in comparison to a null model (Burnham and Anderson 2002). Univariate models from each group with greater relative importance than the null model, and within 2 AIC_c units of the best model were considered supported and were included in the “best” model set (Hovick et al. 2015). The best model set included all supported univariate models, all possible combinations of those variables, and a null model (intercept only), to determine the relative importance of each variable (Loss and Blair. 2011). We calculated model-averaged parameter weights for each supported variable by summing their AIC_c weights [w] in all models within the best model set, then dividing the sum by the total number of models in which that variable occurred within that set (Burnham and Anderson 2002, Hovick et al. 2015). This method allowed us to determine the most informative parameters from multiple competitive models. We calculated confidence intervals for variables in the top model from the final model set to gauge their effect.

Results

We visited 19 leks and conducted 43 sUAS surveys between 9 April and 3 May in 2018 and 2019. Collectively, eight leks were surveyed once, six leks were surveyed twice, five leks were surveyed three times, and two leks were surveyed four times. The number of grouse present on surveyed leks varied, with males averaging 6.3 ± 0.3 (SE) and females averaging 1.0 ± 0.3 . Pre-survey behavior of grouse consisted of resting birds or displaying males. Post-survey observations noted that of 14 leks that scored total disruption, eight had birds returning to leks within an average of $4.4 \text{ min} \pm 1.0$, one had birds return while the sUAS was still in flight, and five had no birds return during the sampling period. Grouse behavior on leks without a total

disruption score included, five where birds returned to displaying within $3.02 \text{ min} \pm 1.48$ of sUAS departure, 10 had birds that continued to display during the flight duration, three had birds displaying immediately following sUAS departure, and five never had birds display again while the lek was being observed. There were six leks where birds remained present but did not display at any given point throughout the sUAS survey.

There was no evidence of correlation between predictor variables of interest. We found altitude and wind speed were most informative at explaining the behavioral response of grouse during sUAS surveys (Table 1). Altitude (parameter importance weight = 0.48) and the quadratic of wind speed (parameter importance weight = 0.48) both occurred in the best model. We observed lower flush scores when we increased survey altitude to 121 m AGL [$\beta_{\text{altitude}} = -6.80$, 95% CI: -29.94 to -1.32] Fig. 2 and Fig. 3]. The quadratic trend of wind speed suggested lower flush scores when surveys occurred at intermediate wind speeds [$\beta_{\text{windspeed}} = -15.36$, 95% CI = 0 to -0.46; $\beta_{\text{windspeed}^2} = 24.22$, 95% CI = 4.11 to 0) Fig. 2 and Fig. 4].

Table 1. Model selection results for sharp-tailed grouse behavioral responses during small unmanned aerial systems surveys conducted in South Dakota during the springs of 2018–2019.

Model	K ^a	ΔAIC_c^b	w^c	log-Likelihood ^d
<i>Weather Models</i>				
Wind speed ²	4	0.00	0.68	-22.63
Cloud cover	3	3.51	0.12	-25.60
Null	2	4.21	0.08	-27.11
Temperature ²	4	5.94	0.03	-25.60
Precipitation	3	6.18	0.03	-26.94
Temperature	3	6.32	0.03	-27.01
Wind speed	3	6.43	0.03	-27.06
<i>Study Design Models</i>				
Altitude	3	0.00	0.81	-24.01
Null	2	3.89	0.12	-27.11
Survey date	3	6.21	0.04	-27.11
Survey date ²	4	6.21	0.04	-25.90
<i>Biological models</i>				
Null	2	0.00	0.42	-27.11
Number of males	3	0.77	0.29	-26.34
Number of females	3	1.92	0.16	-26.91
Pre-flight behavior	3	2.31	0.13	-27.11
<i>Best models</i>				
Altitude + wind speed ²	5	0.00	0.91	-18.34
Altitude	3	6.34	0.05	-24.01
Wind speed ²	4	6.01	0.04	-22.63
Null	2	10.23	0.01	-27.11

^aNumber of model parameters.

^bDifference in AIC_c value between models and the strongest supported model.

^c AIC_c weights.

^dNatural logarithm of the maximum likelihood for model.

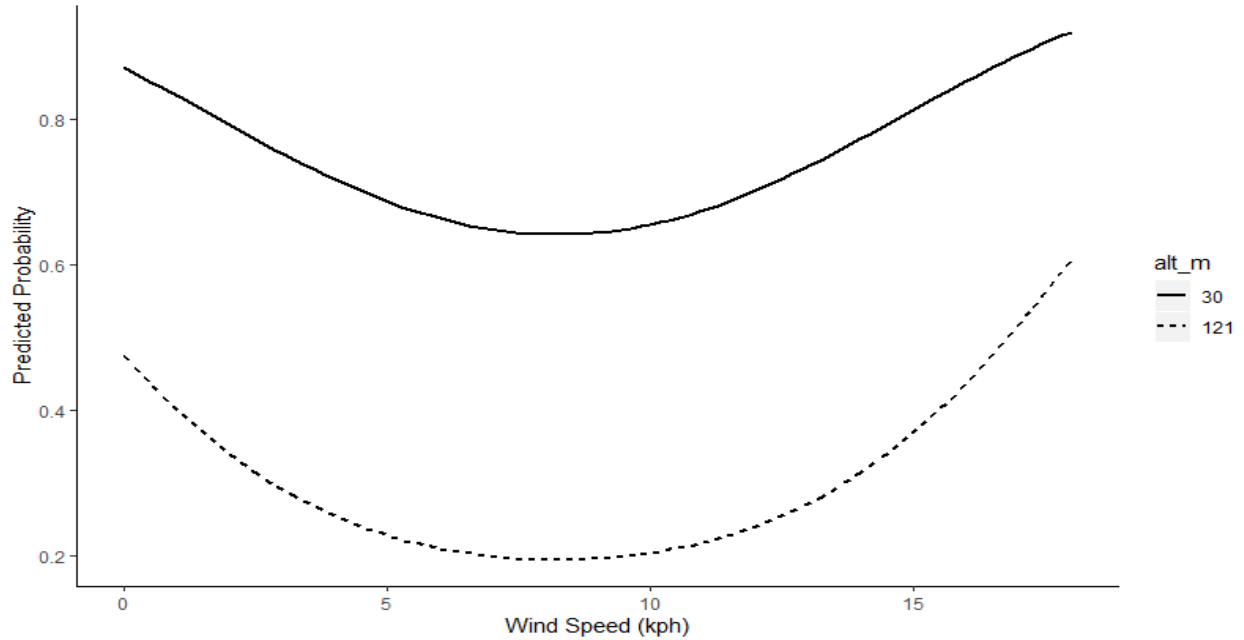


Figure 2. Predicted probability of sharp-tailed grouse producing a flush response relative to above ground levels (altitude at 30 and 121 m) and wind speed (kph) during small unmanned aerial systems (sUAS) lek surveys in South Dakota during the springs of 2018-2019.

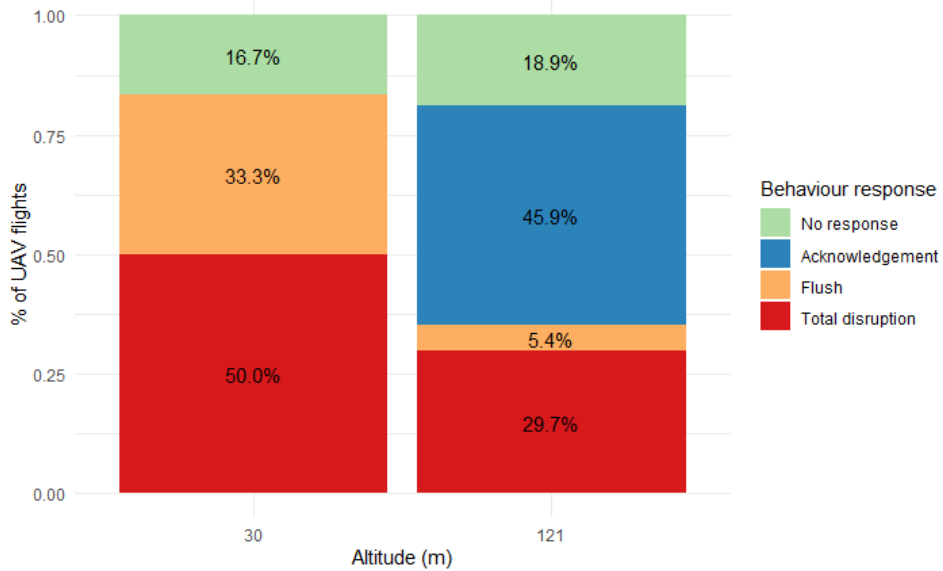


Figure 3. Sharp-tailed grouse flush response to survey altitude (m) during small unmanned aerial systems (sUAS) surveys in South Dakota during the springs of 2018-2019.

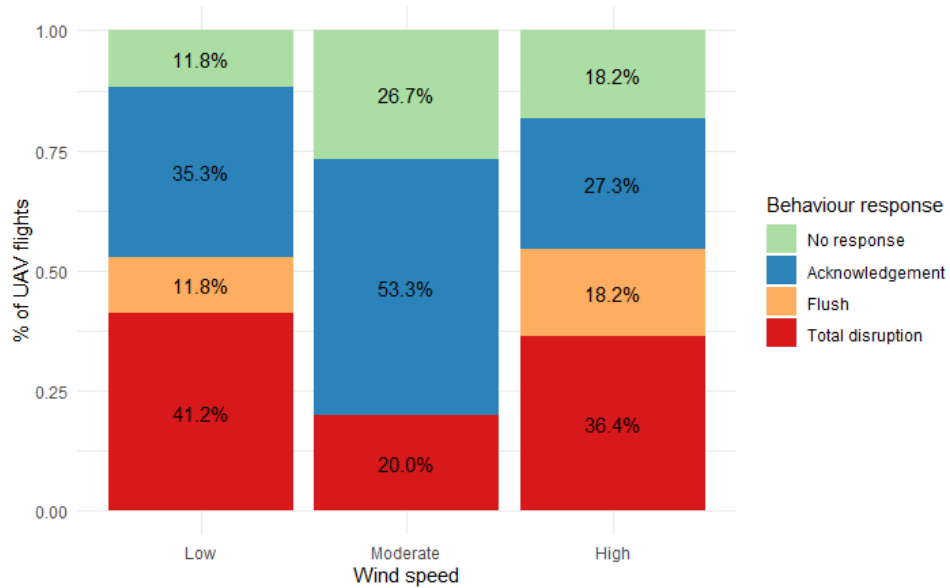


Figure 4. Sharp-tailed grouse behavioral response to wind speed (kph) during small unmanned aerial systems (sUAS) surveys in South Dakota during the springs of 2018-2019. Wind speed (kph) is categorized into Low (< 6 kph), Moderate (≥ 6 kph and < 13 kph), and High (≥ 13 kph).

Discussion

Our main research findings suggest that grouse flushed from lek locations less often when sUAS were flown at greater altitudes and during days with moderate wind speeds. Specifically, we observed lower flush scores from grouse as we increased survey altitude from 30 m to 121 m AGL. One or more grouse flushed from leks 83.3% of the time following sUAS exposure at 30 m AGL and 35.1% at 121 m AGL. Additionally, we found wind speeds ≥ 6 kph and < 13 kph to be best at minimizing grouse flushing and recommend wind be considered in future surveys using sUAS. Despite the behavior response from grouse we observed with our sUAS platform, our experience with sUAS suggest there is potential for their use in aerial lek surveys by improving access to remote locations (Jones et al. 2006) and alleviating dangers associated with manned, aerial surveys. However, it may require more advanced sUAS and sensors that allow for higher altitude observations and greater imagery resolution.

Our results suggest that higher survey AGLs should be considered in future sUAS evaluation but due to FAA restrictions we were unable to survey altitudes >121 m AGL. Flights at similar altitudes to those we evaluated have triggered greater-sage grouse to flush during manned, aerial surveys (Gillette et al. 2013). Small unmanned aerial systems flown at 80 m AGL and lower, have triggered both a behavioral and physiological response to both waterfowl and nesting Arctic sea birds (McEvoy et al. 2016, Weimerskirch et al. 2018). Protocols and changes to FAA regulations, or an exemption permit that allow for increased sUAS survey altitudes >121 m AGL could alleviate this response from grouse and other birds (Hanson et al. 2014). However, identifying less conspicuous grouse (i.e., female greater-sage grouse and sharp-tailed grouse) in still imagery at ≥ 121 m AGL becomes increasingly difficult with sensors rated at ≤ 20 megapixel [Breckenridge et al. 2011 (Fig. 5)]. Small unmanned aerial systems with greater weight capacity would allow for more sophisticated sensors with greater ability to detect grouse at higher altitudes. However, investigators using larger platforms could risk higher detectability from grouse compared to smaller quadcopters (Sardà-Palomera et al. 2012, Watts et al. 2010).



Figure 5. Images taken of sharp-tailed grouse (*Tympanucus phasianellus*) decoys using DJI's Phantom 4 quadcopters 20 megapixel gimbal camera at four above ground level (A: 30 m AGL, B: 60 m AGL, C: 91 m AGL, D: 121 m AGL). Inset images are shown at 500% magnification.

We found a quadratic trend of wind speed, being that at low (< 6 kph) and high (≥ 13 kph) wind speeds more flush scores were recorded than at moderate (≥ 6 kph and < 13 kph) wind speeds. We speculate that during low wind speeds the operating noise produced by the sUAS traveled more efficiently to grouse from the lack of atmospheric distortion. During periods of high wind speeds, the body of the sUAS was forced to increase its flight angle to keep its linear flight path. This resulted in the sUAS's airfoils trailing edge to produce larger amounts of low frequency noise (Brooks et al. 1989). Low frequency anthropogenic noise can influence bird behavior (Goodwin et al. 2010), and could explain grouse behavior during surveys at high wind

speeds. Alternatively, grouse become more alert during high wind speeds, which can make approaching them difficult under those conditions.

We noted that the majority of birds that remained on the lek either sought shelter in the nearest tall vegetation or crouched closer to the ground. This behavioral response could lead to a broken silhouette of grouse in still or video imagery (Chabot et al. 2015). Small unmanned aerial system based thermal imagery presents a potential solution to this problem with wildlife researchers finding them particularly useful for depicting animals in imagery (Potvin and Breton 2005, Carr et al. 2012, Israel 2012, Hanson et al. 2014). Although, this is dependent on wildlife not vacating an area before imagery is able to capture them (Gillette et al. 2013).

Surveys were easy to replicate between leks with DJI's user friendly software, which allowed for easy uploading of preprogrammed linear flight paths. We experienced technical difficulties on several surveys when the sUAS was not calibrating its compass properly. This however did not restrict our ability to complete surveys at any particular lek after the remote pilot began to systematically recalibrate the compass before each sUAS survey.

Small unmanned aerial systems show promise to alleviate concerns with manned, aerial surveys with ease of deployment and alleviate risks during aerial surveys. The Phantom 4 quadcopter was able to survey leks at 32.2 km per/h allowing for an average flight duration of 7.6 min \pm 0.3. We found no difference between flight times for sUAS surveys conducted at 30 m AGL and 121 m AGL. Conversely, we did find a difference between labor times between the two altitudes, but this can largely be attributed to adjustments made after the first year of this study that allowed for more efficient surveys. On three separate occasions we experienced communication difficulties between the sUAS navigation software and remote pilot, but DJI's failsafe system was efficient at preventing damaging accidents. Overall, our sUAS was easy to

deploy, autonomously controlled, and cost efficient. Our research suggests that this sUAS is well suited as an unmanned aircraft in terms of logistics for lek surveys (Hodgson et al. 2010).

However, it was frequently detected by grouse at altitudes ≤ 121 AGL during variable wind speeds.

Our findings suggest that low altitude (≤ 121 m AGL) restrictions to sUAS surveys may limit the potential of sUAS as a substitute for manned, aerial surveys. Despite this, sUAS show promise to alleviate concerns with manned, aerial surveys with ease of deployment, potentially lower operation cost (Wing et al. 2014), and alleviated risks. We extend caution when deploying sUAS on prairie grouse and call for future research in sUAS methodology to identify and alleviate behavioral responses grouse express towards sUAS to determine appropriate sUAS survey protocols. Future research should explore various survey altitudes > 121 m AGL to determine disturbance thresholds for sUAS lek surveys. This will likely require exemption permits or changes to current sUAS regulations set by the FAA. Increasing survey altitude will require more advanced sUAS platforms, so additional sUAS models should be evaluated.

Though much remains unknown about sUAS and wildlife research, our study outlines concerns that need consideration during future research and we hope it will be useful to other researchers that are exploring the use of sUAS in grouse lek surveys.

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CHAPTER 2. DUCK PRODUCTION IN RETIERD CONSERVATION RESERVE PROGRAM LANDS

Introduction

Anthropogenic land use is driving global loss of grasslands (Samson et al. 2004). This has led to significant reductions in habitat for many migratory grassland birds (Askins et al. 2007), which are an important natural resource in North America (US Census Bureau 1996). Despite the ongoing loss of grassland, duck populations in North America have increased over the last several decades (U.S. Fish and Wildlife Service 2019). Federal conservation programs, such as the Conservation Reserve Program (hereafter, CRP) have assisted duck conservation efforts by creating nesting cover on marginal agricultural lands (Reynolds et al. 2001). However, CRP contract stipulations make it subject to disenrollment at the end of a contract period. As a result, total hectares of perennial vegetation associated with these programs has been declining throughout much of United States due to new congressional policies and high commodity prices (SWCS 2008, USDA-FSA 2015). In response, ecologists and land managers need to investigate management practices that incentivize maintaining perennial cover to promote the conservation of grassland dependent waterfowl.

The extensive shallow wetland depressions that make up the Prairie Pothole Region in the northern Great Plains is known as the centralized breeding ground for North American waterfowl and contributes 70% of the continents duck production (Bellrose 1976; Smith et al. 1964). As a consequence, duck production has disproportionately been studied within this region (Klett et al. 1988; Stephens et al. 2005; Williams et al. 1999). This emphasis has undoubtedly benefited duck conservation in the prairie pothole region through improved understanding and subsequent management practices. However, it has generally resulted in a lack of research focus

on the adjacent, Northwestern Great Plains (e.g., Western North and South Dakota). This Northwestern Great Plains region is experiencing some of the highest rates of loss in perennial vegetation cover from landowner disenrollment and contract expiration in CRP (USDA-FSA 2017), which is threatening nesting cover for ducks and other grassland associated biodiversity.

The Conservation Reserve Program was established as part of the 1985 Food Security Act in part to alleviate top soil runoff on marginal crop lands in the United States (USDA, 2018). The Conservation Reserve Program improves soil quality (Karlen et al. 1999), offers drought relief for livestock producers (USDA-Agriculture Act of 2014), and expands perennial cover for wildlife by compensating private landowners for planting perennial cover on their marginal crop land (Reynolds et al. 1994, 2001; Ryan et al. 1998; Herkert 2007, 2009). High commodity prices and reduced caps on enrollment set by the U.S. congress have reduced total CRP hectares by nearly 65% nationwide (Hellerstein and Malcolm 2011; Stubbs 2014; Wachenheim et al. 2018). In North Dakota, roughly 770 thousand hectares of CRP have ended their contract term since 2007 with most returning to crop production (USDA-FSA 2017). For conservation of grassland dependent wildlife to be successful, we need to consider strategies that can maintain post-CRP grassland and minimize conversion of these areas to row-crop agriculture or other land uses. One land use that is compatible with post-CRP lands is grazing. In circumstances where post-CRP is managed for livestock, conservation would benefit from research that attempts to identify management practices that can simultaneously bolster livestock production and nesting grassland birds such as waterfowl.

Working landscapes are defined as lands managed with the intent of producing a commodity (i.e., cattle) while conserving wildlife (Polasky et al. 2005). Our understanding of the conservation value of grazing on gamebirds within working landscapes is incomplete due to

variability in stocking rates (Dettenmaier et al. 2017), grazing systems (Ignatiuk et al. 2001), wildlife species (Holechek et al. 1982), and animal life stages (Taylor et al. 1999). It is generally thought that suitable levels of waterfowl production rely on dense nesting cover associated with idle grasslands (Duebert 1969; Duebert and Lokemoen. 1976). Early evidence of this directed waterfowl conservation plans away from cattle grazing (U.S. Department of the Interior and Environment Canada 1986). However, the lack of disturbance associated with idle management practices can be problematic, as it tends to promote grasslands with limited structural heterogeneity and low levels of biodiversity (Bahm et al. 2011, Kral-O'Brien et al. 2019). Based on some potential negative ecological impacts of idle management, useful insights have been gathered more recently that suggest cattle grazing using moderate to light stocking rates can be compatible with suitable nesting cover for waterfowl (Bloom et al. 2013; Durham and Afton 2003; Warren et al. 2008). However, the limited research investigating waterfowl production in working lands is generally confined to the Prairie Pothole Region (Klett et al. 1988, Horn et al. 2005, Stephens et al. 2005, Bloom et al. 2013, Skone et al. 2016). Research is needed to investigate the influence of grazing on duck production in the adjacent landscapes of the Northwestern Great Plains region as it potentially represents a way to maintain grasslands important to waterfowl nesting.

To address this, we assessed duck production on working landscapes in Southwestern North Dakota over a span of 10 years. Our main objective was to investigate the influence of temporal, biological, and ecological factors influencing nest survival in post-CRP lands with varying management regimes. Based on previous research, we expected management practices that result in greater vegetation density to have a positive effect on nest survival (Bloom et al. 2013; Stephens et al. 2005). Additionally, we expected that nest age would have a positive

influence on survival as previous studies have found that nest survival increases with nest age (Grant and Shaffer 2012; Stephens et al. 2005; Skone et al. 2016). Finally, we expected that landscape features such as crop cover would negatively influence survival (Sheldon et al. 2017) and weather parameters such as maximum temperature or solar radiation would have a negative impact on nest survival (Hovick et al. 2015).

Methods

Site Description

Our study took place on private lands managed for livestock production and wildlife by North Dakota State University's Hettinger Research Extension Center (hereafter HREC; N 46°00'10"; W 102°38'39"), located in Adams County, North Dakota, USA. The area is classified as a cold and temperate climate, with average spring/summer temperatures ranging from -0.55°–21.11°C and an annual precipitation gradient of 25.4–81.28 mm (North Dakota Agriculture Weather Network 2019). Adams County has lost 14,512 hectares of CRP since peak enrollment in 2004 (USDA-FSA 2020). Currently, cow/calf (*Bos taurus*) operations and small grain production occur on much of the landscape, with recent expansion of corn (*Zea mays*) and soybean (*Glycine max*) production.

We conducted research at two, ~186 ha sites that were enrolled in CRP for ≥ 14 years prior to 2006 (Geaumont et al. 2017). Species planted during the establishment of CRP included intermediate wheatgrass (*Elymus hispidus* (P. Opiz) Melderis), alfalfa (*Medicago sativa* L.), crested wheatgrass (*Agropyron cristatum* (L.) Gaertn), and yellow sweet clover (*Melilotus officinalis* (L.) Lam.). Land use, pasture size, and pasture configuration varied throughout the study. From 2006–2011, each site was divided to include a 129 ha pasture, a 32.5 ha hay field and a 32.5 ha idled field (no grazing, haying, or fire). We stocked pastures with Angus x

Hereford cow/calf pairs and grazed them season-long from June–January, targeting 50% total use of vegetation (~ 2.4 Animal Unit Month (AUM) \cdot ha⁻¹). We harvested hay fields once per year in July during the seed set stage. Idled fields were left undisturbed to mimic CRP management. From 2013–2015 both 20% and 40% season long (June-January) total use treatments were evaluated. At each site, the 129 ha pasture was divided into two separate 65 ha pastures. One of two stocking densities were randomly applied to each pasture. The 20% total use pasture was stocked with Angus x Hereford cow/calf pairs at 1.07 AUM \cdot ha⁻¹. The 40% total use pasture was stocked with Angus x Hereford cow/calf pairs stocked at 2.04 AUM \cdot ha⁻¹. We continued to harvest hay once annually in mid-July during seed set stage.

Nest Searches

We searched for upland duck nests 3–4 times per season using the chain drag method (Higgins et al. 1969). We used a 30 m section of 0.78 cm chain connected between two all-terrain vehicles, traveling at a pace of 8–17 km per hr to locate nests. All-terrain vehicle operators used a hand-held Global Position System to track vehicle movements and insure systematic and complete coverage of sites during nest searches. Operators also acted as the visual observers to identify when and where a hen flushed from a nest. Nest searches took place during the peak nesting season, occurring from 6 May through 15 July. Data concerning ducks was not collected in 2012. To increase the probability of encountering an incubating hen, searches occurred between the hours of 0700 and 1300 MST (Klett et al. 1986). Sites had a “rest period” of ≥ 2 weeks in between each nest search to minimize disturbance on incubating hens. All previously located active nests were avoided during subsequent nest searches.

When a nest was located, we recorded the Universal Transverse Mercator coordinate using a Global Position System and flagged the nest with a piece of orange plastic tape 5 m north

of the nest bowl. We determined the time of nest initiation and anticipated hatch date by aging egg embryos. For this, we used a candling technique that uses natural light and a small tube (Weller 1956). We visited all nests at 3–5 day intervals, or until nest fate was determined. During each nest visit, we recorded hen presence/absence, time, date, number of eggs, and the stage of the nest (Ralph et al. 1993). We considered a nest successful if ≥ 1 egg hatched from the nest.

Vegetation and Landscape Sampling

We assessed visual obstruction and maximum vegetation height of live and standing dead vegetation with a Robel pole at 1.25 and 2.5 m from each nest bowl within two days of a successful nesting attempt or after the estimated hatch date for unsuccessful nests (Robel et al. 1970). Visual obstruction readings (hereafter, VOR) were collected by reading the highest strata that was at least 50% obscured from a distance of 4 m and a height of 1 m at each cardinal direction (Robel et al. 1970). We averaged maximum vegetation height, standing dead vegetation, and VOR values that were collected at the same distance from a nest for the analyses (i.e., 1.25 and 2.5 m). We visually estimated standard Daubenmire canopy cover of grasses, forbs, litter, and bare ground (Daubenmire 1959) using a 1 m² frame at each corner of the nest bowl. We recorded management treatments for each pasture searched for nesting waterfowl as season long (i.e., standard, 50% forage utilization), season long 20 (i.e., 20% forage utilization), season long 40 (i.e., 40% forage utilization), idle, or hayed (i.e., one hay harvest after the completion of the nesting season).

Landscape Classification

We quantified landscape characteristics by measuring the distance from each nest to wetland edge, fence lines, and cropland edge. We chose these three landscape features based on their prominent occurrence at our study site and previous research identifying them as important

for nest survival of ducks (Horn et al. 2005; Howerter 2003; Stephens et al. 2005). Wetland and cropland cover was digitized using GeoEye IKONOS imagery in ArcMap 10.6. Annual changes in land cover and fence lines were verified using the historical imagery tool in Google Earth Pro and site maps created annually by the research staff at HREC. We then created distance rasters using the Euclidean distance tool in ArcMap 10.6. The raster grid was then used to measure both linear and quadratic distances from each duck nest to each landscape feature. The relationship between nest survival and landscape feature edge is variable and can have a linear (Howerter 2003) and curvilinear (Stephens et al. 2005) effect.

Data Analysis

We used the nest survival package in program MARK (White and Burnham 1999, Dinsmore and Dinsmore 2007) to evaluate the effects of species, temporal, vegetation, land use, and climatic variables on daily survival rates (hereafter, DSR) of duck nests. We evaluated DSR of duck nests across a 91-day nesting period standardized across years as 6 May to 4 August. We assigned our encounter history to nine groups, representing each year of the study. We created “dummy” variables for management category and species. To evaluate the influence of weather on the survival of duck nests during our study, we obtained daily measures of maximum temperature, solar radiation, precipitation accumulation, and relative humidity for each day of the 91-day nesting period (6 May through 4 August, 2006–2015) from a local weather station at HREC. In addition, we included three temporal and one biological variable that are linked to nest survival [year, nest age, day of the season, and species of duck (Klett et al. 1988, Grant and Shaffer 2012)].

We evaluated DSRs of duck nests through a hierarchical modeling step approach using *a priori* candidate models (Dinsmore and Dinsmore 2007, Hovick et al 2012). We categorized

covariates by placing them into four designated model groups. The nuisance variables model group included year, species, nest age, and Julian date. The vegetation model group consisted of variables collected at distances of either 1.25 m or 2.5 m from the nest including VOR, maximum live vegetation height, and maximum standing litter height. The vegetation model group also included cover of grasses, forbs, litter, and bare ground. Variables measured at 1.25 m and 2.5 m from the nest were treated as different scales during the analyses. The landscape model group consisted of variables measured within and surrounding the study site including pasture management, distance to wetland edge, distance to fence line, and distance to cropland edge. The weather model group included variables measured at the onsite weather station (i.e., listed above).

Prior to fitting models, we assessed variables for multicollinearity using Pearson's correlation, and kept the more interpretable variable from any correlated variable pairs ($r > 0.7$; Coppedge et al., 2008). We then ran univariate models within all four covariate groups and ranked them based on their AIC_c values and in relation to an intercept only (null) model (Burnham and Anderson 2002). We assessed both the linear and quadratic trends of VOR, maximum live vegetation height, maximum standing litter height, distance to fence, distance to wetland edge, and distance to cropland edge (Stephens et al. 2005, Bloom et al. 2013). All covariates including a quadratic trend also included a linear term. Models from each group with greater relative importance than the intercept-only model, and within 2 AIC_c units of the best model within their model group were then used to generate a "best" model set (Hovick et al. 2015). Additionally, models that were hierarchically more complex versions of the top model were not included in the best model set to limit consumption of model weights from the hierarchically simpler model (Arnold 2010, Pagano and Arnold 2009). The best model set

included all supported univariate models, all possible two and three-way combinations of those supported variables, an intercept-only model, and a global model (Loss and Blair 2011). This allowed each supported variable equal opportunity to be included in the top model within the best model set. We calculated model-averaged parameter weights for each variable that was strongly supported in the best model set by summing their AIC_c weights [w] and dividing them by the total number of models each independent variable appeared in (Burnham and Anderson 2002). This method allowed us to determine the most informative parameters from multiple competitive models. We calculated 95% confidence intervals (CI) for variables in the top model from the final model set to gauge their effect. We considered variables whose coefficient estimate included zero in the 95% CI to be uninformative.

Table 2. Summary statistics for variables used to examine duck nest survival at the Hettinger Research Extension Center, ND, USA, 2006-2011 & 2013-2015.

Parameter	Mean (SE)	Range	Definition
Nearby nest (average measurements taken at each cardinal direction within 1.25 and 2.5 m of a nest)			
Vegetation height 1.25 (dm)	6.91 (0.12)	0.00-13.00	Tallest living vegetation 1.25 m from a nest
Standing dead litter 1.25 (dm)	2.69 (0.10)	0.00-10.31	Tallest standing dead litter 1.25 m from a nest
Vegetation height 2.50 (dm)	7.64 (0.14)	2.31-33.25	Tallest vegetation 2.50 m from a nest
Standing dead litter 2.50 (dm)	2.98 (0.11)	0.00-11.00	Tallest standing dead litter 2.50 m from a nest
Visual obstruction 1.25 (dm)	2.73 (0.06)	0.22-6.77	Robel Pole measurement 1.25 m from a nest
Visual obstruction 2.50 (dm)	3.67 (0.06)	0.05-22.94	Robel Pole measurement 2.50 m from a nest
Percent grass	65.77 (1.00)	0.00-100.00	Percent grass canopy cover
Percent forbs	19.87 (0.82)	0.00-88.25	Percent forb canopy cover
Percent litter	17.99 (0.88)	0.00-100.00	Percent litter cover
Percent bare ground	3.99 (0.36)	0.00-50.00	Percent bare ground cover
Landscape feature			
Distance to wetland edge (m)	238.70 (8.26)	0.00-1587.65	Distance from nest to nearest wetland edge
Distance to fence (m)	144.10 (6.34)	0.00-2138.47	Distance from nest to nearest fence line
Distance to cropland edge (m)	279.00 (9.16)	0.00-2056.80	Distance from nest to nearest cropland edge
Weather (data collected from HREC weather station)			
Maximum temperature (°C)	24.37 (0.23)	2.11-42.16	Daily maximum temperature recorded
Solar radiation (MJ/m ² day)	547.75 (5.66)	73.49-768.22	Daily totals of solar radiation
Rain accumulation (cm)	0.25 (0.02)	0.00-6.10	Daily total rainfall accumulation
Relative humidity	65.39 (0.50)	18.74-99.81	Average daily relative humidity
Factor parameter	Factor levels	Observations	Description
Pasture management	SL20	37	Season long grazing targeting 20% use
	SL40	56	Season long grazing targeting 40% use
	SL	189	Season long grazing targeting 50% use
	ID	129	Idled fields serving as wildlife cover
Duck species	HY	60	Hay fields
	BWTE	75	Blue-winged teal (<i>Spatula discors</i>)
	GADW	150	Gadwall (<i>Mareca strepera</i>)
	MALL	136	Mallard (<i>Anas platyrhynchos</i>)
	NOPI	69	Northern pintail (<i>Anas acuta</i>)
	NSHO	20	Northern shoveler (<i>Spatula clypeate</i>)
	AMWI	21	American wigeon (<i>Mareca americana</i>)
Year	2006	45	Number of nests found each year.
	2007	38	
	2008	32	
	2009	51	
	2010	54	
	2011	92	
	2013	51	
2014	54		
2015	54		

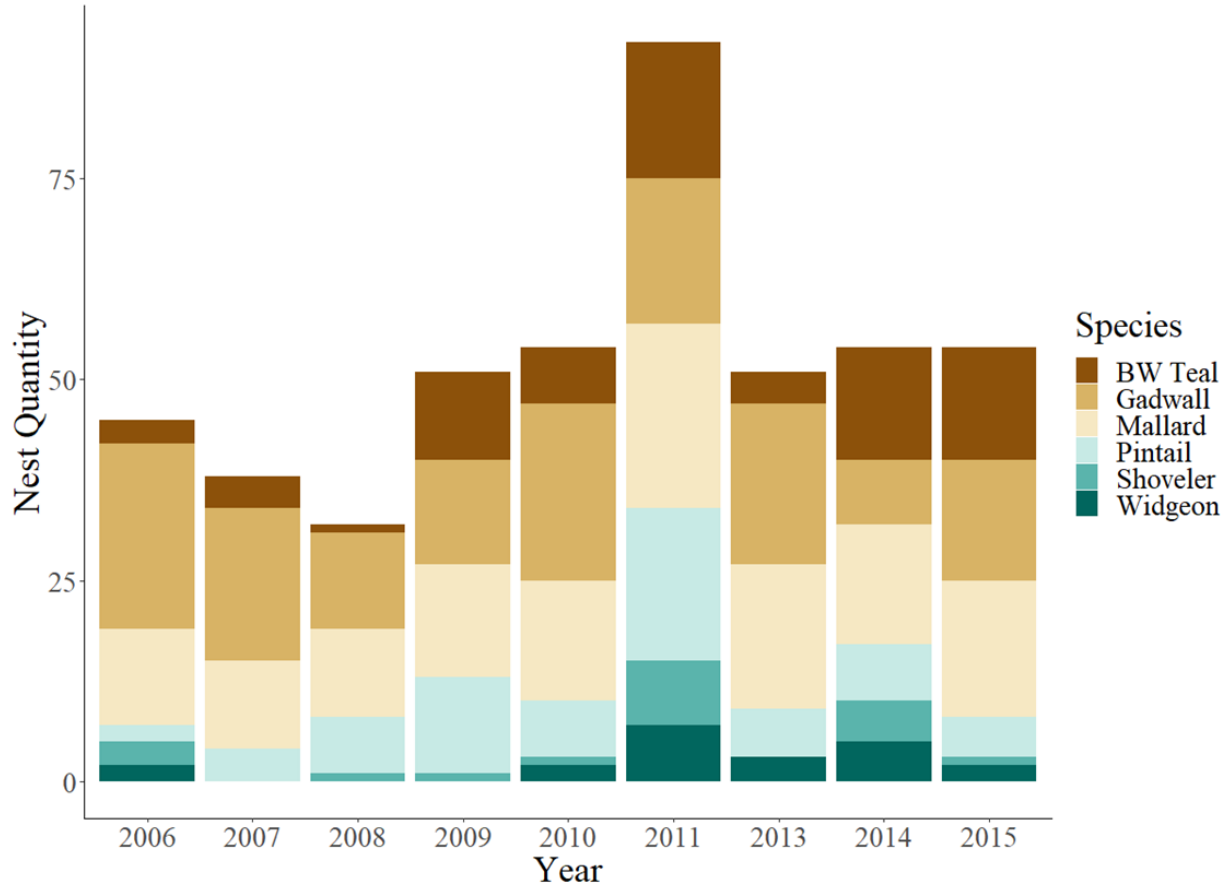


Figure 6. Annual cumulative total of duck nests from all species at Hettinger Research Extension Center, North Dakota, USA, 2006–2011 & 2013–2015.

Results

We found a total of 471 duck nests over the course of our ten-year study. Annual nest totals fluctuated from a low of 32 in 2008 and a high of 92 in 2011 (Table 1 and Fig. 1). Overall species composition of nests was 32% gadwall (*Mareca strepera*), 29% mallard (*Anas platyrhynchos*), 16% blue-winged teal (*Spatula discors*), 15% Northern pintail (*Anas acuta*), 4% American widgeon (*Mareca americana*), and 4% Northern shoveler (*Spatula clypeate*). From 2006–2011 we found 189 duck nests in season long grazing pastures, 85 in idle management pastures, and 38 in hay management pastures. During later portions of the study from 2013–2015 we found 56 duck nests in season long grazing pastures targeting 40% use, 44 in idle

management pastures, 37 in season long grazing pastures targeting 20% use, and 22 in hay management pastures. The constant survival rate for the study was 0.975 and based on a 35-day nesting period the overall probability of nest survival was 41%.

The most informative nest survival model included nest age, vegetation height at 1.25 m from the nest, and relative humidity (Table 2). Three additional models were informative and included nest age, vegetation height at 1.25 m from the nest, relative humidity, the quadratic distance to cropland edge, and the quadratic distance to fence (Table 2). Both the quadratic distance to cropland edge and fence line had 95% CI that included zero and were uninformative parameters. Nest age positively influenced nest survival (parameter importance weight = 0.08), with survival increasing as the nest progressed [$\beta_{\text{nestage}} = 0.03$, 95% CI = 0.01 to 0.04] Fig. 2]. Vegetation height at 1.25 m positively influenced nest survival (parameter importance weight = 0.08), with survival increasing as vegetation height increased [$\beta_{\text{vegheight1.25}} = 0.16$, 95% CI = 0.09 to 0.22] Fig. 2]. Relative humidity positively influenced nest survival (parameter importance weight = 0.04), with survival increasing at greater levels of relative humidity [$\beta_{\text{rh}} = 0.02$, 95% CI = 0.00 to 0.03] Fig. 2].

Table 3. Model selection results of top models in each model group for a study assessing daily survival rates of duck nest at Hettinger Research Extension Center, North Dakota, USA, 2006–2011 & 2013–2015. Parameter definitions can be found in Table 2.

Model	ΔAIC_c^a	w^b	K^c	Deviance	Model Likelihood
Nuisance Variable Models					
Nest age	0.00	0.97	2	1009.33	1.00
Nearby Nest Models					
Vegetation height at 1.25 m from nest	0.00	0.70	2	871.14	1.00
Vegetation height at 1.25 m from nest ²	1.93	0.27	3	871.06	0.38
Landscape Models					
Distance to cropland edge ²	0.00	0.39	3	1020.38	1.00
Distance to fence ²	0.94	0.24	3	1021.32	0.63
Weather Models					
Relative humidity	0.00	0.87	2	1018.77	1.00
Best Models					
Relative humidity + nest age + vegetation height at 1.25 m from a nest ^d	0.00	0.35	4	1000.24	1.00
Nest age + vegetation height at 1.25 m from a nest + nest distance to cropland edge ²	0.88	0.22	5	999.11	0.65
Global	1.71	0.15	8	993.93	0.43
Nest age + vegetation height at 1.25 m from a nest	1.82	0.14	3	1004.07	0.40

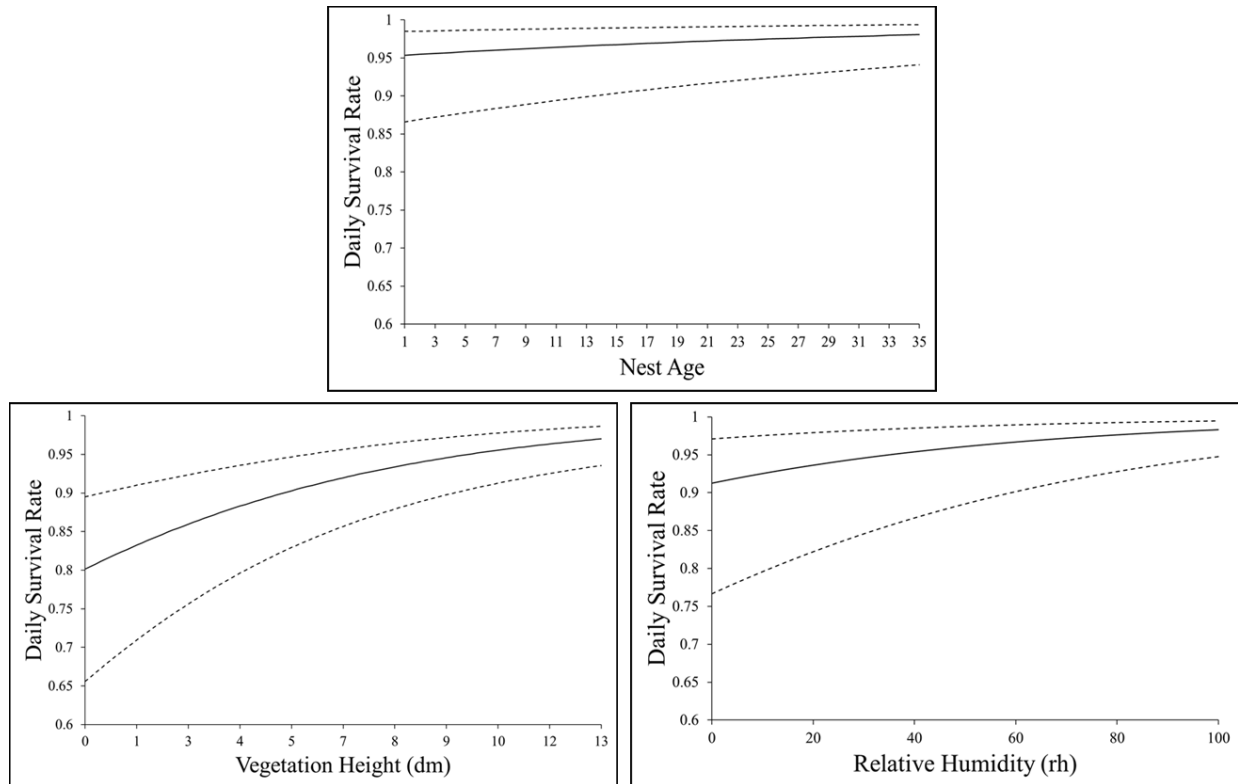


Figure 7. Projected daily survival rates and 95% confidence intervals based on the top model (Nest age +Vegetation height 1.25 m from nest + Relative humidity) for duck nests at Hettinger Research Extension Center, North Dakota, USA, 2006–2011 & 2013–2015.

Discussion

The loss of CRP and conversion to other land cover in the Northwestern Great Plains limits suitable nesting cover for ducks and threatens conservation efforts. Current research in the adjacent Prairie Pothole Region suggests that survival of waterfowl nests is correlated with measures of perennial vegetation cover (Bloom et al. 2013; Higgins et al. 1992; Reynolds et al. 2001; Stephens et al. 2005) and nest age (Stephens et al. 2005). In our investigation of duck nest survival in working landscapes adjacent to the Prairie Pothole Region, we found vegetation height and nest age both had a positive effect on duck nest survival. Additionally, we found that nest survival increased as relative humidity increased. Our study demonstrates that multiple factors can influence duck nest survival, and while management treatments did not have a direct effect on survival, vegetation height is influenced by management actions which emphasizes the need for thoughtful planning in working landscapes. Previously, it has been suggested that grazing is incompatible with upland nesting waterfowl (Higgins 1977; Klett et al. 1988), however, our research provides evidence that conservation based grazing practices and duck nesting can be compatible in post-CRP fields. Moreover, a slight decline in survival or nesting effort in post-CRP fields as a result of grazing far outweighs the downside of these areas converting back to row-crop agriculture. Additionally, grazing can provide benefits for biodiversity conservation in addition to nesting waterfowl (Watkinson and Ormerod 2001, Koper and Schmiegelow 2007). Grassland biodiversity benefits from CRP (Dunn et al. 1993) and with considerate planning, working landscapes that include post-CRP fields could have a similar effect.

Temporal variation in nest survival is common in studies of upland nesting ducks (Grant and Shaffer 2012; Stephens et al. 2005; Skone et al. 2016), and was important in our study. We

found that nest survival increased as the nest aged. As a nest progresses, a hen will spend more time incubating eggs and tending to the nest (Klett and Johnson 1982). The presence of a hen at the nest could discourage small nest predators from attempting to depredate the eggs (Skone et al. 2016). This might explain higher nest survival when we expect less frequent recess events. If a large proportion of the predator community consists of small rodents or reptiles than a nest is most vulnerable to predation during a recess event (Afton and Paulus 1992). Hens can mitigate the risk of predation associated with recess events by selecting nest sites with greater concealment (Crabtree et al. 1989, Bentzen et al. 2009).

Our findings suggest that survival estimates of nests increased as vegetation height around the nest increased. Nest survival increasing with vegetation height and/or density surrounding the nest is a common finding in waterfowl research in the prairie pothole region (Higgins et al. 1992, Durham and Afton 2003, Stephens et al. 2005, Skone et al. 2016) and our study found it important in an adjacent landscape. Taller vegetation structure allows for better nest site screening cover and can lower detection from possible nest predators (Duebbert and Kantrud 1974). Vegetation height is also important for mitigating the thermal environment around a nest which can have direct effects on embryo survival and hen behavior (Walsberg, 1985, Hovick et al. 2014). Parental decisions (i.e., nest site selection) are driven by vegetation characteristics that help stabilize a nest's thermal environment and assist in the incubation of the developing embryos (Carroll et al. 2018). Thus, successful nests are associated with nest site selection behavior that allow for greater nest concealment and thermal mitigation (Lokemon et al. 1984, Borgo and Conover, 2016). If waterfowl conservation is a goal, land managers will need to use practices that leave suitable vegetation structure for the nesting season. Grazing directly alters vegetation structure and composition but we found no evidence in our study that

duck nest survival was effected by land management. These results coincide with previous research that found vegetation height more important than management in nest survival (Koper and Schmiegelow 2007). Grazing will be a more effective tool for duck conservation if producers use stocking rates and use periods that allow for adequate vegetation heights to persist during the nesting season (Koper and Schmiegelow 2007, Warren et al. 2008, Bloom et al. 2013). Land managers should consider low to moderate stocking rates and reduce grazing intensity during the breeding season to manage for waterfowl nesting cover (Bloom et al. 2013).

We found a positive relationship between relative humidity and nest survival. This relationship has been found in a previous study of upland nesting gamebirds where nest survival increased with greater levels of relative humidity (Fogarty et al. 2017). These results contradict the idea behind the moisture-facilitated depredation hypothesis. This hypothesis assumes that water molecules propagate odorant molecules on the surface of eggs and other components of a nest, which then allows olfactory predators to locate nests more effectively (Conover, 2007; Palmer et al. 1993; Roberts et al. 1995). Explanations as to why we didn't see this response in our study may be related to the predator community at our research site (Fogarty et al. 2017). If our study site consisted of lower numbers of olfactory predators, then the vulnerability of a nest would not increase at higher levels of relative humidity. Additionally, in more arid climates, hatchability of duck eggs relies on sufficient moisture (Mayhew 1955). Increased levels of relative humidity could assist in the incubation process and explain why we witnessed increased nest survival at higher levels of relative humidity. The influence of relative humidity was important for our study, but its effect is likely driven by ecological interactions beyond what was measured at the nest site. This could explain variation in the literature in regards to studies finding conflicting effects of weather on nest survival (Fogarty 2017). Regardless of the effect,

our study is consistent in that weather is relevant to upland nesting bird production and should be considered in future assessments (Geaumont et al. 2017; Grisham et al. 2016; Hovick et al. 2015).

Continued loss of perennial grassland cover from row crop production on post-CRP fields will have negative consequences on grassland biodiversity (King and Savidge 1995). Research in the Prairie Pothole Region provide support for continued conservation of perennial vegetation structure for nesting waterfowl (Klett et al. 1988; Stephens et al. 2005; Warren et al. 2008). Our results support these findings in adjacent landscapes. If waterfowl production is a goal, land use that maintains perennial cover should be used. Livestock production appears to be a feasible option depending on how it is applied. This could not only assist duck conservation but also support rural economies (Bloom et al. 2013). This will require grazing systems to incorporate stocking rates and use grazing periods that will leave adequate measures of vegetation structure ≥ 9.5 dm during the nesting season, allowing for better nest concealment (Koper and Schmiegelow 2007, Warren et al. 2008). Furthermore, in addition to temporal and structural attributes, weather variables should be included in future research of duck production.

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**APPENDIX. MODEL SELECTION RESULTS OF MODELS IN EACH MODEL GROUP
FOR A STUDY ASSESSING DAILY SURVIVAL RATES OF DUCK NESTS AT
HETTINGER RESEARCH EXTENSION CENTER, NORTH DAKOTA, USA, 2006–2011
& 2013–2015. PARAMETER DEFINITONS CAN BE FOUND IN TABLE 2.**

Model	ΔAIC_c^a	w^b	K^c	Deviance	Model Likelihood
<i>Nuisance Variable Models</i>					
Nest age	0.00	0.97	2	1009.33	1.00
Year	6.99	0.03	9	1002.30	0.03
Null	15.38	0.00	1	1026.72	0.00
Date	15.63	0.00	2	1024.97	0.00
Date ²	16.49	0.00	3	1023.82	0.00
Species	19.22	0.00	6	1020.55	0.00
<i>Nearby Nest Models</i>					
Vegetation height 1.25	0.00	0.70	2	871.14	1.00
Vegetation height 1.25 ²	1.93	0.27	3	871.06	0.38
Vegetation height 2.50 ²	6.50	0.03	3	875.64	0.04
Vegetation obstruction 1.25 ²	11.68	0.00	3	880.82	0.00
Vegetation obstruction 1.25	12.28	0.00	2	883.42	0.00
Vegetation obstruction 2.50 ²	14.32	0.00	3	883.45	0.00
Vegetation height 2.50	17.77	0.00	2	888.90	0.00
Vegetation obstruction 2.50	20.14	0.00	2	891.28	0.00
Standing dead litter 2.50 ²	23.63	0.00	3	892.76	0.00
Percent bare ground	25.81	0.00	2	896.95	0.00
Null	25.83	0.00	1	898.97	0.00
Standing dead litter 1.25	25.99	0.00	2	897.13	0.00
Standing dead litter 2.50	26.93	0.00	2	898.07	0.00
Percent litter	27.08	0.00	2	898.22	0.00
Percent forbs	27.28	0.00	2	898.42	0.00
Standing dead litter 2.50 ²	27.38	0.00	3	896.51	0.00
Percent grass	27.82	0.00	2	898.96	0.00
<i>Landscape Models</i>					
Distance to cropland edge ²	0.00	0.39	3	1020.38	1.00
Distance to fence ²	0.94	0.24	3	1021.32	0.63
Null	2.33	0.12	1	1026.72	0.31
Distance to cropland edge	3.59	0.06	2	1025.97	0.17
Distance to wetland edge ²	3.63	0.06	3	1024.01	0.16
Distance to wetland edge	3.67	0.06	2	1026.05	0.16
Distance to fence	4.10	0.05	2	1026.49	0.13
Pasture management	8.31	0.01	5	1024.69	0.02

Model	ΔAIC_c^a	w^b	K^c	Deviance	Model Likelihood
<i>Weather Models</i>					
Relative humidity	0.00	0.87	2	1018.77	1.00
Null	5.95	0.04	1	1026.72	0.05
Solar radiation	6.17	0.04	2	1024.94	0.05
Rain accumulation	7.28	0.02	2	1026.05	0.03
Maximum temperature	7.84	0.02	2	1026.61	0.02
<i>Best Models</i>					
Relative humidity + nest age + vegetation height 1.25	0.00	0.35	4	1000.24	1.00
Nest age + Vegetation height 1.25 + Distance to cropland edge ²	0.88	0.22	5	999.11	0.65
Global	1.71	0.15	8	993.93	0.43
Nest age + Vegetation height 1.25	1.82	0.14	3	1004.07	0.40
Nest age + Distance to fence ² + Vegetation height 1.25	2.13	0.12	5	1000.37	0.34
Relative humidity + Distance to cropland edge ² + Vegetation height 1.25	7.85	0.01	5	1006.09	0.02
Relative humidity + Vegetation height 1.25	8.23	0.01	3	1010.47	0.02
Relative humidity + Vegetation height 1.25 + Distance to fence ²	8.92	0.00	5	1007.16	0.01
Vegetation height 1.25 + Distance to cropland edge ²	11.21	0.00	4	1011.45	0.00
Vegetation height 1.25	11.89	0.00	2	1016.13	0.00
Distance to fence ² + Vegetation height 1.25	12.17	0.00	4	1012.41	0.00
Distance to cropland edge ² + Distance to fence ² + Vegetation height 1.25	13.56	0.00	6	1009.79	0.00
Relative humidity + Nest age + Distance to cropland edge ²	17.81	0.00	5	1016.05	0.00
Relative humidity + Nest age + Distance to fence ²	19.19	0.00	5	1017.43	0.00
Relative humidity + Nest age	20.15	0.00	3	1022.40	0.00
Nest age + Distance to cropland edge ²	21.18	0.00	4	1021.42	0.00
Nest age + Distance to fence ²	22.42	0.00	4	1022.66	0.00
Nest age	23.82	0.00	2	1028.06	0.00
Nest age + Distance to cropland edge ² + Distance to fence ²	23.99	0.00	6	1020.22	0.00
Relative humidity + Distance to cropland edge ²	28.70	0.00	4	1028.94	0.00
Relative humidity + Distance to fence ²	29.71	0.00	4	1029.95	0.00
Relative humidity	30.56	0.00	2	1034.81	0.00
Relative humidity + Distance to cropland edge ² + Distance to fence ²	31.58	0.00	6	1027.82	0.00
Distance to cropland edge ²	34.12	0.00	3	1036.37	0.00
Distance to fence ²	35.08	0.00	3	1037.33	0.00
Null	36.44	0.00	1	1042.68	0.00
Distance to cropland edge ² + Distance to fence ²	36.93	0.00	5	1035.17	0.00