GREATER PRAIRIE-CHICKEN (*TYMPANUCHUS CUPIDO*) DEMOGRAPHICS IN FRAGMENTED WISCONSIN LANDSCAPES: EXAMINING LIMITING VITAL RATES

By

Matthew S. Broadway

A Thesis

Submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

IN

NATURAL RESOURCES (WILDLIFE ECOLOGY)

College of Natural Resources

UNIVERSITY OF WISCONSIN-STEVENS POINT

Stevens Point, Wisconsin

December 2015

APPROVED BY THE GRADUATE COMMITTEE OF:

_____

Dr. Jason D. Riddle, Graduate Advisor

Associate Professor of Wildlife

_____

Dr. Scott D. Hull

Wisconsin Department of Natural Resources

_____

Dr. Tim Ginnett

Professor of Wildlife

_____

Dr. Aaron Thompson

Assistant Professor, Natural Resource Planning

EXECUTIVE SUMMARY

The North American Great Plains biome has experienced precipitous human-induced habitat losses exceeding 90% of its original distribution over the last century. These alterations are due to European expansion and concomitant land use practices. As a result, numerous grassland bird species have experienced continued declines throughout their endemic ranges. Not surprisingly, prairie-grouse have experienced range-wide declines and some extant populations persist in highly fragmented landscapes uncharacteristic of their evolutionary history. Such landscapes may limit populations by constraining vital rates (i.e., nest and brood survival). Furthermore, management practices may have unintended negative consequences. The Greater Prairie-Chicken (*Tympanuchus cupido*) population in Wisconsin persists in a highly fragmented landscape where management practices are under review (i.e., disturbance types and intervals); however, current demographic information regarding limiting vital rates for the Wisconsin Greater Prairie-Chicken (GRPC) population is lacking. Aside from apparent nest success estimates provided for the Buena Vista Grassland Management Area (Hamerstrom 1939, Hamerstrom and Hamerstrom 1973, Golner 1997, Toepfer 2006), minimal data on nest or juvenile survival is available. Thus, we sought to investigate the relative effects of environmental characteristics at local-, edge-, and patch-levels on GRPC nest and brood survival to inform future management of GRPC in Wisconsin. During the breeding season (March-May) of 2014 and 2015 we captured and radio-tagged 62 individual female GRPC using walk-in style traps. We subsequently located and monitored 74 GRPC nests of which 23 successfully hatched (i.e., ≥ 1 hatched egg). We used information theory (IT) with Akaike's Information Criterion adjusted for small

samples (AIC_c) and the nest survival option in Program MARK to analyze the

relationship between nest daily survival rate (DSR) and visual obstruction of the nest,

residual cover at the nest and nest area, distance to nearest edge, patch shape, patch size,

and percent core area in grass cover. We considered models competitive if ΔAIC_c values

were ≤ 2 AIC_c units of the top model. The most parsimonious model, $S_{(residual)}$, considered

nest DSR a function of residual vegetation at the nest and surrounding area ($\hat{S} = 0.9763$,

SE = 0.003, [95% CI = 0.9685, 0.9822], $w_i = 0.28$) and was ~ 2.5 times more likely than

the second competing model ($S_{(.)}$). The mean residual cover at successful and

unsuccessful nests was 31.9% and 44.1%, respectively. There was some model

uncertainty because the null ($S_{(.)}$; $\hat{S} = 0.9762$, SE = 0.003, [95% CI = 0.9684, 0.9820], $w_i =$

0.11) was competitive ($\Delta AIC_c = 1.83$). The top two models estimate success of ~ 43

percent.

We tracked females of successful nests ≥ 5 days/week ($n = 23$) via radio telemetry

from hatch to 90 days of age and performed weekly flush counts of broods until 70 days

of age, collar shedding, transmitter failure, hen mortality, or brood loss. We considered a

brood lost if 2 consecutive flushes yielded zero counts. We used the Young Survival

model in Program MARK which is based on the Lukacs model of young survival. This

particular model accounts for imperfect detection during counts. Using this model we

employed an IT approach with AIC_c to compare the importance of each a priori model.

GRPC survival was best explained when detection (p) and survival (Phi) estimates varied

across 3 and 4 intervals, respectively. Detection probability was considered different

across 3 intervals: p_1 (count 1), p_2 (counts 2-7), and p_3 (count 8-10). Conversely, survival

(Phi) was best explained using 4 age intervals: Phi_1 (0-14 days), Phi_2 (15-21 days), Phi_3

(22-28 days), and *Phi*$_4$ (29-70 days). Juvenile survival estimates were best explained by additive effects of residual and forb cover estimates at flush locations *(Phi*$_1$ = 0.96, SE = 0.02; *Phi*$_2$ = 0.84, SE = 0.04; *Phi*$_3$ = 0.66, SE = 0.08; Phi$_4$ = 0.82, SE = 0.03). We estimate survival probability during the study at ~ 0.16 (95% CI = 0.11, 0.22). Contrary to other studies, juvenile survival at our sites declined from hatch until 28 days of age which suggests predation may be a limiting factor. Vegetation characteristics best explained juvenile survival in our study and may exacerbate or mediate mortality from abiotic (i.e., extreme weather events) or biotic (i.e., predation) events. We recommend spatially and temporally altering current management practices (e.g. prescribed fire and grazing) that best mimic historical disturbances and promote desirable local-level vegetation characteristics.

DEDICATION

Although, this has been a definitively self-orchestrated endeavor, I am unequivocally indebted to numerous professionals I have become acquainted with during my brief career. Several of whom I also now call my best friends; my life has been forever altered and immeasurably more fulfilled by those friendships. I am immensely grateful to Shane Wellendorf for hiring me at Tall Timbers Research Station and Land Conservancy immediately after graduating from Auburn University. I surmise my position was finagled into existence subsequently affording me an opportunity that, otherwise, would not have existed. Certainly, that served to catalyze incredible future experiences. I suppose I may never have enjoyed the pleasure of working for Dan Gibson on Greater Sage-Grouse, Marcus Lashley and Colter Chitwood on white-tailed deer, or Greg Wann on white-tailed ptarmigan to name a few. I toured the country living out of a mobile Toyota-home; a vagabond of sorts. But, such is the life of a traveling technician. I challenged my body and mind to complete all contests without exemption and found my greatest work came during the most difficult times. I have acquired countless fond memories and as many regrets. However, I am thankful for every occasion that led me to Stevens Point to study under my graduate advisor, Dr. Jason Riddle. I cannot have imagined working for someone who would teach me so much of professionalism, character, patience, and consideration. I am thankful for my family, especially my parents, whose love and support were never limited by distance traveled. To those I mentioned, and many more unmentioned, this thesis is dedicated to them and everything they have done for me, consciously or otherwise.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

for *Phi* intervals 1-3, respectively. Estimates of forb cover at *Phi* intervals 1-3 were 27%

(±5.06), 31% (±5.83), and 32% (±6.65), respectively. 74

CHAPTER I: THE RELATIVE IMPORTANCE OF HABITAT CHARACTERISTICS AT MULTIPLE SPATIAL SCALES: GREATER PRAIRIE-CHICKEN NEST SURVIVAL IN FRAGMENTED AGRICULTURAL LANDSCAPES OF WISCONSIN

Abstract: Once the largest biome in North America, the Great Plains region is the most altered ecosystem in the United States. Habitat loss, degradation, and fragmentation likely have negative effects on population vital rates (i.e., nest and brood survival). Greater Prairie-Chickens (*Tympanuchus cupido*; GRPC) in Wisconsin persist in highly fragmented landscapes where nest survival may limit populations. Thus, we sought to identify environmental characteristics limiting GRPC nest survival. We trapped, radio-tagged, and monitored 62 female GRPC throughout the breeding, nesting and brood rearing seasons (April-September) of 2014 and 2015. Subsequently, we monitored 74 GRPC nests and derived nest DSR estimates with respect to environmental variables at multiple spatial scales (e.g., local-, edge-, and patch-level) using an IT approach in Program MARK. We considered models with ΔAIC_c values ≤ 2 AIC_c units of the top model to be competitive. The most parsimonious model $S_{(residual)}$ considered nest DSR a function of residual vegetation at the nest and surrounding area ($\hat{S} = 0.9763$, SE = 0.003, [95% CI = 0.9685, 0.9822], $w_i = 0.28$) and was ~ 2.5 times more likely than the next most competitive model. The relationship of nest DSR and residual cover was negatively linear ($\beta = -0.011$, SE = 0.005, [95% CI = -0.0233, -0.0002]). Some model uncertainty exists because the constant model ($S_{(.)}$; $\hat{S} = 0.9762$, SE = 0.003, [95% CI = 0.9684, 0.9820], $w_i = 0.11$)) was competitive ($\Delta AIC_c = 1.83$). Edge- and patch-level covariates did not explain nest DSR. Management and conservation activities should better mimic ecological

processes historically present at the local scale by spatially and temporally altering

management practices (e.g., prescribed fire, grazing, etc.).

Key words: Greater Prairie-Chicken, *Tympanuchus cupido*, Great Plains, grassland,

grassland birds, fragmentation, vital rates, nest survival, daily survival rate

INTRODUCTION

Prairie biomes depend on regular periodic disturbances supporting spatially and

temporally heterogeneous floral mosaics conducive to life-histories of grassland bird

assemblages (Anderson 1990, Fuhlendorf and Engle 2001, Powell 2008). However,

despite once being the most expansive vegetative communities in North America, native

prairie ecosystems are now the most altered in North America (Klopatek et al. 1979,

Johnsgard 2002) experiencing precipitously range declines following European

expansion (Samson and Knopf 1994, Svedarsky et al. 2000). The intensification of

concomitant land use practices caused ubiquitous landscape changes, habitat loss, and

degradation (Sampson and Knopf 1994, Fuhlendorf et al. 2002). Not surprisingly,

grassland bird communities have experienced population declines throughout endemic

ranges (Taylor and Guthery 1980, Knopf 1992, Herkert 1994, 1995; Vickery et al. 1999).

Specifically, Greater Prairie-Chicken (*Tympanuchus cupido*) declines attributed to habitat

loss, degradation, and fragmentation associated with anthropogenic disturbance are well

documented throughout historic ranges (Johnsgard and Wood 1968, Svedarsky et al.

2000, 2003; Johnson et al. 2011).

The range-wide history of Greater Prairie-Chicken (GRPC) abundance and

distribution also reflects that of Wisconsin, where populations became isolated after

extensive agrarian expansion and forest succession simultaneously fragmented suitable

habitat (Hamerstrom and Hamerstrom 1961, Svedarsky et al. 2000). Currently, the extant GRPC population in Wisconsin occupies the southern portion of the Central Wisconsin Grassland Conservation Area (CWGCA; Figure 1). This peripheral Wisconsin population suffered significant inbreeding depression before supplementing populations via translocations (Bateson et al. 2014). However, successfully integrating unique genetic material may not release populations from other demographic limitations. Nest survival is a limiting demographic parameter of prairie-grouse populations (Peterson and Silvy 1996, Wisdom and Mills 1997). Additionally, nest survival is a commonly studied population possibly impacted by fragmentation (Wilcove 1985, Paton 1994, reviewed in Stephens et al. 2005).

Fragmentation defines the process of landscape change or the resultant spatial pattern (Wiens 1995) and can negatively impact wildlife populations via formation of novel spatial physiognomies and patterns (Wilcove 1985, Andrén and Angelstem 1988, Faaborg et al. 1999). Those patterns are determined by size, shape, and spatial arrangement of dissimilar cover-types. Patch size may be important for area-dependent grassland birds serving as viable umbrella species, such as the GRPC (Samson 1980, Poiani 2001). However, patch-size incompletely describes multidimensional landscape features where area equivalent habitat patches may still be incongruent (i.e., same size, but different shapes). Thus, irregularly shaped patches creating edge quantities disproportionate to area may be better predictors of nest survival than area alone (Helzer and Jelinski 1999, Shake et al. 2012). The juxtaposition of suitable habitat and surrounding matrix form corollary ecotones that may influence predator behavior (Johnson and Temple 1990, Winter et al. 2000, Chalfoun et al. 2002, Hilty and

Merenlender 2004). These 'edge-effects' are well documented on forest nesting birds (Wilcove et al. 1986, Andrén and Angelstam 1988) and Fuhlendorf et al. (2002) found edge density was an important determinant of prairie-grouse population trends. Indeed, fragmentation has negative consequences on prairie-grouse occupancy (Samson 1980), movement and distribution (Pruett et al. 2009, Hovick et al. 2014, Shaffer et al. 2015), and population dynamics (Ryan et al. 1998, Hagen et al. 2003, McNew et al. 2012).

Furthermore, local-level vegetation characteristics likely influence site selection (Ryan et al. 1998, McNew et al. 2013) and nest survival rates. For example, available residual cover (Hamerstrom and Hamerstrom 1957, Kirsch 1974, Buhnerkempe et al. 1984, but see McKee et al. 1998), forb cover (McKee et al. 1998, Fields et al. 2006), vegetation height (Riley et al. 1992, Lutz et al. 1994), and visual obstruction (Pitman et al. 2005, Davis 2009) are considered conducive to quality nesting cover for prairie-grouse and may supersede, or obscure, the importance of immediate landscape characteristics. Indeed, grassland bird conservation requires simultaneous consideration of multiple spatial scales (Weins 1989, 1995; Bakker et al. 2002, Bissonette and Storch 2003).

Therefore, the Wisconsin DNR implemented the Central Wisconsin Grassland Conservation Area (CWGCA; Figure 1.1) to address grassland habitat management for GRPC and other grassland obligates at multiple spatial scales; however, no site-specific research elucidates the influence of spatial physiognomies on GRPC demographics in Wisconsin. Thus, our objectives were to determine the relative importance of local-, edge-, and patch-level characteristics best explaining nest daily survival rates (DSR) of the Wisconsin GRPC population by employing a multi-model selection technique and an information-theoretic approach. Previously, apparent nest success estimates have been

15

provided for one study area (Hamerstrom 1939, Hamerstrom and Hamerstrom 1973, Golner 1997, Toepfer 2006); however, apparent nest success estimates are subject to inherent bias (Mayfield 1961, 1975). Thus, we provide the first nest DSR estimates while considering environmental covariates for the Wisconsin population. Our research results provide insight to GRPC conservation at multiple spatial scales by considering the relative importance of local-, edge-, and patch-level spatial characteristics in a highly fragmented landscape where the state-threatened GRPC is a conservation priority.

METHODS

Study Site

Our study was conducted in the 3,600 km^2 Central Wisconsin Grassland Conservation Area in central Wisconsin, USA (N 516877, W 466134) and included sampling two distinct populations in close geographic proximity (i.e.,, 15 km). Both prairie-chicken populations are associated with two state-owned and managed wildlife areas, the Paul J. Olson Wildlife Area and Buena Vista Grassland Management Area (Figure 1.1). Paul J. Olson Wildlife Area (PJOWA) is located in eastern Wood and northwestern Portage Counties and is approximately 1,236 ha constituted by scattered parcels from 6.5 ha to 347 ha (mean = 59 ha). The Buena Vista Grassland Management Area (BVGMA) is located in southwestern Portage and northern Wood Counties. The BVGMA includes 5,140 ha owned and managed by the Wisconsin Department of Natural Resources. State-owned parcels range from 4.4 ha to 1,253 ha in size (mean = 178 ha). The BVGMA site is formerly a tamarack swamp and the result of a failed drainage project and some PJOWA properties are seasonally wet. Descriptions of plant communities are provided in

Niemuth (2000). Soil characteristics and topography are described by Otter and Fiala (1978).

Study sites are bisected by landscape features including urban development, forest, and the Wisconsin River which likely contribute to their physical separation. The mean daily maximum and minimum temperatures during January are ~ -4°C and -14°C. In July, those temperatures change to ~ 15°C and 26°C, respectively. The median growing season is approximately 145 days (range=123-159 days). Average annual precipitation averages 32.7 (BVGMA) and 31.9 cm (PJOWA), respectively. Climate data were retrieved from the National Oceanic and Atmospheric Administration (available at http://www.ncdc.noaa.gov/).

Capture and Monitoring

We captured female Greater Prairie-Chickens using walk-in style traps (Schroeder and Braun 1991) on established leks from March-May 2014 and 2015. We opened traps at astronomical dawn (available from the National Oceanic and Atmospheric Administration at http://www.esrl.noaa.gov/gmd/grad/solcalc/glossary.html) and continued trapping each day until lek dispersal or male activity ceased for ≥45 minutes. We captured and marked individuals with a serial-numbered metal state-band and aged via characteristics of primaries 9 and 10 (Johnson et al. 2011). We weighed females with a Pesola© spring scale to the nearest ± 5 grams, determined morphometrics of the tarsus (±0.01 mm) with digital calipers and wing chord (± 1 mm) using a Universal Standard Wing Ruler (30cm, Avinet, Inc., Dryden, New York). We radio-tagged female prairie-chickens with a 16g necklace-style VHF transmitter (Model #A3960, 796 day battery,

Advanced Telemetry Systems, Inc., Isanti, MN) equipped with a 6 hour mortality switch. We immediately released individuals at the capture location after processing.

We monitored hens via triangulation of VHF radio signals and homing techniques using portable receivers and hand-held Yagi antennas throughout the nesting (April-June) and brood rearing seasons (June-September). We calculated error ellipses and location coordinates using Program Radio-Tracker which utilizes methods from Lenth (1981). Sampling intervals were ≤ 30 minutes between first and third azimuth readings of marked individuals and bearing accuracy was recorded to ± 1° with a handheld compass. We used homing techniques to locate nesting females after hens localized based on previous locations and we flushed hens from nests after 3 consecutive equivalent locations.

Nest processing and monitoring. We flushed females from nests during early incubation to determine clutch size and incubation stage via egg floating techniques (McNew et al. 2009). Observers wore rubber boots and sterile nitrile gloves to reduce scent deposition during nest processing. We recorded nest locations with handheld GPS units to ±3 m in Wisconsin Transverse Mercator and affixed Thermochron iButton data-loggers (Model DS 1921G, iButtonLink, Whitewater, WI, USA) in nest bowls to record temperatures every 30 minutes; a second data-logger was secured to the ground ≤ 100 m from the nest to simultaneously record ambient temperatures. We monitored nesting females via triangulation and homing ≥ 5 times/week from distances exceeding 100 meters (McNew et al. 2012) unless nests were ≤100 meters from a road. Observers monitored hens via homing of radio signals ~ 20 meters away on the projected hatch date and every other day until females hatched or failed (Augustine and Sandercock 2011). If a hen was relocated away from her respective nest on 2 consecutive occasions, we visited

nests immediately to determine reproductive status. Nest fates were classified as failed

abandoned, failed destroyed, or successful (i.e., hatching ≥ 1 egg). We used differences

between nest and ambient Thermochron data loggers to determine timing of nest failures

to ± 30 minutes (Hartman and Oring 2006).

Nest data. We recorded local-level vegetative characteristics at the nest and

paired random points within 7 days of nest fates. Local-level covariates were obtained

using variations on digital imagery techniques. Specifically, we estimated visual

obstruction of the nest bowl by vegetation from taking digital images of a red sphere of

known pixel count placed in the nest. We took digital photos of the sphere from each

cardinal direction at a distance of 4 m and a height of 1 m. The visible red pixels in each

photo were totaled. That number was then divided by 4 times the pixel count of the

unobstructed spherical object, or

$$VO = \frac{P_N + P_W + P_S + P_E}{4(P_U)}$$

where P_i equals the number of visible red pixels from each cardinal direction (N, W, S, E),

or the unobstructed spherical object (U).

We processed obstruction photos using GNU Image Manipulation Program

(GIMP) (Kimball and Mattis 2006, open software package). Further use of digital

imagery was employed to acquire photos of the nest area. We visually estimated percent

residual cover (i.e., dead vegetation remaining from previous growing season) from

digital images of 1 m^2 frames (Daubenmire 1959) centered on nest bowls and 5 meters in

each cardinal direction. We did not distinguish between ground-level horizontal and

standing vertical vegetation strata within plots (Aldridge and Brigham 2002).

Subsequently, we derived mean residual cover estimates across all nest area photos.

Landscape characteristics at the edge- and patch-levels include percent grassland cover in female core area (i.e., 13 ha; McNew et al. 2013), patch-size, patch perimeter-area ratio (Helzer and Jelinksi 1999, Shake et al. 2009), and distance to nearest edge regardless of edge-type. We aggregated land-cover types that were structurally similar (i.e., hay/alfalfa, idle grasses, CRP) where predators likely do not perceive an edge (Winter et al. 2000). We defined patch size based on the total contiguous area of analogous cover-types. The perimeter-area ratio was a function of these aggregations and was calculated using methods equivalent to Shake et al. (2012). All distance measures were acquired using the Near tool in ArcToolbox in ArcGIS (ver. 10.3; Environmental Systems Research Institute, Redlands, CA). We extracted spatial information using the 2013 Central Wisconsin Grassland Conservation Area data layer (WDNR 2013). This vector data layer is remotely sensed and satellite imagery informed using National Agriculture Imagery Program (NAIP; U. S. Department of Agriculture 2013) of the CWGCA supplemented with ground-truthing methods to provide ~ 85 % accuracy of land cover classifications. Further, we visually inspected areas surrounding nest locations and corrected any polygon misclassifications according to site-specific knowledge and ground-truthing methods. Consequently, we reclassified agriculture cover types if they differed temporally from data layer production years.

Model Selection and Analyses

We determined biologically relevant a priori models using aforementioned covariates at multiple spatial scales to explain variation in nest DSR at each site. We constructed a

model lacking covariates (i.e., null) as our simplest model, single-variable, and interactive models investigating effects of local-level habitat and surrounding landscape attributes on nest survival. We used arcsin-transformations if mean covariate values approached theoretical limits (<0.3, >0.7; Zar 1999). We assumed an average exposure period of 36 days based on average female reproductive characteristics in our study. Specifically, we assumed a laying rate of 1 egg/day, average clutch size of 12 (range: 6-19, $x = 11.55$, $n = 70$), and an incubation period of 24 days (range: 21-29 days, $x = 24.5$, $n = 23$). We generated maximum likelihood estimates of GRPC nest daily survival rate (DSR) using the Nest Survival Model in Program MARK Version 7.1 (White and Burnham 1999). Unlike previous methods used to model nest survival, the nest survival model in Program MARK allows consideration of biologically relevant covariates (Dinsmore et al. 2002). We used an information-theoretic (IT) approach to quantify the relationship between nest survival and univariate and 6 independent variables as well as interactions thereof (Table 1.1). We considered the top model (i.e., that with the lowest AIC_c value) and models with ΔAIC_c values ≤ 2 as competitive. We calculated relative importance values for each variable based on the cumulative model weights in which a particular variable was present (Burnham and Anderson 2002). We provide the statistical results of our study ($\pm$ SE).

RESULTS

Descriptive Data

We captured 62 (20, PJOWA; 42, BVGMA) female GRPC during the breeding seasons (March-May of 2014, 2015) and monitored individuals via radio-telemetry until mortality, collar shedding, or transmitter failure. We detected and monitored 74 nests

from radio-tagged females and opportunistically found 2 nests from unmarked females that were included in analyses. We pooled nest data across sites and years ($n = 74$) because we included yearly ($S_{(year)}$) and site ($S_{(site)}$) models in analyses. The mean clutch size (11.56 eggs/clutch, range: 6-19) and mean hatching success (~ 85%) were similar to those reported by others (Hamerstrom and Hamerstrom 1973, Johnson et al. 2011, McNew et al. 2012). We estimated apparent nest success rates to 34% and field evidence suggests the majority of nest failures were mammalian depredations (57.7%). Other nest failures appeared to be caused by avian (7.7%) and reptilian (1.9%) depredations, trampling (1.9%), abandonment (1.9%), and mechanical implements (3.8%; e.g., haying or mowing implements). One nest was censored after being incidentally flushed early in laying because the observer suspected the female abandoned in response to i-Button placement (M.S. Broadway personal observation).

Nest Survival

Model $S_{(residual)}$ was the most parsimonious model (Table 1.1; $\hat{S} = 0.9763$, SE = 0.003, [95% CI = 0.9685, 0.9822], $w_i = 0.28$) and was approximately 2.5 times more likely than the next competing model. However, there was some model uncertainty with $S_{(.)}$ (constant model) being the second most competitive ($\Delta AIC_c = 1.83$, $\hat{S} = 0.9762$, SE = 0.003, [95% CI = 0.9684, 0.9820], $w_i = 0.11$). The mean percent residual cover at the nest and nest area was negatively related to nest DSR ($\beta = -0.011$, SE = 0.005, [95% CI = -0.0233, -0.0002]; Figure 1.2). The mean residual cover at successful and unsuccessful nests was 31.9% and 44.1%, respectively (Figure 1.2; Table 1.2). No interactive models were competitive and those including edge- and patch-level covariates generally received less support than models including local-level covariates (Table 1.3). Also, residual cover

alone received more support than all edge- and patch-level variables combined. The extrapolated apparent nest success estimate using a 36 day exposure period and $\hat{S}$ from model $S_{(residual)}$ is ~ 42% suggesting our apparent nest success estimates are biased low for these populations.

Likewise, nest survival ($\hat{S}$) parameter estimates (0.9762) for the $S_{(.)}$ model were similar and extrapolated to ~ 42% apparent nest success. Aside from residual cover estimates at the nest and nest area, no other environmental covariate explained variation in nest survival data better than the null model. The second best environmental covariate (third-ranked model) quantified visual obstruction of the nest bowl (i.e., $S_{(vo)}$; Table 1.1). Furthermore, model performance decreased with inclusion of interactive terms and variation in nest survival was not explained by site or year effects.

DISCUSSION

The results of our study suggest local-level quantities of residual vegetation reliably predict nest DSR in the Wisconsin GRPC population. The negative relationship between nest DSR and residual cover surrounding nests is consistent with previous research and suggestions that grasslands with excessive residual cover from previous growing seasons may provide poor prairie-chicken nesting cover (Hamerstrom et al. 1957, Yeatter 1963, McKee et al. 1998). McKee et al. (1998) showed excessive quantities of residual cover at GRPC nests predicted failure beyond a maximum threshold of ~ 25 percent. Additionally, Mathews et al. (2013) demonstrated decreased nest survival below the recommended 50% success rate (Westemeier 1973) when standing dead vegetation exceeded 25 percent. Nest DSR estimates in our study declined below ~ 0.98 (i.e., 50%) when residual cover exceeded the maximum threshold identified by McKee et al. (1998; Figure 2).

There are several possible mechanisms whereby residual cover influences nest survival. Excessive residual cover may catalyze failure events through indirect effects. For example, copious litter accumulation may reduce available sunlight to grasses and forbs thereby delaying spring vegetation growth and effectively limiting vertical vegetative cover for nests (Westemeier 1973). For example, Coates and Delahanty (2008) found incubation constancy increased with visual obstruction of Greater Sage-Grouse (*Centrocercus urophasianus*) nests and nest areas (i.e., 25 meter radii). Additionally, vegetation cover at nests may influence thermal conditions at nest sites and therefore metabolic demands on incubating females (Ar and Sidis 2002). Hovick et al. (2014) attributed significant differences in operative temperatures between nest sites and random locations within 2 meters of nests to thermal elasticity of adequate vegetation structure. Additionally, Guthery et al. (2005) showed nesting Northern Bobwhite Quail (*Colinus virginianus*) respond to thermal stress via gular flutter at approximately 30° Celsius. Incubating females may respond to such abiotic conditions (i.e., thermal environments) by increasing recess frequency (Afton 1980). Larger-bodied galliforme species may experience thermal stress at lower temperatures than Northern Bobwhite Quail (Hovick et al. 2014). Thus, female GRPC selecting nest sites with superfluous residual cover and minimal vertical and aerial cover may be exposed to thermal extremes requiring similar thermoregulatory behavior possibly contributing to nest detection by predators.

Furthermore, delayed or limited vegetation growth may reduce food availability near nests, thereby requiring incubating females to engage in more frequent or longer incubation recesses (Rastogi et al. 2006, Chalfoun and Martin 2007, Smith et al. 2007). During our study, mean incubation periods were similar to other reports (Johnson et al.

2011, McNew et al. 2013) but incubation ranged from 21-27 days based on nest bowl temperatures from iButton Thermochron data-loggers (M.S. Broadway personal observation). Extended incubation recesses may induce embryo cooling requiring longer incubation periods to hatch (Martin et al. 2007) and longer incubation periods may expose nesting females to increased predation rates. Behavioral responses to abiotic and biotic factors may increase predator detection of nests. These relationships may be exacerbated by plant community effects on alternative prey species. For instance, the presence of residual cover may attract opportunistic predators that incidentally depredate nests (Vickery et al. 1992). While the effect of litter accumulation varies among small mammal species (Kaufman et al. 1989), increased litter accumulation may provide high quality small mammal habitat (Svedarsky 1979, Westemeier and Buhnerkempe 1983) consequently attracting mesocarnivores that could opportunistically depredate GRPC nests. Local-level effects of vegetation structure may influence predator searching behavior resulting from increased prey availability and evidence suggests local-level characteristics supersede the importance of edge- and patch-level characteristics on GRPC nest survival at our study sites.

Our results corroborate those of McKee et al. (1998) and Pitman et al. (2005) who detected no edge-effect on GRPC nest survival. Additionally, Renfrew et al. (2005) detected no edge-effect and reported consistently low grassland bird nesting success. Furthermore, Walk et al. (2010) demonstrated that proximity to edge had no negative influence on Dickcissel (*Spiza americana*) and Eastern Meadowlark (*Sturnella magna*) nest success. Likewise, we found no effect of patch-size on GRPC nest survival; however, the importance of patch-size is arbitrated by spatial arrangement (Lefkovitch

and Fahrig 1985, Wiens 1989, Dunning et al. 1992) or patch quality (Dunning et al. 1992, Davis 2004). Thus, the lack of support for edge- and patch-level spatial physiognomies in our results should not negate their potential importance to GRPC and other grassland birds over broader temporal and spatial scales because study duration and scale of investigation may influence the detection of fragmentation effects (Stephens et al. 2003) and these effects may be species dependent (Johnson and Temple 1990, Winter and Faaborg 1999).

Conclusion

The results of our analyses suggest local-level nest vegetation characteristics are the best predictor of GRPC nest DSR at our sites. This further supports the importance of regular, intense management, such as prescribed fire and other disturbance mechanisms that reduce residual cover. Greater Prairie-Chickens evolved under selective pressures and ecological processes that were driven by regular disturbance and intense grazing by large ungulates (i.e., pyric herbivory; Fuhlendorf and Engle 2001). Although, discrepancies exist between minimum habitat recommendations for prairie-grouse (Hamerstrom et al. 1957, Taylor and Guthery 1980, Fuhlendorf et al. 2002), there is little disagreement regarding the necessity of management practices to duplicate the suite of vegetative characteristics conducive to life-history (Samson and Knopf 1994). We recommend limiting mowing practices that accelerate litter accumulation (McCoy et al. 2001) and suggest disturbance intervals of ~ 3 years (Millenbah et al. 1996, McCoy et al. 2001). We recommend practices more effective at removing residual cover and litter accumulation, such as discing (Greenfield et al. 2003) and burning (King and Savidge 1995) which may improve plant community structure and diversity (Collins and Gibson 1990). However,

plant communities may interact differentially with soil, climate, topography, and timing of fire (Gibson and Hulbert 1987, Sparks et al. 1998, Brockway et al. 2002). For example, forb and C4 grass net primary production (NPP) may be limited by soil moisture or other abiotic factors (Briggs and Knapp 1995). Because soil characteristics of these sites are dissimilar to tallgrass prairie regions, caution should be exercised on when implementing fire to avoid promoting undesirable plant species or vegetation structure characteristics. Future research at our sites should focus on the effects of variable disturbance intervals and types on GRPC nest site selection. Additionally, we suggest projects focused on the effects of disturbance type and intervals on vegetation structure, diversity and species richness, and insect and plant food availability.

ACKNOWLEDGEMENTS

volunteers at the University of Wisconsin-Stevens Point for help during the 2015 trapping season. All field protocols were approved by and conducted in accordance with the University of Wisconsin-Stevens Point Institute for Animal Care and Use Committee (Protocol #2013.11.1).

LITERATURE CITED

Afton, A. D. (1980). Factors affecting incubation rhythms of Northern Shovelers. The
   Condor 82:132-137.

Akaike, H. (1973). Maximum likelihood identification of Gaussian autoregressive
   moving average models. Biometrika 60:255-265.

Aldridge, C. L., & Brigham, R. M. (2002). Sage-grouse nesting and brood habitat use in
   southern Canada. The Journal of Wildlife Management 66:433-444.

Anderson, R. C. (1990). The historic role of fire in the North American grassland, pp 8-
   18 in, S.L. Collins and L.L. Wallace, eds., Fire in North American tallgrass
   prairie.

Andrén, H., & Angelstam, P. (1988). Elevated predation rates as an edge effect in habitat
   islands: experimental evidence. Ecology 69:544-547.

Augustine, J. K., & Sandercock, B. K. (2011). Demography of female Greater Prairie-
   Chickens in unfragmented grasslands in Kansas. Avian Conservation and
   Ecology 6:2.

Bakker, K. K., Naugle, D. E., & Higgins, K. F. (2002). Incorporating landscape attributes
   into models for migratory grassland bird conservation. Conservation Biology
   16:1638-1646.

Bateson, Z. W., Dunn, P. O., Hull, S. D., Henschen, A. E., Johnson, J. A., &
   Whittingham, L. A. (2014). Genetic restoration of a threatened population of
   Greater Prairie-Chickens. Biological Conservation 174:12-19.

Briggs, J. M., & Knapp, A. K. (1995). Interannual variability in primary production in
   tallgrass prairie: climate, soil moisture, topographic position, and fire as

determinants of aboveground biomass. American Journal of Botany 82:1024-1030.

Brockway, D. G., Gatewood, R. G., & Paris, R. B. (2002). Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. Journal of Environmental Management 65:135-152.

Buhnerkempe, J. E., Edwards, W. R., Vance, D. R., & Westemeier, R. L. (1984). Effects of residual vegetation on prairie-chicken nest placement and success. Wildlife Society Bulletin 12:382-386.

Burnham, K. P., and D. R. Anderson. (2002). Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

Chalfoun, A. D., Thompson, F. R., & Ratnaswamy, M. J. (2002). Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306-318.

_____, _. _., & Martin, T. E. (2007). Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. Animal Behaviour 73:579-585.

Collins, S. L., & Gibson, D. J. (1990). Effects of fire on community structure in tallgrass and mixed-grass prairie. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, 81-98.

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

Davis, S. K. (2004). Area sensitivity in grassland passerines: effects of patch size, patch

shape, and vegetation structure on bird abundance and occurrence in southern

Saskatchewan. The Auk 121:1130-1145.

Dinsmore, S. J., White, G. C., & Knopf, F. L. (2002). Advanced techniques for modeling

avian nest survival. Ecology 83:3476-3488.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect

populations in complex landscapes. Oikos 65:169-175.

Fields, T. L., White, G. C., Gilgert, W. C., & Rodgers, R. D. (2006). Nest and brood

survival of Lesser Prairie-Chickens in west central Kansas. Journal of Wildlife

Management 70:931-938.

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands:

Ecosystem Management Based on Evolutionary Grazing Patterns. BioScience

51:625-632.

_____, _. _., Woodward, A. J., Leslie, D. M., & Shackford, J. S. (2002). Multi-scale

effects of habitat loss and fragmentation on lesser prairie-chicken populations of

the US Southern Great Plains. Landscape Ecology 17:617-628.

Gibson, D. J., & Hulbert, L. C. (1987). Effects of fire, topography and year-to-year

climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-

185.

Golner, D. P. (1997). Analysis of habitat selection by female Greater Prairie Chickens in

Central Wisconsin. M.S. Thesis. University of Wisconsin-Stevens Point.

Greenfield, K. C., Chamberlain, M. J., Burger Jr, L. W., & Kurzejeski, E. W. (2003).

Effects of burning and discing Conservation Reserve Program fields to improve

habitat quality for Northern Bobwhite (*Colinus virginianus*). The American

midland naturalist 149:344-353.

Guthery, F. S., Rybak, A. R., Fuhlendorf, S. D., Hiller, T. L., Smith, S. G., Puckett Jr, W.

H., & Baker, R. A. (2005). Aspects of the thermal ecology of bobwhites in north

Texas. Wildlife Monographs 159:1-36.

Hamerstrom, F. N. (1939). A study of Wisconsin prairie chicken and sharp-tailed

grouse. The Wilson Bulletin 51:105-120.

Hamerstrom, F., Mattson, O. E., & Hamerstrom, F. (1957). A guide to prairie chicken

management (No. 15). Game Management Division, Wisconsin Conservation

Department.

_____, F., & Hamerstrom, F. (1961). Status and problems of North American

grouse. Wilson Bulletin 73:284-294.

_____, Jr, F. N., & Hamerstrom, F. (1973). The greater prairie-chicken in

Wisconsin-highlights of a 22 year study of counts, behavior, movements,

turnover, and habitat. Wisconsin Dept. Natural Resources. Technical Bulletin, 64.

Hartman, C. A., & Oring, L. W. (2006). An inexpensive method for remotely monitoring

nest activity. Journal of Field Ornithology 77:418-424.

Helzer, C. J., & Jelinski, D. E. (1999). The relative importance of patch area and

perimeter-area ratio to grassland breeding birds. Ecological Applications 9:1448-

1458.

Herkert, J. R. (1994). The effects of habitat fragmentation on midwestern grassland bird

communities. Ecological Applications 4:461-471.

_____, _. _. (1995). An analysis of midwestern breeding bird population trends: 1966-1993. American Midland Naturalist 134:41-50.

Hilty, J. A., & Merenlender, A. M. (2004). Use of riparian corridors and vineyards by mammalian predators in northern California. Conservation Biology 18:126-135.

Hovick, T. J., Elmore, R. D., Allred, B. W., Fuhlendorf, S. D., & Dahlgren, D. K. (2014). Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse. Ecosphere 5:3.

_____, _. _., Elmore, R. D., Fuhlendorf, S. D., & Dahlgren, D. K. (2015). Weather constrains the influence of fire and grazing on nesting Greater Prairie-Chickens. Rangeland Ecology & Management 68:186-193.

Johnsgard, P. A. (2002). Grassland grouse and their conservation. Smithsonian Institution Press, Washington, D.C., USA.

_____, _. _., & Wood, R. E. (1968). Distributional changes and interaction between prairie chickens and sharp-tailed grouse in the midwest. The Wilson Bulletin 80:173-188.

Johnson, Jeff A., Schroeder, M. A. and Robb, L. A. (2011). Greater Prairie-Chicken (*Tympanuchus cupido*), The Birds of North America Online, A. Poole, ed. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/036 doi:10.2173/bna.36

Johnson, R. G., & Temple, S. A. (1990). Nest predation and brood parasitism of tallgrass prairie birds. The Journal of Wildlife Management 54:106-111.

Kaufman, D. W., Kaufman, G. A., & Finck, E. J. (1989). Rodents and shrews in un-

    grazed tallgrass prairie manipulated by fire. Proceedings of the Eleventh North

    American Prairie Conference 173-177.

King, J. W., & Savidge, J. A. (1995). Effects of the Conservation Reserve Program on

    wildlife in southeast Nebraska. Wildlife Society Bulletin 23:377-385.

Kirsch, L. M. (1974). Habitat management considerations for prairie chickens. Wildlife

    Society Bulletin 2:124-129.

Lefkovitch, L. P., & Fahrig, L. (1985). Spatial characteristics of habitat patches and

    population survival. Ecological Modelling 30:297-308.

Lenth, R.V. (1981). On finding the source of a signal. Technometrics 23:149-154.

Lutz, R. S., Lawrence, J. S., & Silvy, N. J. (1994). Nesting ecology of Attwater's prairie-

    chicken. The Journal of Wildlife Management 58:230-233.

Martin, T. E., Auer, S. K., Bassar, R. D., Niklison, A. M., & Lloyd, P. (2007).

    Geographic variation in avian incubation periods and parental influences on

    embryonic temperature. Evolution 61:2558-2569.

Mathews, T. W., Tyre, A. J., Taylor, J. S., Lusk, J. J., & Powell, L. A. (2013). Greater

    prairie-chicken nest success and habitat selection in southeastern Nebraska. The

    Journal of Wildlife Management 77:1202-1212.

Mayfield, H. (1961). Nesting success calculated from exposure. The Wilson Bulletin

    73:255-261.

_____, H. F. (1975). Suggestions for calculating nest success. The Wilson Bulletin

    87:456-466.

McCoy, T. D., Kurzejeski, E. W., Burger Jr, L. W., & Ryan, M. R. (2001). Effects of conservation practice, mowing, and temporal changes on vegetation structure on CRP fields in northern Missouri. Wildlife Society Bulletin 29:979-987.

McKee, G., Ryan, M. R., & Mechlin, L. M. (1998). Predicting greater prairie-chicken nest success from vegetation and landscape characteristics. The Journal of Wildlife Management 62:314-321.

McNew, L. B., Gregory, A. J., Wisely, S. M., & Sandercock, B. K. (2009). Estimating the stage of incubation for nests of greater prairie-chickens using egg flotation: a float curve for grousers. Grouse News 38:12-14.

_____, _. _., Gregory, A. J., Wisely, S. M., & Sandercock, B. K. (2012). Demography of greater prairie-chickens: Regional variation in vital rates, sensitivity values, and population dynamics. The Journal of Wildlife Management 76:987-1000.

_____, _. _., Gregory, A. J., & Sandercock, B. K. (2013). Spatial heterogeneity in habitat selection: Nest site selection by Greater Prairie-Chickens. The Journal of Wildlife Management 77:791-801.

_____, _. _., Hunt, L. M., Gregory, A. J., Wisely, S. M., & Sandercock, B. K. (2014). Effects of wind energy development on nesting ecology of Greater Prairie-Chickens in fragmented grasslands. Conservation Biology 28:1089-1099.

Millenbah, K. F., Winterstein, S. R., Campa III, H., Furrow, L. T., & Minnis, R. B. (1996). Effects of Conservation Reserve Program field age on avian relative abundance, diversity, and productivity. The Wilson Bulletin 108:760-770.

National Oceanic and Atmospheric Administration. 2015. Available at: http://www.ncdc.noaa.gov/. Accessed September 2015.

Niemuth, N. D. (2000). Land use and vegetation associated with Greater Prairie-Chicken leks in an agricultural landscape. The Journal of Wildlife Management 64:278-286.

Otter, A. J., Fiala, W. D. (1978). Soil survey of Portage County, Wisconsin. U. S. Department of Agriculture and Soil Conservation Service. Washington D. C. 135pp.

Paton, P. W. (1994). The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.

Peterson, M. J., & Silvy, N. J. (1996). Reproductive stages limiting productivity of the endangered Attwater's prairie chicken. Conservation Biology 10:1264-1276.

Pitman, J. C., Hagen, C. A., Robel, R. J., Loughin, T. M., & Applegate, R. D. (2005). Location and success of Lesser Prairie-Chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 69:1259-1269.

Poiani, K. A., Merrill, M. D., & Chapman, K. A. (2001). Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. Conservation Biology 15:513-522.

Powell, A. F. (2008). Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41-52.

Pruett, C. L., Patten, M. A., & Wolfe, D. H. (2009). Avoidance behavior by prairie grouse: implications for development of wind energy. Conservation Biology 23:1253-1259.

Rastogi, A. D., Zanette, L., & Clinchy, M. (2006). Food availability affects diurnal nest
   predation and adult antipredator behaviour in song sparrows, *Melospiza
   melodia*. Animal Behaviour 72:933-940.

Renfrew, R. B., Ribic, C. A., & Nack, J. L. (2005). Edge avoidance by nesting grassland
   birds: a futile strategy in a fragmented landscape. The Auk 122:618-636.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. (1970). Relationships
   between visual obstruction measurements and weight of grassland vegetation.
   Journal of Range Management 23:295–297.

Rotella, J. J. [online]. 2005. Nest survival models. *In* Cooch, E. and G. C. White [EDS.],
   Program MARK: a gentle introduction. 6th ed.
   <http://www.phidot.org/software/mark/docs/book/> (1 October 2013).

Riley, T. Z., Davis, C. A., Ortiz, M., & Wisdom, M. J. (1992). Vegetative characteristics
   of successful and unsuccessful nests of lesser prairie chickens. The Journal of
   Wildlife Management 56:383-387.

Ryan, M. R., Burger, W., Jr., Jones D. P., and Wywialowski, A. P. (1998). Breeding
   ecology of greater prairie-chickens (*Tympanuchus cupido*) in relation to prairie
   landscape configuration. American Midland Naturalist 140:111–121.

Samson, F. B. (1980). Island biogeography and the conservation of prairie birds.
   In Proceedings of the Seventh North American Prairie Conference 7:293-299.

_____, F., & Knopf, F. (1994). Prairie conservation in North America. BioScience
   44:418-421.

Schroeder, M. A., and Braun, C. E. (1991). Walk-in traps for capturing greater prairie-
   chickens on leks. Journal of Field Ornithology 62:378-385.

Shaffer, J. A. and Buhl, D. A. (2015). Effects of wind-energy facilities on breeding

    grassland bird distributions. Conservation Biology 00:1-13.

    doi: 10.1111/cobi.12569

Shake, C. S., Moorman, C. E., Riddle, J. D., & Burchell, M. R. (2012). Influence of patch

    size and shape on occupancy by shrubland birds. The Condor 114:268-278.

Shochat, E., Patten, M. A., Morris, D. W., Reinking, D. L., Wolfe, D. H., & Sherrod, S.

    K. (2005). Ecological traps in isodars: effects of tallgrass prairie management on

    bird nest success. Oikos 111:159-169.

Smith, P., Gilchrist, A., Grant, A., & Smith, J. N. (2007). Effects of nest habitat, food,

    and parental behavior on shorebird nest success. The Condor 109:15-31.

Sparks, J. C., Masters, R. E., Engle, D. M., Palmer, M. W., & Bukenhofer, G. A. (1998).

    Effects of late growing-season and late dormant-season prescribed fire on

    herbaceous vegetation in restored pine-grassland communities. Journal of

    Vegetation Science 9:133-142.

Stephens, S. E., Koons, D. N., Rotella, J. J., & Willey, D. W. (2004). Effects of habitat

    fragmentation on avian nesting success: a review of the evidence at multiple

    spatial scales. Biological Conservation 115:101-110.

Svedarsky, W. D. (1979). Spring and summer ecology of female greater Prairie Chickens

    in northwestern Minnesota. Ph.D. thesis. University of North Dakota, Fargo.

_____, _. _. (1988). Reproductive ecology of female Greater Prairie-Chickens in

    Minnesota. Pp. 193–239 in, A. T. Bergurud and M. W. Gratson, ed., Adaptive

    strategies and population ecology of northern grouse. Vol. I. University of

    Minnesota Press, Minneapolis, MN.

_____, _. _., Westemeier, R. L., Robel, R. J., Gough, S., & Toepher, J. E. (2000). Status and management of the greater prairie-chicken *Tympanuchus cupido pinnatus* in North America. Wildlife Biology 6:277-284.

_____, _. _., J. E. Toepfer, R. L. Westemeier, and R. J. Robel. (2003). Effects of management practices on grassland birds: Greater Prairie-Chicken. Northern Prairie Wildlife Research Center, Jamestown, ND.

Taylor, M. A., & Guthery, F. S. (1980). Fall-winter movements, ranges, and habitat use of Lesser Prairie Chickens. The Journal of Wildlife Management 44:521-524.

Toepfer, R. L. (2006). Status and management of the Greater Prairie-Chicken in Wisconsin-2006. The Passenger Pigeon 69:259-288.

U. S. Department of Agriculture. (2013). Geospatial data gateway. Available at: http://datagateway.nrcs.usda.gov. Accessed September 2014.

Vickery, P. D., Hunter Jr, M. L., & Wells, J. V. (1992). Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281-288.

_____, _. _., Tubaro, P. L., Da Silva, J. C., Peterjohn, B., Herkert, J. R., & Cavalcanti, R. B. (1999). Conservation of grassland birds in the western hemisphere, 2-26.

Walk, J. W., Kershner, E. L., Benson, T. J., & Warner, R. E. (2010). Nesting success of grassland birds in small patches in an agricultural landscape. The Auk 127:328-334.

Westemeier, R. L. (1973). Prescribed burning in grassland management for prairie chickens in Illinois, in, R. Komarek, ed., *Proceedings of the Tall Timbers Fire Ecology Conference*, pp. 317–338. Tall Timbers Research Station, Tallahassee, Florida, USA.

_____, _. _., and J. E. Buhnerkempe. (1983). Responses of nesting wildlife to
    prairie grass management on prairie chicken sanctuaries in Illinois. Pp. 39-46 in
    R. Brewer, editor. Proceedings of the Eighth North American Prairie Conference.
    Western Michigan University, Kalamazoo, Michigan.

White, G. C., and K. P. Burnham. (1999). Program MARK: survival estimation from
    populations of marked animals. Bird Study 46:S120–S139.

Wiens, J. A. (1989). Spatial scaling in ecology. Functional Ecology 3:385-397.

_____, _. _. (1995). Habitat fragmentation: island v landscape perspectives on bird
    conservation. Ibis 137:S97-S104.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory
    songbirds. Ecology 66:1211-1214.

Winter, M., & Faaborg, J. (1999). Patterns of Area Sensitivity in Grassland-Nesting
    Birds. Conservation Biology 13:1424-1436.

_____, _., Johnson, D. H., & Faaborg, J. (2000). Evidence for edge effects on multiple
    levels in tallgrass prairie. The Condor 102:256-266.

Wisconsin Department of Natural Resources. (2013). Central Wisconsin Grassland
    Conservation Landsat Data Layer.

Wisconsin Department of Natural Resources. 2015. Central Wisconsin Greater Prairie-
    Chicken Survey.

Wisdom, M. J., & Mills, L. S. (1997). Sensitivity analysis to guide population recovery:
    prairie-chickens as an example. The Journal of Wildlife Management 61:302-312.

Zar, J. H. (1994). Biostatistical analysis. 2nd. Prentice Hall USA.

FIGURES
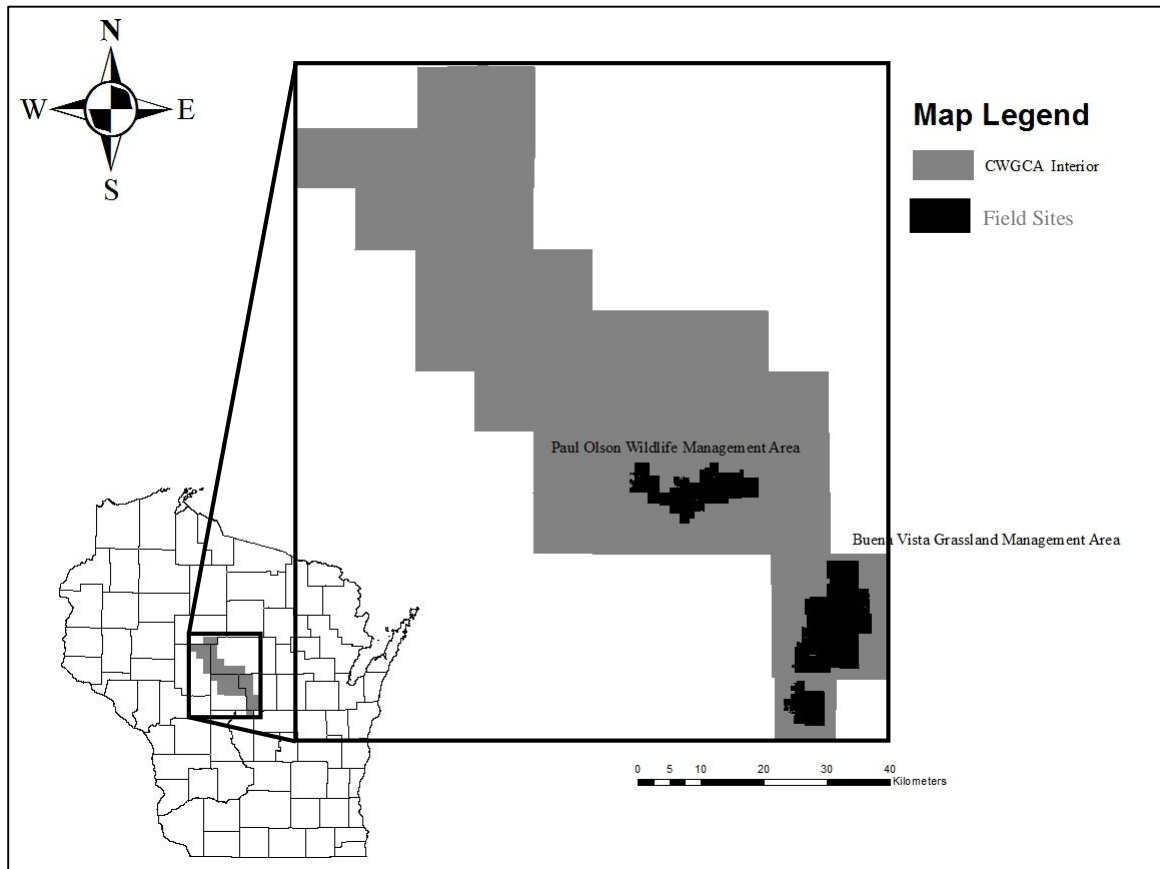
Figure 1.1. The Central Wisconsin counties comprising the Central Wisconsin Grassland

Conservation Area (CWGCA). The CWGCA Interior represents the Wisconsin

Department of Natural Resources priority grassland management areas where the

remaining Greater Prairie-Chicken population persists in low numbers.

Mean Percent Estimates for Local-level Vegetation
Variables at Successful and Unsuccfull GRPC Nests
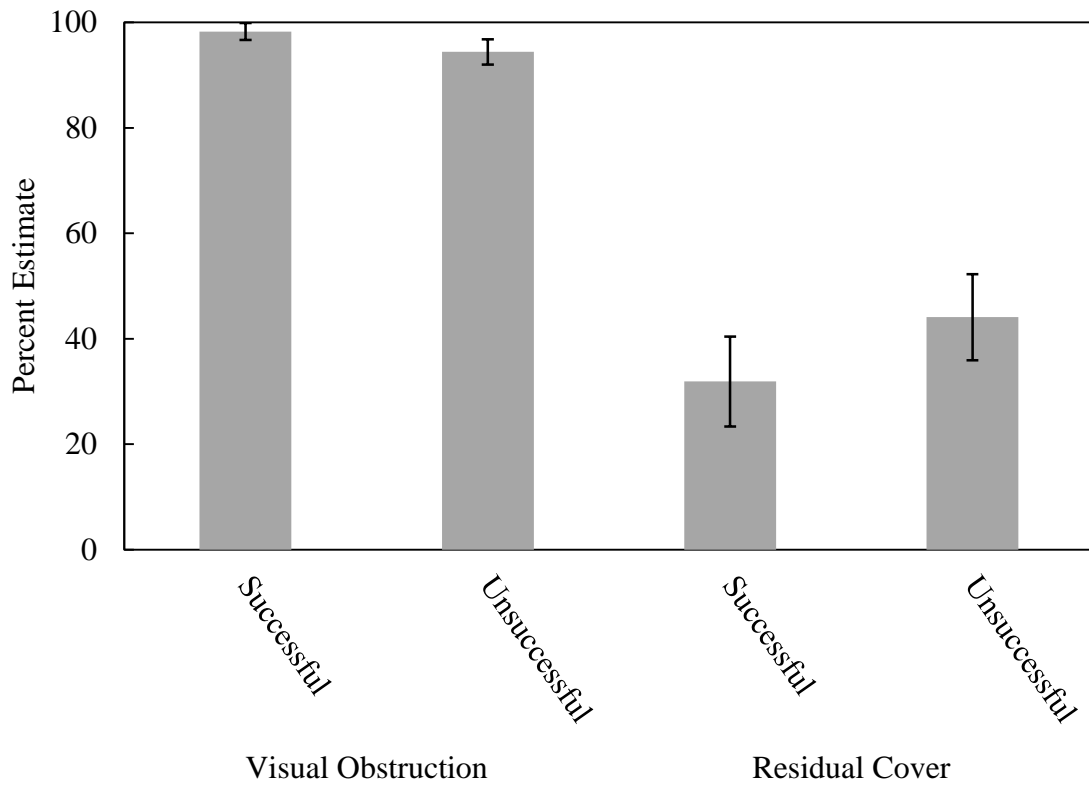
Figure 1.2. The raw estimates for visual obstruction (VO) and residual cover at successful

and unsuccessful nests with 95% confidence intervals.

TABLES

Table 1.1. Model selection using AICc adjusted for small samples shown in descending order of AICc value. Model statistics include ΔAICc, model weight (w_i), model likelihood, number of parameters (K), and deviance.

Model Structure	Model Statistics					
	AICc	ΔAICc	w_i	Model Likelihood	K	Deviance
$S_{(residual)}$	430.86	0.00	0.28	1.00	2	426.86
$(.)$	432.69	1.83	0.11	0.40	1	430.69
$S_{(VO)}$	432.99	2.12	0.10	0.35	2	428.98
$S_{(site)}$	433.72	2.86	0.07	0.24	2	429.72
$S_{(shape)}$	433.89	3.02	0.06	0.22	2	429.88
$S_{(residual\ x\ year)}$	434.34	3.48	0.05	0.18	4	426.32
$S_{(VO\ x\ year)}$	434.56	3.70	0.04	0.16	4	426.54
$S_{(nearest)}$	434.59	3.72	0.04	0.16	2	430.58
$S_{(VO\ x\ residual)}$	434.61	3.75	0.04	0.15	4	426.59
$S_{(core)}$	434.63	3.77	0.04	0.15	2	430.63
$S_{(size)}$	434.64	3.78	0.04	0.15	2	430.63
$S_{(year)}$	434.68	3.81	0.04	0.15	2	430.67
$S_{(site\ x\ size)}$	436.76	5.90	0.01	0.05	4	428.74
$S_{(site\ x\ shape)}$	437.00	6.13	0.01	0.05	4	428.98
$S_{(site\ x\ nearest)}$	437.03	6.17	0.01	0.05	4	429.01
$S_{(site\ x\ year)}$	437.52	6.66	0.01	0.04	4	429.50
$S_{(size\ x\ nearest)}$	437.59	6.72	0.01	0.03	4	429.57

Table 1.2. The mean values of each environmental covariate ± SE.

	Mean	±SE
Visual Obstruction	89.49	0.20
Residual Cover	33.95	490.43
Distance to Nearest Edge (m)	98.88	6037.04
Patch Size (ha)	216.12	27820.50
Patch Shape	2.64	40.84
Percent Core Grass	0.74	0.06

Table 1.3. Relative importance values for each covariate used in analysis of GRPC nest DSR estimates.

Covariate	RI Value
Residual	0.36
Year	0.15
VO	0.13
Site	0.11
Patch Shape	0.08
Nearest Edge	0.07
Patch Area	0.07
Core Grass	0.05

CHAPTER II: THE RELATIVE IMPORTANCE OF HABITAT

CHARACTERISTICS AT MULTIPLE SPATIAL SCALES TO JUVENILE

GREATER PRAIRIE-CHICKEN SURVIVAL IN WISCONSIN

Abstract: Grassland bird species have declined throughout their endemic ranges, especially in the Midwest. Similarly, Greater Prairie-Chickens (GRPC) have experienced precipitous declines for the last century throughout its range, including the state of Wisconsin. Several authors have identified nest and brood survival as limiting vital rates of prairie-grouse. However, little current information on brood survival during early ontogeny exists at our study sites. Hence, we sought to identify environmental variables contributing to juvenile survival. We used radio-tagged female Greater Prairie-Chickens in 2014 and 2015 to locate, flush, and count broods ($n = 23$) at weekly intervals until 70 days of age. We used the Young Survival option in Program MARK which estimates survival rates and accounts for detection probability. Further, we employed an information theoretic (IT) approach using AIC_c to compare the relative importance of our a priori models. Preliminary analyses suggested GRPC juvenile survival was best explained when detection (*p*) and survival (*Phi*) estimates varied across 3 and 4 intervals, respectively. After employing covariates, juvenile survival estimates (± SE) were best explained with the addition of residual and forb cover estimates at flush sites *(Phi$_1$= 0.96, ±0.02; Phi$_2$ = 0.84, ±0.04; Phi$_3$ = 0.66, ±0.08; Phi$_4$ = 0.83, ±0.03)*. We estimate the probability of a juvenile surviving the study at ~ 0.16 (± 0.03). Brood survival was strongly positively related to increases in residual and forb cover during the first survival period (*Phi$_1$*). Additionally, juvenile survival continued to decline from hatch to 28 days of age suggesting predation may be a limiting factor. We recommend management

practices promoting heterogeneous mixtures of forbs that maximize trade-offs between mobility and cover availability.

Key words: Grassland, Greater Prairie-Chicken, *Tympanuchus cupido*, prairie-grouse Program MARK, juvenile survival, detection probability

INTRODUCTION

Grassland ecosystems of the Great Plains are perhaps the most degraded in North America following agriculture expansion and modern land use practices contributing to habitat fragmentation (Klopatek et al. 1979, Samson and Knopf 1994). Effects of landscape change are evident in grassland bird species which have declined precipitously since the mid-20th century (Herkert 1995, Powell 2008). For example, pinnated grouse populations have declined throughout their range (Griffon et al. 1997, Fuhlendorf and Engle 2001, Johnsgard 2002) with Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) declining in near proportion to habitat loss (Taylor and Guthery 1980). Likewise, European settlement and intensification of concomitant land use practices caused extensive contraction and isolation of Greater Prairie-Chicken (*Tympanuchus cupido*; GRPC) populations have occurred (Hammerstrom and Hammerstrom 1961, Applegate and Horak 1999, Svedarsky et al. 2000). Currently, peripheral populations persist in fragmented landscapes with novel landscape matrix characteristics that influence prairie-grouse population demographics (Ryan et al. 1998, Fuhlendorf et al. 2002, Herkert et al. 2003, Hovick et al. 2014).

Fragmented landscapes may limit populations through tangential effects. For instance, fragmentation may intensify predator searching behavior proximate to ecotones (Wiens 1995, Winter et al. 2000, Chalfoun et al. 2002, Hilty and Merenlender 2004) and

such behavioral adaptations may negatively influence grassland bird demography (Wilcove 1985, Andrén and Angelstem 1988, Burger et al. 1994).

Juvenile survival and recruitment to subsequent breeding seasons is an important demographic metric in avian species (Saether and Bakke 2000, Hannon and Martin 2006). Further, several authors suggest nest and brood survival as limiting vital rates in GRPC populations (Bergerud and Gratson 1988, Peterson and Silvy 1996, Wisdom and Mills 1997; but, see McNew et al. 2012). Estimates of GRPC apparent nest success are available over a broad temporal scale in Wisconsin (Hamerstrom 1939, Hamerstrom and Hamerstrom 1973, Golner 1997, Toepfer 2006); however, no published estimates of juvenile survival parameters are available.

This necessitates additional information to direct management and conservation practices targeting extant GRPC populations in the highly fragmented landscapes of Wisconsin. Here only ~ 250 breeding males occupy the southeastern portion of the Central Wisconsin Grassland Conservation Area (Figure 2.1) (CWGCA; Wisconsin Department of Natural Resources 2015). The landscape matrix surrounding surrogate grassland patches in central Wisconsin is dominated by agricultural production, pine-barrens, early succession forests, wetlands, and shrublands (Sample et al. 2003). These fragmented landscapes may have negative effects on grassland bird population demographics, such as nest survival (Winter et al. 2000, Renfrew et al. 2005, Mathews et al. 2013). Similar ecological effects on brood survival are possible. However, few studies report the simultaneous relative effects of local-, edge-, and patch-level habitat characteristics and documentation of cause-specific mortality is minimal (Hannon and Martin 2006).

Our objectives were to 1) better understand temporal patterns in juvenile survival during the first 70 days and 2) identify environmental covariates best explaining juvenile survival during the aforementioned period in the Wisconsin GRPC population.

METHODS

Field Sites

Our study sites were state-owned and managed wildlife areas located within the 3,600 km^2 CWGCA (N 516877, W 466134) and included sampling two genetically distinct populations, Buena Vista Grassland Management Area (BVGMA) and Paul J. Olson Wildlife Area (PJOWA; Figure 2.1). Specifically, sites were approximately 15.5 km apart. The BVGMA boundary includes nearly 19,000 ha with 5,140 ha owned and managed by the Wisconsin Department of Natural Resources and located in southwestern Portage County, Wisconsin. State-managed grassland areas range from 4.4 ha to 1,253 ha (mean = 178 ha) and are surrounded by commercial row-crop production and forest cover. The PJOWA is comprised by scattered parcels ranging from 6.5 ha to 347 ha (mean = 59 ha) in eastern Wood and northwestern Portage counties. The landscape matrix around PJOWA consists of forested tracts, small-scale private grain and forage production, as well as small dairy operations. Detailed descriptions of plant communities are available in Niemuth (2000). Additionally, Otter and Fiala (1978) provide accounts of regional soil type and topography. We selected these sites because they represent the last remaining GRPC populations in Wisconsin.

BVGMA and PJOWA are bisected by landscape features including urban development, forest, and the Wisconsin River. Climate is typically continental with distinct seasonal changes. The estimated annual precipitation at each site is ~ 32 cm/year

and mean daily maximum and minimum temperatures during January are -4°C and -14°C. In contrast, mid-summer (i.e., July) mean daily maximum and minimum temperatures are 26°C and 15°C, respectively. Growing seasons at our sites are approximately 145 days (range=123-159 days). Climate data were retrieved from the National Oceanic and Atmospheric Administration (available at http://www.ncdc.noaa.gov/).

Capture and Monitoring

Our study was conducted March-September of 2014 and 2015. We captured female Greater Prairie-Chickens using walk-in style traps (Schroeder and Braun 1991) on leks that maintained an average male lek attendance ≥ 5. We marked all captured individuals with serial numbered metal state-bands and aged via characteristics of primaries 9 and 10 (Johnson et al. 2011). We weighed females with a Pesola© spring scale to the nearest ± 5 grams, recorded morphometrics and radio-tagged female prairie-chickens with a 16g necklace-style VHF transmitter with a 796 day battery (Model #A3960, 6hr mortality switch, Advanced Telemetry Systems, Inc., Isanti, MN). We released individuals at the capture location immediately after processing.

We located females via triangulation of VHF radio signals and homing techniques using hand-held Yagi antennas and portable receivers ≥ 5 per week. Error ellipses and location coordinates were calculated in the field using Program Radio-Tracker (Lenth 1981). Intervals were ≤ 30 minutes between first and third and azimuth readings. We recorded bearings with handheld compasses to ± 1° accuracy. We began using homing techniques after a hen was believed to have localized based on triangulated locations.

We determined female reproductive status by flushing hens from nests early in laying after 3 consecutive homing locations. After flushing females, we counted clutches and used floating techniques to back-date the onset of incubation (McNew et al. 2009) and project hatch dates based on a 24-day incubation period. During nest processing we anchored Thermochron iButton data-loggers (Model DS 1921G, iButtonLink, Whitewater, WI, USA) inside and flush with the contour of nest bowls to record temperatures every 30 minutes. We also anchored iButtons synchronized with the associated nest iButtons within 100 meters of each nest to record ambient temperatures. We consulted temperature data from iButton data-loggers to determine timing ± 30 minutes of hatch (Hartman and Oring 2006) and dates of successive flush events.

We used homing of female radio signals to locate brood hens within 30 minutes of sunrise at regular weekly intervals (Goddard and Dawson 2009) from hatch to 70 days of age. We cautiously approached when flushing females and counted as many chicks as possible immediately after brood hens flushed. Observers wore rubber boots to reduce scent deposition, recorded brood locations with handheld GPS units (±3 m in Wisconsin Transverse Mercator), and marked flush locations with orange survey flags. After, observers exited the area in the opposite direction of broods and the attending female. A brood was considered lost if two consecutive flushes produced zero counts and was corroborated by female behavior (e.g., excessive flight distances without return). If hen behavior was inconclusive a third flush was used to confirm brood status. Additionally, we captured broods at night with nets and hand-held lights at 45 and 90 days of age. We randomly selected chicks in each brood to affix 7 g necklace-style collars (ATS, Inc., Isanti, MN, Model #3930, 221 day battery) at 45 days of age. We subsequently

recaptured collared chicks at approximately 90 days of age to replace collars with adult-sized models equipped with 6 hour mortality switches (Model #A3960, 16g, 796 day battery, Advanced Telemetry Systems, Inc., Isanti, MN). Chick processing, morphometric measurements, and body condition assessment was identical to adult captures. We monitored radio-tagged brood hens and juveniles ≥7 days/week until 90 days of age, collar shedding, or mortality occurred.

Vegetation sampling. We visually estimated residual and forb cover at weekly brood-flush locations (local-level) until 28 days of age. We delayed vegetation sampling if a hen was ≤ 50 meters of a flush location to minimize disturbance and completed sampling within 7 days of each flush. These vegetation measures were obtained using variations on digital imagery techniques. We sampled vegetation surrounding the brood location using digital images of $1 \ m^2$ frames (Daubenmire 1959) centered at the brood flush location and at 5 meters from center in four cardinal directions. We visually estimated the percent cover of vegetation classes in each frame similar to Aldridge and Brigham (2001), subsequently deriving a mean percent cover estimate of residual cover, forb cover, and bare ground. The latter was discarded from analyses because it rarely contributed values >0. Our vegetation cover data were non-normally distributed near upper and lower extremes (i.e., < 0.3, >0.7) and required arcsin transformations (Zar 1999).

Landscape covariates. We selected metrics at multiple spatial scales (local-, edge-, and patch-level independent variables) that could potentially explain variation in juvenile survival in Wisconsin. Spatial covariates at edge- and patch-levels included distance to nearest edge ($\phi_{(edge)}$), patch-shape ($\phi_{(shape)}$; Shake et al. 2012), and patch-size

($\phi_{(size)}$) respective of brood flush locations. Although, predator use may increase near

particular edges (Winter et al. 2000, Hilty and Merenlender 2004) we assumed edge-

effects were similar regardless of edge-type. We defined patch size based on the total

contiguous area of analogous cover-types (e.g., hay/alfafa, warm and cool season

grasses). We also considered the possibility that brood movement may expose young to

increased metabolic demands or predation risk, thus we considered the distance moved

between flush counts as a predictor of survival. We acquired all spatial data using

ArcMap (ver. 10.2; Environmental Systems Research Institute, Redlands, CA) and the

Central Wisconsin Grassland Conservation Area data layer (WIDNR 2013). This data

layer was used in combination with 2013 National Agriculture Imagery Program (NAIP)

data layers (U. S. Department of Agriculture 2013) and ground truthing methods.

Accuracy assessment of the layer showed strong agreement between field observations

and cover-type classifications (>85 %). Additionally, we corrected disagreements and

modified the data layer via ground-truthing methods to account for temporal

disagreement in crop-types between data-layer production (2013) and study years (2014

and 2015).

Statistical Analyses

We explored juvenile survival (ϕ) and detection (p) in two stages. In the first stage, we

considered 10 a priori models that allowed for various levels of biologically reasonable

temporal variation in survival and detection using AIC_c (Table 2.1; Akaike 1973,

Burnham and Anderson 2002). We considered models that included survival periods

paralleling those previously used (Pitman et al. 2006, Fields et al. 2006, Goddard and

Dawson 2009). Specifically, we hypothesized juvenile survival would follow 1 of 3

trends: juvenile survival would 1) be constant (null) through time (ϕ(.); 1 estimate); 2) would remain equal among but different in two 2 week intervals through the first 4 weeks, stabilizing and climaxing at different estimates thereafter ($\phi(t_3)$; 3 estimates); 3) would be constant from hatch to week 2, different in week 3, different in week 4 and then different but constant thereafter ($\phi(t_4)$; 4 estimates). Detection probability (p) was modeled in combination with the aforementioned ϕ models. We hypothesized p would either 1) be constant in time p(.), or 2) follow a pattern corresponding to juvenile growth and development ($p(t_3)$). In the latter model ($p(t_3)$), we anticipated lower detection probabilities at 7-day flush counts when not all chicks are capable of flight and/or may be obstructed by vegetation. The Young Survival Model in Program MARK uses hatch counts as the initial brood size and derives detection probability estimates (p) at prior counts (p_i) based on the number of individuals detected on subsequent counts (p_{i+1}) (Lukacs et al. 2005). Thus, we included counts conducted at 7 days of age and beyond where not all individuals are necessarily detectable. Further, we assumed detection would increase and remain constant from 14-49 day flush counts as chicks acquired flight capability and detection would decrease at 56-70 day flush counts as chicks became more independent (Robel et al. 1970) and less likely to be detected. This resulted in 3 parameter estimates for detection probability. To avoid confounding between the final ϕ and p parameter estimates, we fixed final p estimates equal to the proportional average of p parameter estimates in the top model. We considered site and year effects and fully time varying models in stage 1. However, fully time varying models were discarded because they failed to provide viable estimates ϕ and p. We included the model best

explaining variation in ϕ and p without environmental variables as a base (i.e., $\phi(t_i)\bullet p(t_i)$) in stage two.

Stage 2 focused on determining which environmental covariates most influenced survival during the 4 periods identified in stage one. In stage 2 we continued to employ an information theoretic approach using Akaike's Information Criterion adjusted for small samples (AIC_c; Akaike 1973, Burnham and Anderson 2002). We ranked models based on AIC_c weights (w_i) and considered models within 2 AIC_c units of the most parsimonious model as competitive. To account for site and year effects on survival, we included a site ($\phi(site)$), year ($\phi(year)$), and site-year interactive model ($\phi(site \ x \ year)$) in our analyses. We also included a null or (constant) model lacking covariates. When allowing survival to remain constant, or vary by site and/or year, we continued to employ the best detection probability model structure (i.e., $p(t_3)$) from stage one. Finally, we constructed a priori additive and interactive models that considered the aforementioned vegetation, movement, and spatial characteristics associated with broods we thought were biologically reasonable predictors of juvenile survival and mortality. We provide results of model parameter estimates ($\pm$ SE).

RESULTS

We captured, radio-tagged, and monitored 62 females on leks March-May of 2014 and 2015. Subsequently, we monitored 74 nests until success or failure, including renests. Mean clutch size during our study was ~ 12 and mean incubation period of successful nests was ~ 24 days. We monitored 23 broods (2014: 6; 2015: 17) during the brood rearing seasons of our study (June-September) consequently estimating survival from 68 and 154 chicks in 2014 and 2015, respectively (total = 222). Two females with broods

shed their collars prior to monitoring period end (2015) and one brood female was depredated when chicks were 38 days old (2014). Consequently we censored the remaining flush encounters for those broods. In total, 8 broods survived to 10 weeks (2014: 5; 2015: 3). We detected one whole-brood failure (4.3%) before 14 days of age in 2014 and 7 whole-brood failures (30.4%) before 7 days of age during the 2015 season.

Base model. The best fit model ($\phi(t_4) \cdot p(t_3)$) allowed survival to differ between 4 intervals (Phi_{1-4}) and detection probability to differ across 3 intervals (p_{1-3}; Table 2.1). The probability of surviving the study was estimated at ~ 13% ($\pm$ 0.02; [95% CI = 0.09, 0.18], w_i = 0.99). Using our base model lacking covariates, we estimated weekly survival at 0.701 ($\pm$ 0.019), 0.903 ($\pm$ 0.031), 0.624 ($\pm$ 0.045), and 0.852 ($\pm$ 0.023) for intervals 1-4, respectively. Detection probability estimates considered week 1 counts (p_1), weeks 2-7 (p_2), and weeks 8-10 (p_3) different from one another (Figure 2.2). Again, because the last survival and detection parameters are confounded in this and other population models (e.g., Cormack-Jolly-Seber Model) we fixed the last detection probability estimate based on the proportional mean of our other detection estimates in the top model. Additionally, ϕ and p parameters were inestimable using fully time-varying models and were therefore removed from the final model set. There was no support for site or year effects after preliminary modeling of survival and detection probability and no model uncertainty.

Juvenile Survival and environmental covariates. We analyzed survival through 4 distinct periods using 11 a priori models including individual environmental covariates. One model, an interaction between forb and residual cover, was discarded because it failed to produce mathematically reasonable estimates for multiple survival periods. The top model ($\phi(t_4 \ residual + forb) \cdot p(t_3)$; Table 2.2) considered survival a function of the

56

additive relationship between residual and forb cover at flush locations during survival period 1 (Phi_1 = 0.96, SE = 0.02, [95% CI = 0.90, 0.98]), period 2 (Phi_2 = 0.84, SE = 0.04, [95% CI = 0.74, 0.91]), and period 3 (Phi_3 = 0.66, SE = 0.08, [95% CI = 0.49, 0.79], w_i = 1.00). The β estimates of each covariate in the top model were strongly positive during survival period 1 (Phi_1) but weakened in subsequent survival periods (Table 2.3). The top model showed a decline in juvenile survival estimates between survival intervals 1-3 (Phi_{1-3}) of brood rearing but increased thereafter (Figure 2.3). Forb cover estimates increased slightly across each survival period; however, residual cover estimates increased from survival period 1-2 and decreased in the third survival period (Phi_3; Figure 2.4). Because we did not collect vegetation data beyond 28 days, vegetation characteristics were not considered in the final survival period (i.e., Phi_4). The weekly survival probability during the post-fledging period was low (i.e., 29-70 days; Phi_4 = 0.82, SE = 0.03, [95% CI = 0.76, 0.87]) and the probability of a chick surviving the duration of our study was 0.16 (± 0.03, [95% CI = 0.11, 0.22). There was no model uncertainty and no other model received support.

DISCUSSION

Our results suggest juvenile survival during the first 4 weeks is best explained by additive positive effects of local-level habitat characteristics (i.e., forb cover and residual cover). The effects were strongest during the first survival period and strength of effects weakened during the second and third survival periods (Table 2.2). There are several potential mechanisms by which residual and forb cover could impact juvenile survival.

First, some residual cover in our study was primarily horizontal at ground level thereby functioning as bare ground (M.S. Broadway personal observation). If this

allowed for easier juvenile mobility, then increased residual cover may facilitate escape

from predators, increase foraging efficiency, and decrease energy expenditures associated

with movement. This could be especially important during the first 2 weeks of ontogeny

when chicks are flightless (Johnson et al. 2011). Other studies have addressed the

relationship between chick foraging ecology and vegetation structure. For example,

Doxon and Carroll (2010) demonstrated increased foraging rates and diet breadth of ring-

necked pheasant and bobwhite chicks in CRP fields with less dense vegetation.

Furthermore, Anderson et al. (2015) demonstrated GRPC brood hens used sites with

greater and more homogeneous litter depth but also with heterogeneous structure and

intermediate obstruction estimates suggesting females select areas compromising

tradeoffs between food and cover.

Second, increased forb cover may provide vegetable foods to chicks during early

growth and development. For example, Blomberg et al. (2013) demonstrated through

stable isotope analysis of Greater Sage-Grouse (*Centrocercus urophasianus*) chick

plumage that individuals with diets comprised of both plant and animal biomass exhibited

higher growth rates than those with diets dominated by arthropods. These vegetable foods

may be crucial as young grouse transition through early ontogeny (i.e. 0-28 days). Other

studies also have demonstrated that brooding female prairie-grouse, including GRPC, use

areas with greater forb abundance (Jamison et al. 2002, Fields et al. 2006, Goddard et al.

2009, Mathews et al. 2011, Anderson et al. 2015). Finally, forb communities may support

a more abundant arthropod population (Jones 1963, Jamison et al. 2002). Insects are

important dietary components to precocial gallinaceous chicks (Rumble et al. 1988,

Savory 1989, Griffon et al. 1997) and provide nutrients necessary for plumage

development and muscular growth (Aulie 1976). Higher chick growth rates likely have a

positive impact on survival in grouse (Erikstad 1985) as young are capable of more

efficient foraging, independent thermoregulation, and escape from predators. Again, we

did not measure individual juvenile movements, foraging efficiency, diet preference, or

arthropod abundance. However, we posit these as potential mechanistic explanations

from other studies possibly explaining the strong relationship between survival, residual

cover, and forb cover in our study. Regardless of the mechanism, residual and forb cover

were the only covariates associated with juvenile survival in our study.

Conclusion

Juvenile survival of prairie-grouse is consistently a limiting factor of population

growth rates (i.e., λ; Wisdom and Mills 1997). Our results suggest that GRPC brood

survival in Wisconsin is low and may be limiting the population growth rate (i.e., λ).

Specifically, our results suggest that local vegetation communities are more important

than edge- and patch-level characteristics to juvenile survival. GRPC evolved under

mechanistic abiotic factors creating heterogeneous plant communities through periodic

disturbance and management practices should emulate the spatial and temporal variation

of historic disturbance patterns in mixed and tallgrass prairie ecosystems. Currently, the

Wisconsin DNR limits active management to $\leq$ 20% of grassland area at each site and

management practices may be constrained by abiotic conditions at our sites (i.e., soil

organic matter, weather). However, disturbance intervals of $\geq$ 5 years may be insufficient

based on our findings. Future management prescriptions should focus on promoting

vegetation structure providing overhead cover while simultaneously minimizing ground-

level obstruction. We recommend the spatial and temporal variation of current

management practices that increase forb production and bare ground while reducing woody encroachment such as prescribed burning (Wright and Baily 1982, Collins and Gibson 1990). McCoy et al. (2001) observed twice the bare ground in warm season CRP plantings compared to cool season CRP and mowing practices accelerated litter accumulation. Alternatively, Greenfield et al. (2003) demonstrated that increased strip-discing positively increased plant species richness and bare-ground while decreasing litter. Historic disturbances (i.e., fire and grazing) likely occurred in grassland prairies between 3-5 years (Knapp et al. 1998). Similar disturbance intervals have been suggested for CRP lands (Millenbah et al. 1996, McCoy et al. 2001). While we cannot extricate the exact mechanism determining brood survival, we recommend future research focus on the impacts of insect abundance, plant species composition, and cause-specific mortality of juvenile Greater Prairie-Chicken in Wisconsin.

P) and the University of Wisconsin-Stevens Point. This manuscript was approved by the funding agencies prior to submission and publication.

LITERATURE CITED

Akaike, H. (1973). Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60:255-265.

Aldridge, C.L. & Brigham, R.M. (2001). Nesting and reproductive activities of greater sage grouse in a declining northern fringe population. The Condor 103:537–543.

Anderson, L. C., Powell, L. A., Schacht, W. H., Lusk, J. J., & Vodehnal, W. L. (2015). Greater prairie-chicken brood-site selection and survival in the Nebraska sandhills. The Journal of Wildlife Management 79:559-569.

Andrén, H., & Angelstam, P. (1988). Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69:544-547.

Applegate, R. D., & Horak, G. J. (1999). Status and management of the Greater Prairie Chicken in Kansas. The greater prairie chicken: A national look. Minnesota Agricultural Experiment Station, University of Minnesota, Misc. Publication, 99-1999.

Aulie, A. (1976). The pectoral muscles and the development of thermoregulation in chicks of willow ptarmigan (*Lagopus lagopus*). Comparative Biochemistry and Physiology Part A: Physiology 53:343-346.

Bergerud, A. T. (1988). Population ecology of North American grouse. Pages 578–777 in A. T. Bergerud, and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, USA.

Burger, L. D., Burger Jr, L. W., & Faaborg, J. (1994). Effects of prairie fragmentation on predation on artificial nests. The Journal of Wildlife Management 58:249-254.

Burnham, K. P., and D. R. Anderson. (2002). Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Chalfoun, A. D., Thompson, F. R., & Ratnaswamy, M. J. (2002). Nest predators and fragmentation: a review and meta-analysis. Conservation Biology 16:306-318.

Collins, S. L., & Gibson, D. J. (1990). Effects of fire on community structure in tallgrass and mixed-grass prairie. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, 81-98.

Daubenmire, R. (1959). A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

Doxon, E. D., & Carroll, J. P. (2010). Feeding ecology of ring-necked pheasant and northern bobwhite chicks in conservation reserve program fields. Journal of Wildlife Management 74:249-256.

Erikstad, K.E. (1985). Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. Scandinavian Journal of Ornithology 16:181–190.

Fields, T. L., White, G. C., Gilgert, W. C., & Rodgers, R. D. (2006). Nest and brood survival of lesser prairie-chickens in west central Kansas. Journal of Wildlife Management 70:931-938.

Fuhlendorf, S. D., and D. M. Engle. (2001). Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. BioScience 51:625–632.

_____, _. _., Woodward, A. J., Leslie, D. M., & Shackford, J. S. (2002). Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landscape Ecology 17:617-628.

Goddard, A. D., & Dawson, R. D. (2009). Factors influencing the survival of neonate sharp-tailed grouse *Tympanuchus phasianellus*. Wildlife Biology 15:60-67.

_____, _. _., R. D. Dawson, and M. P. Gillingham. (2009). Habitat selection by nesting and brood-rearing sharp-tailed grouse. Canadian Journal of Zoology 87:326–336.

Golner, D. P. (1997). Analysis of habitat selection by female Greater Prairie Chickens in Central Wisconsin. M.S. Thesis. University of Wisconsin-Stevens Point.

Greenfield, K. C., Chamberlain, M. J., Burger Jr, L. W., & Kurzejeski, E. W. (2003). Effects of burning and discing Conservation Reserve Program fields to improve habitat quality for northern bobwhite (*Colinus virginianus*). The American midland naturalist 149:344-353.

Griffon, C. P., M. E. Morrow, and N. J. Silvy. (1997). Insects as a possible limiting factor for Attwater's prairie-chicken *Tympanuchus cupido attwateri*. Wildlife Biology 3:288.

Hamerstrom, F. N. (1939). A study of Wisconsin prairie chicken and sharp-tailed grouse. The Wilson Bulletin 51:105-120.

_____, F., & Hamerstrom, F. (1961). Status and problems of North American grouse. Wilson Bulletin 73:284-294.

Hamerstrom Jr, F. N., & Hamerstrom, F. (1973). The greater prairie-chicken in Wisconsin-highlights of a 22 year study of counts, behavior, movements, turnover, and habitat. Wisconsin Dept. Natural Resources. Technical Bulletin, 64.

Hannon, S. J., & Martin, K. (2006). Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology 269:422-433.

Hartman, C. A., & Oring, L. W. (2006). An inexpensive method for remotely monitoring nest activity. Journal of Field Ornithology 77:418-424.

Herkert, J. R. (1995). An analysis of Midwestern breeding bird population trends: 1966-1993. American Midland Naturalist 134:41-50.

_____, J. R., Reinking, D. L., Wiedenfeld, D. A., Winter, M., Zimmerman, J. L., Jensen, W. E., & Robinson, S. K. (2003). Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17:587-594.

Hilty, J. A., & Merenlender, A. M. (2004). Use of riparian corridors and vineyards by mammalian predators in northern California. Conservation Biology 18:126-135.

Hovick, T. J., Elmore, R. D., Dahlgren, D. K., Fuhlendorf, S. D., & Engle, D. M. (2014). Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. Journal of Applied Ecology, 51:1680-1689.

Jamison, B. E., R. J. Robel, J. S. Pontius, and R. D. Applegate. (2002). Invertebrate biomass: associations with lesser prairie-chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin 30:517–526.

Johnsgard, P. A. (2002). Grassland grouse and their conservation. Smithsonian Institution Press, Washington, D.C., USA.

Johnson, Jeff A., M. A. Schroeder and L. A. Robb. (2011). Greater Prairie-Chicken (*Tympanuchus cupido*), The Birds of North America Online (A. Poole, Ed.).

Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/036 doi:10.2173/bna.36

Jones, R. E. (1963). Identification and analysis of lesser and greater prairie chicken habitat. Journal of Wildlife Management 27:757–778.

Klopatek, J. M., Olson, R. J., Emerson, C. J., & Joness, J. L. (1979). Land-use conflicts with natural vegetation in the United States. Environmental Conservation 6:191-199.

Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Lenth, R.V. (1981). On finding the source of a signal. Technometrics 23:149-154.

Lukacs, P. M., Dreitz, V. J., Knopf, F. L., & Burnham, K. P. (2004). Estimating survival probabilities of unmarked dependent young when detection is imperfect. The Condor 106:926-931.

Matthews, T. W., A. J. Tyre, J. S. Taylor, J. J. Lusk, and L. A. Powell. (2011). Habitat selection and brood survival of greater prairie-chickens. Pages 179–191 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39). University of California Press, Berkeley, USA.

Matthews, T. W., Tyre, A. J., Taylor, J. S., Lusk, J. J., & Powell, L. A. (2013). Greater prairie-chicken nest success and habitat selection in southeastern Nebraska. The Journal of Wildlife Management 77:1202-1212.

McCoy, T. D., Kurzejeski, E. W., Burger Jr., L. W., & Ryan, M. R. (2001). Effects of conservation practice, mowing, and temporal changes on vegetation structure on CRP fields in northern Missouri. Wildlife Society Bulletin 29:979-987.

McNew, L. B., Gregory, A. J., Wisely, S. M., & Sandercock, B. K. (2009). Estimating the stage of incubation for nests of greater prairie-chickens using egg flotation: a float curve for grousers. Grouse News 38:12-14.

McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. (2012). Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. Journal of Wildlife Management 76:987–1000.

Millenbah, K. F., Winterstein, S. R., Campa III, H., Furrow, L. T., & Minnis, R. B. (1996). Effects of Conservation Reserve Program field age on avian relative abundance, diversity, and productivity. The Wilson Bulletin 108:760-770.

Niemuth, N. D. (2000). Land use and vegetation associated with greater prairie-chicken leks in an agricultural landscape. The Journal of Wildlife Management 64:278-286.

Otter, A. J. and W. D. Fiala. (1978). Soil survey of Portage County, Wisconsin. U. S. Department of Agriculture and Soil Conservation Service. Washington D. C. 135pp.

Peterson, M. J., & Silvy, N. J. (1996). Reproductive stages limiting productivity of the endangered Attwater's prairie chicken. Conservation Biology 10:1264-1276.

Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. (2006). Survival of juvenile lesser prairie-chickens in Kansas. Wildlife Society Bulletin 34:675–681.

Powell, A. F. (2008). Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41-52.

Renfrew, R. B., Ribic, C. A., & Nack, J. L. (2005). Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. The Auk 122:618-636.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

Rumble, M. A., Newell, J. A., & Toepfer, J. E. (1988). Diets of Greater Prairie Chickens on the Sheyenne National Grasslands. Pages 49-54 in, A. J. Bjugstad (technical coordinator), Prairie chickens on the Sheyenne National Grasslands. U.S. Department of Agriculture Forest Service General Technical Report RM-159. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Ryan, M. R., W. Burger, Jr., D. P. Jones, and A. P. Wywialowski. (1998). Breeding ecology of greater prairie-chickens (*Tympanuchus cupido*) in relation to prairie landscape configuration. American Midland Naturalist 140:111–121.

Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Sample, D. W., Ribic, C. A., & Renfrew, R. B. (2003). Linking landscape management with the conservation of grassland birds in Wisconsin. Landscape ecology and resource management: linking theory with practice, 359-385.

Samson, F., and F. Knopf. (1994). Prairie conservation in North America. Bioscience 44:418–421.

Savory, C. J. (1977). The food of red grouse chicks *Lagopus l. scoticus*. Ibis 119:1-9.

Schole, A. C., T. W. Matthews, L. A. Powell, J. J. Lusk, and J. S. Taylor. (2011). Chick

    survival of greater prairie-chickens. Pp. 247–254 in B. K. Sandercock, K. Martin,

    and G. Segelbacher (editors). Ecology, conservation, and management of grouse.

    Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Schroeder, M.A., and Braun, C.E. (1991). Walk-in traps for capturing greater prairie-

    chickens on leks. Journal of Field Ornithology 62:378-385.

Shake, C. S., Moorman, C. E., Riddle, J. D., & Burchell, M. R. (2012). Influence of patch

    size and shape on occupancy by shrubland birds. The Condor 114:268-278.

Svedarsky, W. D., Westemeier, R. L., Robel, R. J., Gough, S., & Toepher, J. E. (2000).

    Status and management of the greater prairie-chicken *Tympanuchus cupido*

    pinnatus in North America. Wildlife Biology 6:277-284.

Taylor, M. A., & Guthery, F. S. (1980). Status, ecology, and management of the lesser

    prairie chicken. U.S. Forest Serv. Gen. Tech. Rep. RM-77. Rocky Mountain

    Forest and Range Experiment Station, U.S. Dep. Agriculture, Fort Collins,

    Colorado.

Toepfer, R. L. (2006). Status and management of the Greater Prairie-Chicken in

    Wisconsin-2006. The Passenger Pigeon 69:259-288.

U. S. Department of Agriculture. (2013). Geospatial data gateway. Available at: http://

    datagateway.nrcs.usda.gov. Accessed September 2014.

Wiens, J. A. (1995). Habitat fragmentation: island v landscape perspectives on bird

    conservation. Ibis 137:S97-S104.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory

    songbirds. Ecology 66:1211-1214.

Winter, M., Johnson, D. H., & Faaborg, J. (2000). Evidence for edge effects on multiple

      levels in tallgrass prairie. The Condor 102:256-266.

Wisconsin Department of Natural Resources. 2015. Central Wisconsin Greater Prairie-

      Chicken Survey.

Wisdom, M. J., & Mills, L. S. (1997). Sensitivity analysis to guide population recovery:

      prairie-chickens as an example. The Journal of Wildlife Management 61:302-312.

Wright, H. A., & Bailey, A. W. (1982). Fire ecology: United States and southern Canada.

      John Wiley & Sons.

Zar, J. H. (1999). Biostatistical analysis. Pearson Education India.
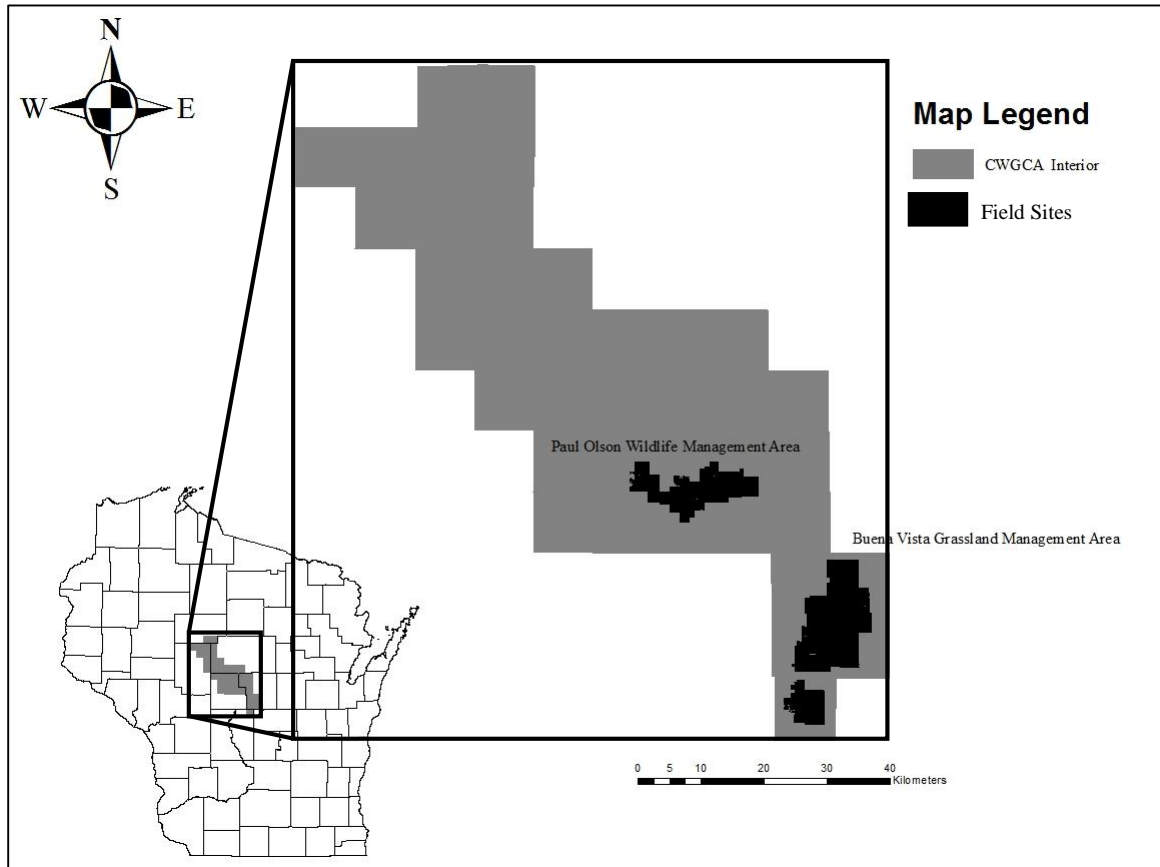
FIGURES

Figure 2.1. The central Wisconsin Grassland Conservation area (CWGCA) is comprised of 7 central Wisconsin Counties. The CWGCA interior was defined by the Wisconsin Department of Natural Resources in 2004 and contains ~ 8,900 hectares of managed public lands.

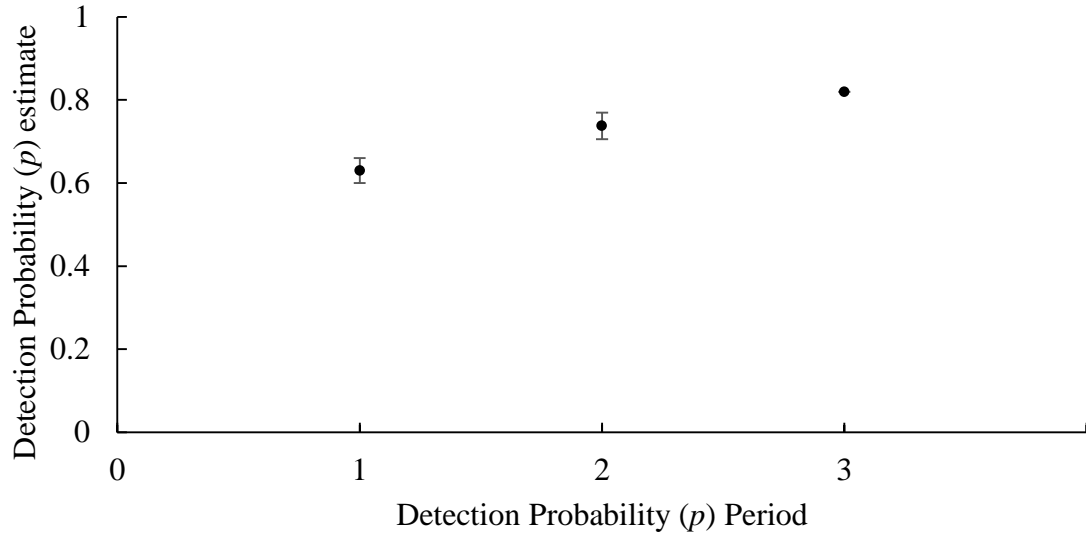GRPC Juvenile Detection Probability Estimates for
Distinct Periods

Figure 2.2. Juvenile detection probabilities for the top model ($\phi(t_4)$ $p(t_3)$) from

preliminary analyses of juvenile survival and detection probability. Intervals (p_{1-3})

correspond to flush day 7, 14-49, and 56-70, respectively. The final p estimate was fixed

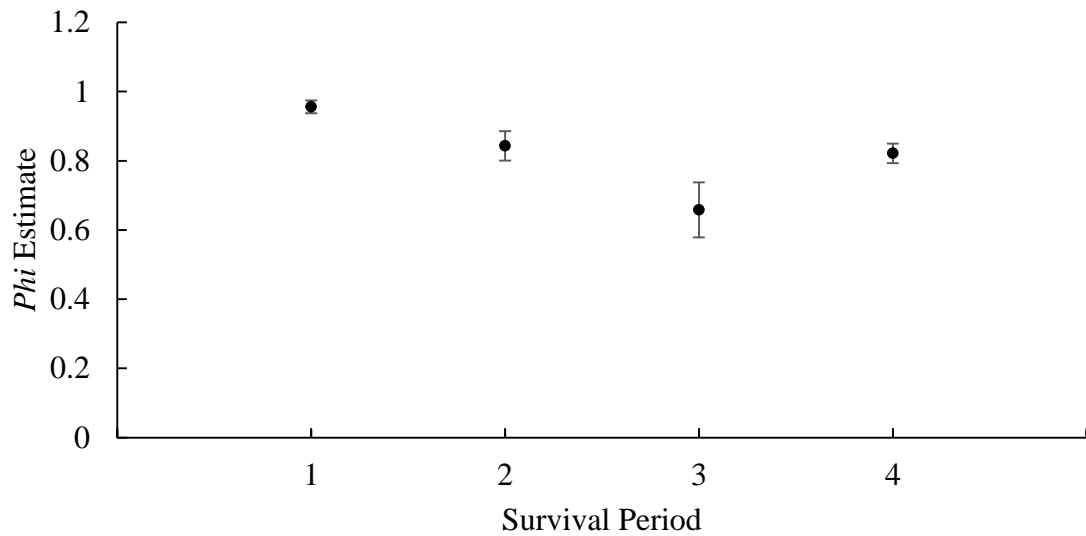to avoid confounding with the last survival estimate (*Phi4*).

Figure 2.3. Greater Prairie-Chicken Juvenile average survival estimates from the top

model (ϕ(t_4 + *residual* + *forb*)•p(t_3)are shown for each survival period (*Phi*$_{1-4}$)

corresponding to days 0-14 (*Phi*$_1$, 0.95 ±0.02), 15-21(*Phi*$_2$, 0.84 ±0.04), 22-28(*Phi*$_3$, 0.66

±0.03), and 29-70(*Phi*$_4$, 0.83 ±0.03), respectively. Residual and forb cover were not

measured during the *Phi*$_4$ survival period.

Figure 2.4. The mean percent residual cover and forb cover with 95% confidence

Mean Percent Cover of Vegetation Categories at Brood Survival Intervals
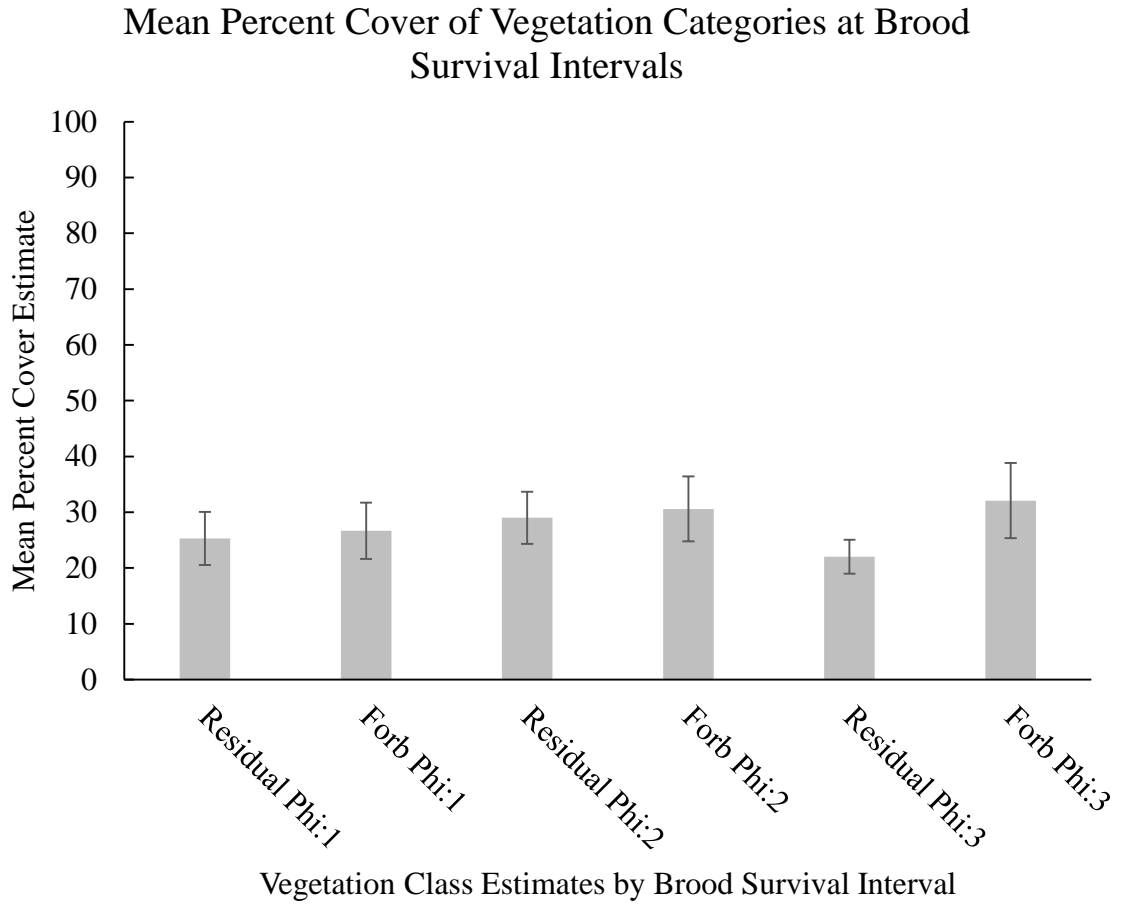
intervals. Residual cover estimates were 25% (±4.77), 29% (± 4.68), and 22% (± 3.05) for *Phi* intervals 1-3, respectively. Estimates of forb cover at *Phi* intervals 1-3 were 27% (±5.06), 31% (±5.83), and 32% (±6.65), respectively.

TABLES

Table 2.1. Preliminary models of survival and detection probability (p) ranked by AICc value and ordered according to their ΔAICc (difference in AICc from the top-ranked model). The number of parameters (K), model likelihood, and deviance also are included.

	MODEL STATISTICS					
Model Structure	AIC_c	ΔAIC_c	w_i	Model Likelihood	K	Deviance
$\phi(t^4)\,p(t^3)$	1046.9	0.00	0.99	1.00	6	796.53
$\phi(t^3)\,p(t^3)$	1056.3	9.41	0.01	0.00	5	808.07
$\phi(.)\,p(t^3)$	1067.6	10.78	0.00	0.00	3	823.63
$\phi(t^3)\,p(.)$	1085.4	38.58	0.00	0.00	4	839.35
$\phi(.)\,p(.)$	1086.6	39.74	0.00	0.00	2	844.66
$\phi(site)\,p(site)$	1086.9	40.04	0.00	0.00	4	840.81
$\phi(year)\,p(year)$	1087.4	40.52	0.00	0.00	4	841.29
$\phi(site\ x\ year)\,p(site\ x\ year)$	1090.4	43.55	0.00	0.00	6	840.08

Table 2.2. Model statistics include AICc (Akaike's Information Criterion adjusted for small samples), ΔAICc, model weight (w_i), model likelihood, number of parameters (K), and deviance.

Model Structure	Model Statistics					
	AICc	ΔAIC_c	w_i	Model Likelihood	K	Deviance
$\phi(t^4 + residual + forb)\bullet p(t^3)$	782.93	0.00	1.00	1.00	12	757.24
$\phi(t^4 + distance\ x\ forb)\bullet p(t^3)$	885.83	102.9	0.00	0.00	16	850.81
$\phi(t^4 + residual)\bullet p(t^3)$	886.77	103.8	0.00	0.00	9	867.81
$\phi(t^4 + shape + distance)\bullet p(t^3)$	908.47	125.5	0.00	0.00	14	878.17
$\phi(t^4 + distance)\bullet p(t^3)$	908.98	126.0	0.00	0.00	10	887.79
$\phi(t^4 + size)\bullet p(t^3)$	948.26	165.3	0.00	0.00	10	927.08
$\phi(t^4 + hatch)\bullet p(t^3)$	954.07	171.1	0.00	0.00	8	937.30
$\phi(t^4 + forb)\bullet p(t^3)$	954.78	171.8	0.00	0.00	9	935.82
$\phi(t^4)\bullet p(t^3)$	967.26	184.3	0.00	0.00	6	954.82
$\phi(t^4 + shape)\bullet p(t^3)$	969.28	186.3	0.00	0.00	10	948.10
$\phi(t^4 + edge)\bullet p(t^3)$	971.51	188.6	0.00	0.00	10	950.32
$\phi(year)\bullet p(t^3)$	999.89	216.95	0.00	0.00	4	991.68
$\phi(site)\bullet p(t^3)$	1001.98	219.05	0.00	0.00	4	993.77
$\phi(.)\bullet p(.)$	1036.67	253.7	0.00	0.00	2	1032.61

Table 2.3. Beta (β) estimates of each environmental covariate (i.e., residual and forb cover) in the top model (i.e., $\phi(t_4 + residual + forb) \cdot p(t_3)$) are ordered chronologically. Survival (*Phi*) periods 1-3 consider days 0-14, 15-21, and 22-28 days.

		Beta	SE	95% Confidence Interval	
				Lower	Upper
Residual	*Phi*$_1$	0.454	0.064	0.328	0.580
Forb	*Phi*$_1$	0.212	0.031	0.151	0.273
Residual	*Phi*$_2$	-0.043	0.024	-0.091	0.005
Forb	*Phi*$_2$	-0.048	0.022	-0.090	-0.005
Residual	*Phi*$_3$	0.045	0.030	-0.013	0.103
Forb	*Phi*$_3$	0.027	0.018	-0.009	0.062