AN ANALYSIS OF GREATER PRAIRIE-CHICKEN DEMOGRAPHY IN KANSAS: THE EFFECTS OF HUMAN LAND USE ON THE POPULATION ECOLOGY OF AN OBLIGATE GRASSLAND SPECIES

by

LANCE B. MCNEW, JR.

B.S., Eastern Illinois University, 2001
M.S., Southern Illinois University, 2003

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
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Abstract

Greater prairie-chicken (*Tympanuchus cupido*) populations have been reduced by >70% since the turn of the 20th century due to large-scale conversion of native prairie habitats to cultivated agriculture and other human development. Although Kansas is considered a stronghold for greater prairie-chickens, statewide populations have declined >30% in the last 30 years. Goals of this dissertation were to determine the demographic mechanisms for apparent population declines and evaluate how regional variations in landscape composition and grassland management affect the demography, habitat use, life-history, and population viability of three populations of greater prairie-chickens. First, I found that, despite high reproductive potential, poor reproductive success prevented populations from being self-sustaining. All three populations were projected to decline but finite rates of population declines were different among populations ($\lambda = 0.49$, 0.54, and 0.74). I found that grassland fragmentation and rangeland management practices influence nearly every aspect of greater prairie-chicken population ecology and dynamics. A population in a contiguous prairie landscape managed with annual spring burning and intensive early stocking of cattle (South) was characterized by delayed breeding, low nest and brood survival (0.08–0.18 and 0.27, respectively), high annual survival of mature females (0.64–0.71), projected age-ratios heavily skewed toward adults, and longer generation times. Conversely, a population in grasslands heavily fragmented by cultivation and managed with longer fire-return intervals and moderate grazing (Smoky) initiated nests earlier, had higher nest and brood survival rates (0.16–0.31 and 0.34, respectively), produced significantly larger eggs, and had low annual survival (0.34–0.42) and shorter generation times. A site with intermediate levels of fragmentation, burning and grazing (North) had intermediate demography. Finite population change was more sensitive to changes in adult survival at all sites, but the relative influence of fecundity parameters on projected population change was not similar among study populations. Data indicate that differences in rates of decline among populations were largely due to variation in adult survival mediated by human landscape alteration. Human-mediated changes to grasslands impact the demography and viability of prairie-chicken populations, influence population sensitivities to changes in vital rates, and mediate changes in the life-history strategies of a grassland-sensitive species.

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Dedication

This work is dedicated to the “friggin’ cows” of Kansas who did their best to thwart it.

CHAPTER 1 - INTRODUCTION

Three subspecies of greater prairie-chickens historically occurred in North America (Schroeder and Robb 1993). The extinct heath hen (*Tympanuchus cupido cupido*) once occupied a vast range in coastal New England. The Attwatter's prairie chicken (*T. c. attwatteri*) is currently on the brink of extinction and is maintained in only two isolated locations in Texas via a captive breeding program (Silvy et al. 1999). Similarly, the interior greater prairie-chicken (*T. c. pinnatus*) has shown significant population declines across its continually shrinking range over the last century (Braun et al. 1994, Schroeder and Robb 1993). Greater prairie-chicken populations, which were once known to occur in 20 states and 4 provinces, have been reduced to several isolated subpopulations by extensive agricultural development, and are listed or extirpated in at least 15 states and provinces (Braun et al. 1994, Schroeder and Robb 1993, Svedarsky et al. 2000). More than 95% of the American tallgrass prairie was lost to cultivation or development during the last century (Knapp et al. 1998), and prairie-chicken populations declined an estimated 75-80% as a result (Johnsgard 2002). States currently supporting greater prairie-chicken populations include Colorado, Illinois, Iowa, Kansas, Minnesota, Missouri, Nebraska, North Dakota, Oklahoma, South Dakota, and Wisconsin, with hunted populations in Kansas, Nebraska, Oklahoma, and South Dakota. With the exception of Colorado, most statewide populations have generally continued to decline due to habitat loss or degredation, and translocations from core areas to populations in Illinois, Iowa, and Missouri have been necessary to maintain population viability (Westemeier and Gough 1999).

The core of the extant distribution of the greater prairie-chicken has been the prairies of Kansas (Johnsgard 2002; Fig. 1.1). Greater prairie-chickens historically occurred in $\geq$79 counties throughout the tallgrass and mixed-grass prairies of Kansas (Horak 1985), but the majority of their current distribution occurs within two geologically-defined ecoregions: the Flint Hills and the Smoky Hills (Fig. 1.1). Although considered tallgrass prairie ecosystems, much variation in land cover composition and patterning, as well as grassland management, exists across these two ecoregions. The Flint Hills ecoregion is characterized by shallow limestone soils which make much of the area unsuitable for cultivation. However, the area supports an economically important cattle-grazing industry and historical grazing and fire regimes have generally maintained a relatively large (>1.6 million ha) and contiguous tallgrass prairie ecosystem. Thus, the Flint Hills region is often considered a stronghold for grassland obligate birds such as the greater prairie-chicken (Svedarsky et al. 1999, Johnsgard 2002). Despite large tracts of relatively intact grassland, the best available data from surveys conducted by Kansas Department of Wildlife and Parks (KDWP) indicate that prairie-chicken numbers have been declining in the Flint Hills over the past 30 years (Haukos and Church 1996, Applegate and Horak 1999, Rodgers 2009; Fig. 1.2), possibly in response to changing rangeland management practices (Robbins et al. 2002, Patten et al. 2007). Unlike the Flint Hills, much (≥40%) of the Smoky Hills region is tillable, and native prairies are moderately to highly fragmented by row crop agriculture (Fig. 1.1). Despite the commonly-observed negative impacts of fragmentation on grassland birds (Askins 2000), lek surveys conducted by KDWP suggest that populations in this region may be stationary or increasing (Rodgers 2009; Fig. 1.2). It is unknown why populations have been relatively stationary in the fragmented grasslands of the Smoky Hills while decreasing sharply in contiguous grasslands of the Flint Hills, but significant differences in rangeland management may be the cause. Grasslands in the Flint Hills are intensively managed for cattle production, and declines of prairie-chickens coincide with the wide-spread implementation of intensive early stocking and annual spring burning (IESB) in the region (Smith and Owensby 1978, With et al. 2008). Grazing by cattle is common on Smoky Hill pastures, but IESB is not; pastures are typically burned irregularly and cattle stocking occurs later in the spring at lower densities than in the Flint Hills (see Chapter 2).

Despite being an obligate grassland bird and indicator species for unfragmented tallgrass prairie at the core of species' distribution, relatively little is known about the vital population processes of greater prairie-chickens in Kansas. No studies have taken a comprehensive approach to quantifying the demography of greater prairie-chickens or evaluated the relative influences of human-driven variation in habitat conditions on population dynamics and viability. Although a few recent studies have quantified nest success (Nooker 2007) or offspring survival (Matthews et al., in press, Schole et al., in press) in the Flint Hills, no single study quantifying the complete life-history of greater prairie-chickens over a broad spatial extent has been attempted. Conservation of this species urgently requires baseline data representing these vital rates and their respective influence on population growth or decline in native habitats. My goal was to evaluate how regional variations in landscape composition and grassland management affect the demography, habitat use, life-history, and population viability of greater prairie-chickens. My specific objectives were to: 1) assess how variation in human land use and habitat alteration impacts the phenology and demography (e.g., fecundity, survival) of greater prairie-chickens, 2) use stochastic population models to evaluate variation in the rate of population change across a gradient of human landscape alteration, 3) evaluate how human manipulations of habitats have influenced the long term dynamics of greater prairie-chicken populations, 4) describe how human land management mediates selection for life-history traits, and 5) combine various quantitative methods to evaluate the efficacy of various conservation strategies in reducing or reversing population declines of greater prairie-chickens.

This dissertation is organized into four core chapters. In Chapter 2, I describe the reproductive chronology and breeding ecology of three declining populations of greater prairie-chickens occurring over a gradient of landscape alteration and rangeland management within the core of the species extant range. I found that the reproductive phenology of greater prairie-chickens in Kansas occurred earlier and lasted longer than in other populations and that clutch initiation was delayed in areas where most residual cover was removed through extensive annual spring burning and early cattle stocking. In Chapter 3, I used multiseason occupancy models and information-theoretic model selection procedures to evaluate the long-term occupancy, and the ecological factors influencing changes in the probabilities of colonization and local extinction of greater prairie-chickens at Konza Prairie Biological Station, a tallgrass prairie preserve in northeastern Kansas. I found that the probability of detecting greater prairie-chickens during surveys was highly variable and always <1, and that prairie-chicken occupancy declined precipitously over the 28-year study period due to increasing probabilities of local extinction as a result of grassland management practices. In Chapter 4, I tested for anthropogenic effects on the life-history evolution of greater prairie-chickens breeding at three sites across a gradient of landscape alteration. I found that reproductive effort varied significantly among the study sites in agreement with life-history theory. Variation in the life history traits of prairie-chickens was most consistent with site differences in predation rates and mortality of adult females which were apparently mediated by the anthropogenic effects of road development and conversion of grasslands to cropland. In Chapter 5, I estimated 12 demographic rates for the three populations of greater prairie-chickens, applied them to stage-based matrix models to estimate regional rates of population change, and evaluated their relative influences on population growth. I found that all populations of prairie-chickens are projected to decline under observed demographic conditions, that rates of population declines among the populations were not similar, and that rates of declines were much more sensitive to adult survival than other demographic parameters. Overall my results suggest that that 1) populations of prairie-chickens in Kansas are not sustainable without immigration, 2) rates of population decline vary among areas under different land management practices, 3) human land-use patterns may impact the relative influences of vital rates on population trajectories, and 4) anthropogenic effects on population demography may influence the regional life history strategies of a short-lived game bird. In Chapter 6, I summarize and discuss the major findings of my intensive population study and make recommendations for management and future research.

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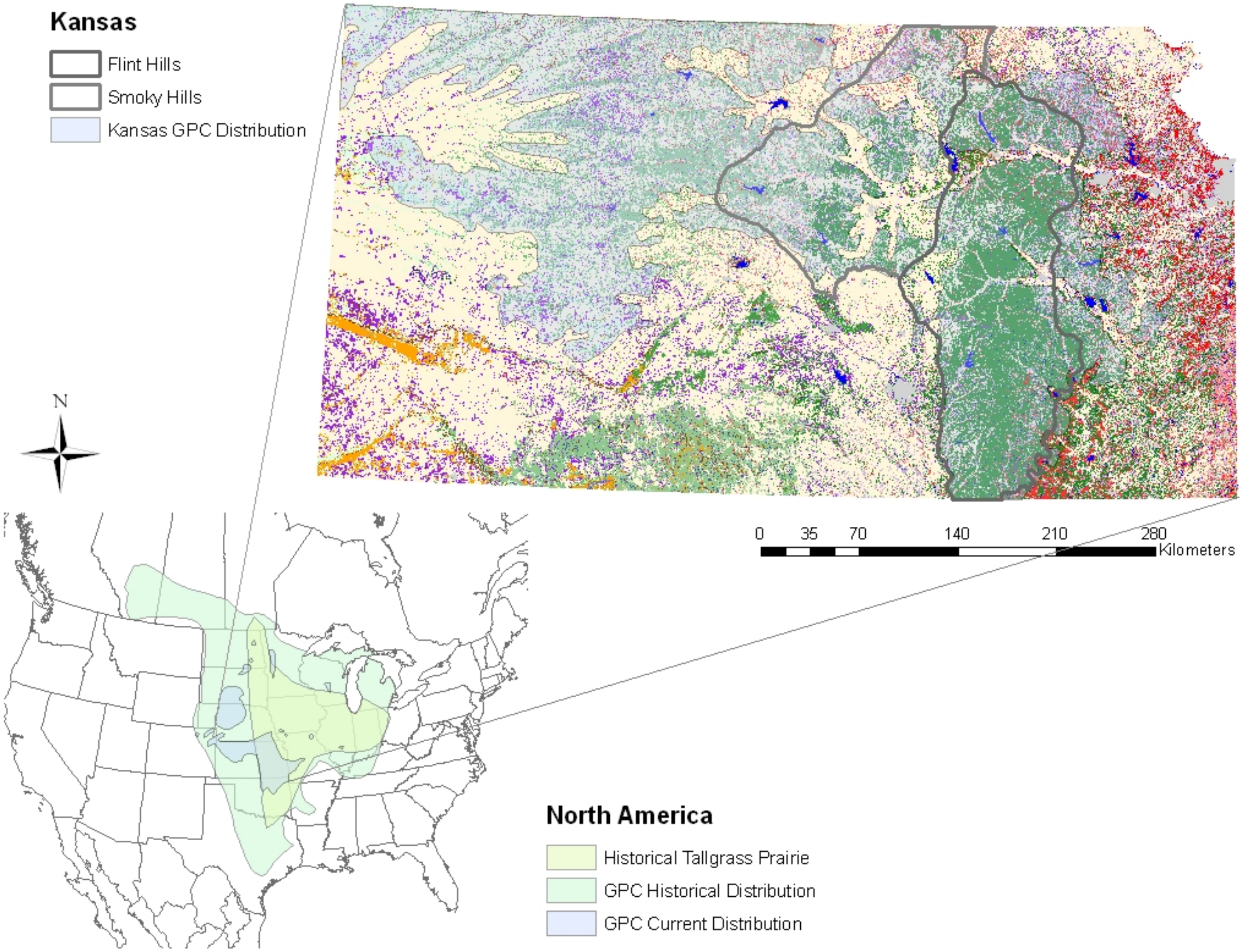

Figure 1.1. Historical and current distributions of greater prairie-chickens (GPC) in North America and Kansas. Kansas landcover data and statewide prairie-chicken range boundary were developed by the Kansas Applied Remote Sensing Laboratory at the University of Kansas, Lawrence.

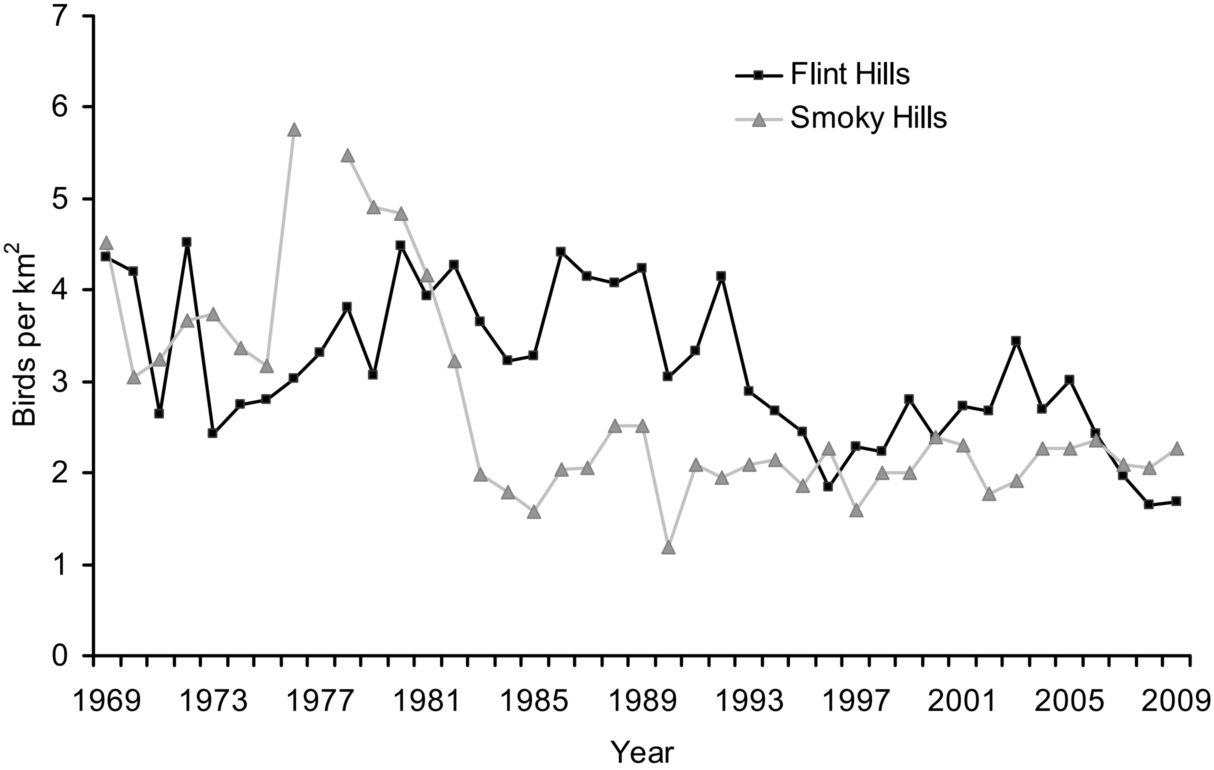

Figure 1.2. Population trends of greater prairie-chickens in the Flint Hills and Smoky Hills ecoregions of Kansas derived from annual lek counts conducted by the Kansas Department of Wildlife and Parks, 1969–2009.

CHAPTER 2 - REPRODUCTIVE CHRONOLOGY AND BREEDING ECOLOGY OF GREATER PRAIRIE-CHICKENS IN KANSAS

Abstract

We conducted a 3-year study of the breeding chronology of greater prairie-chickens (*Tympanuchus cupido*) to determine seasonal patterns of lek attendance and clutch initiation, and the duration of egg-laying and incubation for birds at the core of the species distribution. Our field study included three sites differing in landscape composition and rangeland management in the Flint Hills and Smoky Hills of Kansas. Counts of birds on leks were 30% higher when using counts from blinds compared to flush counts. Timing of lek attendance did not differ among study sites. Males attended leks from 2 March–19 May, females were observed at leks from 20 March–16 April, and peak lek attendance for both sexes was 9–10 April. Mean date of clutch initiation of first and renesting attempts was 26 April and 24 May, respectively, with active nests documented from 1 April–8 July. Females delayed initiation of first nests at the most southerly study site, possibly because of a lack of suitable nesting cover early in the season due to range management practices. Although previously undocumented for prairie-chickens, egg laying rates >1 egg/day suggested that intraspecific nest parasitism occurred in 6–15% of clutches. The probability of a female renesting after first nest failure was 50%, declined with date of nest failure, but was unaffected by stage of loss or study site. On average, females initiated renests 8 d after failure of first nests. Hatch dates ranged from 18 May–8 July, brood-rearing extended from 18 May–22 July, and juveniles were independent by 7 September at 60 d of age. Overall, the reproductive phenology of greater prairie-chickens in Kansas occurred earlier and lasted longer than in other populations. Our research results will be useful to wildlife biologists planning surveying or trapping activities, researchers conducting studies of nesting and brood ecology, and land managers concerned with minimizing the impacts of prescribed burning, cutting for hay or other types of rangeland management.

Introduction

Greater prairie-chickens (*Tympanuchus cupido*) have shown significant population declines across their continually shrinking range over the last century. Agriculture practices have caused a drastic decline of available usable habitat since the early 20th century (>95%; Braun et al. 1994, Schroeder and Robb 1993), and prairie-chicken populations declined an estimated 75–80% as a result (Johnsgard 2002). The relatively intact tallgrass prairie of east-central Kansas, southern Nebraska, and northeast Oklahoma has been identified as a stronghold for greater prairie-chickens (hereafter "prairie-chickens"; Johnsgard 2002). This area, referred to as the Flint Hills, is characterized by rocky soils that are unsuitable for cultivation but support an economically important cattle grazing industry and encompasses over 1.6 million ha. For this reason, many authors consider the Flint Hills to be vital to the long-term persistence of grassland birds (Svedarsky et al. 1999, With et al. 2008). Despite large tracts of relatively intact grassland, annual lek surveys conducted by the Kansas Department of Wildlife and Parks (KDWP) show that statewide prairie-chicken populations have declined annually from 4.5 birds/km^2 in 1980 to 1.5 birds/km^2 in 2008 (Applegate and Horak 1999, Rodgers 2008). The definitive cause for population declines remains unknown but timing of declines coincide with the introduction of the range management practice of intensive early stocking and annual spring burning (IESB; Westemeier and Gough 1999, Robbins et al. 2002). A combination of early annual spring burning (Mar-Apr) and intensive cattle stocking of rangelands has been implemented annually by ranchers across the Flint Hills for nearly three decades (Launchbaugh et al. 1983). IESB benefits cattle production by increasing grass production and allowing ranchers to stock ranges with cattle early. IESB may negatively affect prairie grouse production if complete burns of large contiguous range result in significant decreases in availability of quality nesting sites (Robbins et al. 2002, Patten et al. 2007). To date, studies of the effects of rangeland management on prairie-chicken breeding ecology have been limited to the selection of nest sites and its relative effects on nest survival (McKee et al. 1998, Patten et al. 2007). Data are lacking regarding how these practices impact other aspects of prairie-chicken breeding behavior, such as breeding phenology.

The timing of reproductive events of grassland birds is important; especially for short-lived species whose population dynamics are sensitive to variation in reproductive success (Wisdom and Mills 1997). For prairie grouse, such as greater prairie-chickens, productivity may be determined by seasonal variation in the ability of females to locate mates at mating arenas or leks, and the environmental conditions at nesting and brood-rearing habitats. For example, timing of breeding and clutch initiation should be late enough to ensure that suitable vegetative cover exists for concealment of first nesting attempts, but early enough to ensure that renesting attempts can occur if needed and that juveniles are independent before inclement winter conditions (Horak 1985, Svedarsky et al. 2003). In addition, timing of nest initiation has implications for recruitment because chick development and survival is affected by abundance and seasonal phenology of insect food items (Johnson and Boyce 1990, Park et al. 2001, Gregg and Crawford 2009). Thus, timing of reproductive events is critical for maximizing fitness of prairie-chickens and may vary among areas of different habitat conditions.

Reproductive chronology of prairie-chickens also has implications for population monitoring, research and range management. Knowledge of the timing of reproductive events is necessary for wildlife biologists planning population surveys of leks or females with broods, researchers studying nesting and brood ecology, and land managers scheduling burning, grazing or haying activities. Knowledge of reproductive chronology is particularly important for species with broad geographic ranges but regional variation in rates of population decline, such as the greater prairie-chicken (Rodgers 2008). Reproductive chronology has been described for isolated populations in Minnesota (Svedarsky 1983, 1988) and Wisconsin (Hamerstrom and Hamerstrom 1973), but relatively little is known about the timing of reproductive events of prairie-chickens breeding in Kansas (Robel 1970, Horak 1985). Recent changes in regional land management practices (i.e., grazing and prescribed burning) over the last three decades may have altered the breeding phenology of prairie-chickens in the Flint Hills, as these practices have changed the seasonal availability of lekking, nesting, and brood-rearing habitat (Patten et al. 2007). The landscapes of Kansas provide a unique opportunity to evaluate whether land management practices impact the breeding phenology of prairie-chickens because land use and range management practices vary significantly across the species range within the state. In addition to occupying the large unfragmented grasslands of the Flint Hills, prairie-chickens also occur in the more developed Smoky Hill ecoregion (Rodgers 2008). Although grasslands in the Smoky Hills are highly fragmented by row crop agriculture (>35% of the landscape) and improved roads (1.04 km per ha), they are not as intensively managed as grasslands in the Flint Hills and may be of better quality due to lower cattle stocking rates and less frequent burning (J. Pitman, Kansas Department of Wildlife and Parks, pers. comm.).

In this paper, we describe the reproductive chronology of three declining populations of greater prairie-chickens (*T. c. pinnatus*) occurring over a gradient of landscape alteration and rangeland management within the core of the species extant range in Kansas. We expected (1) timing of breeding events to occur earlier than previous reports for northern populations and, (2) differences in regional land use to affect the seasonal phenology and reproductive rates in our study populations. If prairie-chickens require suitable cover in order to initiate nests (Pitman et al. 2005, Fields et al. 2006), clutch initiation, duration of laying and incubation, renesting propensity, and timing of brood rearing and fledging might be delayed in areas where most residual cover is removed through extensive annual spring burning and early cattle stocking. We discuss the ecological and management implications of regional variation in the seasonal breeding chronology of prairie-chickens in Kansas.

Study Sites

Our field study was conducted at three sites in Kansas; two sites in the Flint Hills and one site in the Smoky Hills (Fig. 2.1). The three study sites differed in landscape composition and pattern, as well as rangeland management practices (Table 2.1). The Southern Flint Hill site (South) was burned annually in the spring, and managed with intensive early stocking (IESB, 1 head/0.8 ha for 90 days; Smith and Owensby 1978, With et al. 2008). The second study area was located in the northern Flint Hills (North). Annual spring burning is common at North and lands are managed with a mixture of IESB and season-long stock grazing and annual burning (SLSB; 1 head/1.6 ha for 180 days). The third study area (Smoky) was located in the Smoky Hills ecoregion and is more fragmented by agricultural land uses (Table 2.1). Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at Smoky are burned infrequently at fire return intervals >1 year, are grazed at low intensity (1 head / >2 ha for 90 days), and cattle stocking occurs later in the season than at the Flint Hill sites.

Methods

Lek Attendance

During the spring lekking period (February–May), counts of birds at leks were conducted using two methods: (1) birds were flushed from untrapped leks between 0600 and 0930 hrs, and (2) prairie-chickens were observed from blinds while birds were trapped at leks. We attempted to obtain counts of males and females prior to flushing by viewing leks with binoculars from >100 m when possible. For both methods, the maximum numbers of males, females, and total birds were recorded. Multiple flush counts were conducted for each lek within a breeding season but not on consecutive days. To assess whether survey method affected lek counts, we used analysis of variance (ANOVA) to compare counts of prairie-chickens when leks were flushed or trapped, and among our three study sites. A Tukey-Kramer HSD was used to compare lek counts among sites at $\alpha = 0.05$ level.

We calculated the date of peak lek attendance for males and females at each study site by weighting the Julian date of lek observation (day 1 = 1 Jan) by the average number of birds attending leks:

$$\text{Day of Peak Lek Attendance} = \frac{\sum\left(D_i \frac{A_i}{\overline{A}_{1-N}}\right)}{N},$$

where D_i is the Julian day i of lek observation, A_i is the mean lek attendance by males or females for day i, $\overline{A}_{1-N}$ is the mean lek attendance for all days of observation, and N is the total number of observation days per sex. Low numbers of surveys per day at each study area precluded comparisons of peak lek attendance among sites by year. We pooled daily surveys among years of study and compared timing of peak lek attendance among study sites using ANOVA. Female lek attendance data were log-transformed to meet the normality assumption of ANOVA (Sokal and Rohlf 2000).

Egg-laying and Incubation

We captured prairie-chickens with walk-in traps and drop-nets at leks during March–May of 2006–2008 (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage characteristics (Henderson et al. 1967). Females were fitted with 11-g necklace-style VHF radio transmitters with an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). We located females $\geq$3 times per week during the breeding and brood-rearing seasons (March–August), and daily once females began nesting. Once a female had localized in an area for three consecutive days, we used a portable radio receiver and handheld Yagi antenna to locate and flush the bird. Nest sites were visited $\leq$2 times during laying and early incubation to determine clutch size and stage of incubation. Nests were not visited again until females had departed and were located away from the nest for ≥2 consecutive days. Once a female departed, we classified nest fate as either successful because ≥1 eggs successfully hatched chicks, or failed because the clutch was depredated, abandoned or destroyed for other reasons. Date of hatching was the last day the female was estimated to be incubating at a successful nest by triangulation with radio-telemetry. Field methods were approved by Kansas State University's Institutional Animal Care and Use Committee (Protocol numbers 2474 and 2781).

To estimate duration of incubation in days, we subtracted the date of known clutch completion from the date of hatch. We assessed the influence of study site, nesting attempt, clutch size, and day of nest initiation on duration of incubation using forward stepwise regression. Alpha (α) levels of 0.05 and 0.1 were specified for entry and removal of factors from the model.

Nest and Brood Chronology

First nests were defined as the first nest discovered for an individual female within a breeding season, whereas renests were nesting attempts by radio-marked females where the first nest was known to have failed. If the clutch size increased between visits, the date of clutch initiation was determined by backdating by the number of eggs from the first visit assuming one egg laid per day (Svedarsky 1988). If clutch size did not change between successive visits, the date of clutch initiation was determined by backdating from the hatch date assuming an incubation period of 24 days (Schroeder and Robb 1993), or from the stage of incubation determined by egg floatation (McNew et al. 2009; Appendix A). We used forward stepwise regression to model dates of clutch initiation as a function of study year, study site, and nesting attempt. Alpha (α) levels of 0.05 and 0.1 were specified for entry and removal of factors from the model. We then fitted a linear model with the resulting significant predictor variables and assessed model fit.

We used logistic regression to evaluate the relationship between the probability of renesting and study site, clutch size of the first nest, day of incubation when the initial attempt failed, and the date of nest failure. Date of failure was considered to be the midpoint between the last day the nest was known to be active and the day it was identified as failed. The average interval (± SD) between the last day a nest was known to be active and the day it was determined to have failed was 4 + 4 d. We excluded females that were unavailable to renest if they died while incubating first nests, could not be located after first nests failed, or lost their transmitters within two weeks of failure of the first nest. We also excluded 10 nests for which explanatory data were missing. We fit 13 *a priori* models to data from 82 failed first nest attempts. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for model selection, and models where $\Delta AIC_c \leq 2$ were considered to be equally parsimonious (Burnham and Anderson 1998). Logistic regression analyses were conducted using the logistic procedure in SAS 9.1 (SAS Institute, Cary, NC).

We located radio-marked hens with broods daily via triangulation. Brood flushes were conducted at 14-d post-hatching to estimate pre-fledge brood survival. Prairie-chickens can sustain short flights at 14-d of age (Schroeder and Robb 1993). Although juveniles can survive without the brood female once they are 40-d old, they are still generally associated with the female and brood mates until 60-80-d post hatch (Bowman and Robel 1977; L. B. McNew, unpubl. data). Therefore, dates of fledging and independence were estimated for successful broods and compared to predicted dates for all hatched broods. Sample sizes of successful broods were too small to conduct statistical analyses and descriptive statistics are presented. Statistics were calculated with procedures of program JMP IN (Ver. 4.0.4, SAS Institute, Cary, NC).

Results

Lek Attendance

During 2006–2008, we conducted 673 lek surveys at our three study sites from 2 March–19 May. We conducted 408 lek observations from blinds during trapping activities and 265 flush counts where no traps were deployed. To assess whether our trapping activities impacted lek attendance, a random sample of 265 trapped lek observations were selected and compared to flush counts. The maximum number of prairie-chickens observed was greater during lek observations of trapped leks (10.9 + 0.4SE birds per day) than flush counts (7.2 + 0.4; $F_{1,522} = 56.8$, $P < 0.001$). Similarly, female lek attendance was greater for observations conducted during trapping (1.3 + 0.9 birds per day) than during flush counts (0.4 + 0.1; $F_{1,367} = 30.7$, $P < 0.001$); suggesting that trapping activities did not negatively impact lek attendance and that counts from lek observations of trapped leks were suitable for further analysis.

The peak of male lek attendance was 9 April across all years and study sites in Kansas, with males present on leks during the entire 79-d observation period (2 March–19 May; Fig. 2.1). Peak female attendance at leks was 10 April when data were pooled among years and sites, with 95% of female lek visitations occurring during a 28-d period between 20 March–16 April (Fig. 2.1). Timing of peak lek attendance did not differ among study sites for males ($F_{2,172} = 0.38$, $P = 0.68$) or females ($F_{2,172} = 0.32$, $P = 0.73$), but the duration of female lek attendance appeared to be a shorter period at the South site (Fig. 2.2). Copulations (n = 13) were observed during a 37–d period from 3 April–9 May.

Timing of Clutch Initiation and Renesting

During 2006–2008, we located 231 nests of 155 females. A total of 167 nests were first nests, 61 nests were first renests, and three nests were third nesting attempts. Mean date of clutch initiation for first nests at all sites was 26 April (range = 1 April–22 May; N = 162). Mean date of clutch initiation for known renest attempts was 24 May (range = 29 April – 4 July; N = 64). Forward stepwise regression revealed that nesting attempt and the interaction between study site and nesting attempt were significant predictors of date of clutch initiation ($r^2 = 0.45$, $P < 0.01$). Study year and site alone did not improve model fit and were removed from the model. Mean ($\pm$SE) date of clutch initiation differed significantly among study sites (South = 2 May $\pm$ 1.9 d, North = 30 Apr $\pm$ 1.5 d, Smoky = 24 Apr $\pm$ 1.7 d; $F_{2,150} = 3.4$, P = 0.03), but timing of renests did not differ among study sites (Fig. 2.3). Mean date of hatching for all sites pooled was 6 June for first nests (range = 18 May–21 June) and 26 June for renests (7 June–8 July, Fig. 2.4). Date of hatching did not differ among study sites ($F_{2,40} = 2.0$, $P = 0.15$) and years ($F_{2,21} = 0.23$, $P = 0.79$).

The probability of a prairie-chicken initiating a renesting attempt was influenced by the date of failure for the first nest (Fail Day) and the stage of incubation at failure (First Nest Age). An additive model with these two factors was the minimum AIC_c model, and models that included Fail Day had 98% of the relative support of the data (Table 2.2). However, the regression coefficient for First Nest Age ($\beta = -0.002$) was not significantly different than zero (95% CI = -0.06 to 0.06) and was considered spurious. Females losing first nests late in the season had a lower probability of renesting ($\beta = -0.11$, 95% CI = -0.17 to -0.05; Fig. 2.5), and the odds of a female attempting a renest decreased by 11% per day during the nesting season.

Prairie-chickens renested with an average interval between failure of the first nest and initiation of a renesting attempt was 7.8 $\underline{+}$ 1.1 days (range = 0–27 d, n = 45).

The fledging period, defined as the period between the dates of fledging for our first and last brood, at all study sites ranged across a 53-d period from 31 May–22 July (mean day of fledging was 30 June). Timing of fledging did not differ for broods that successfully fledged and the dates predicted for unsuccessful broods (difference = 2 d). Prairie-chicken chicks at the Smoky site tended to fledge earlier than the other two sites but the difference was not significant ($F_{2,40} = 2.1$, $P = 0.13$). Dates of independence for prairie-chicken young at 60 days of age would be predicted to occur from 16 July–7 September.

Egg-Laying and Incubation

On average, prairie-chickens laid an egg every 1.1 $\underline{+}$ 0.3 days, but in 10 of 67 cases (15%), the estimated rates of egg-laying were >1 egg/day (range = 1.1–2.0). When we adjusted clutch initiation dates to account for the uncertainty of our egg floatation technique ($\underline{+}$ 2 d; McNew et al. 2009), egg laying rates at 6 of 10 nests still were >1 egg per day. Thus, 6-15% of prairie-chicken clutches in our study showed evidence of intraspecific nest parasitism by other female prairie-chickens. Clutch sizes of first nests (12.4 $\underline{+}$ 2.3 eggs) were larger than renests (10.5 $\underline{+}$ 2.4 eggs). Prairie-chickens incubated nests for 25.0 $\underline{+}$ 2.5 days on average (range = 22–29 d, n = 38). Forward stepwise regression indicated that duration of incubation was not affected by study site ($F_{2,34} = 0.5$, $P = 0.63$), date of nest initiation ($r^2 = 0.07$, P = 0.11, df = 1, n = 35), or nesting attempt ($F_{1,34} = 3.4$, $P = 0.08$; second and third nests pooled). Duration of incubation was positively related to clutch size by:

$$Duration\ of\ Incubation = 20.9 + 0.32\ (Clutch\ Size),$$

but most of the variation was unexplained ($r^2 = 0.12$, $P = 0.03$, df = 1, n = 35).

Discussion

Compared to populations of prairie-chickens in the northern extent of their range (Hamerstrom and Hamerstrom 1973, Svedarsky 1983; 1988), the seasonal timing of lek attendance and clutch initiation was earlier in Kansas, the duration of the nesting and brood-rearing periods was longer, and rates of renesting were higher. Moreover, regional differences in landscape pattern and rangeland management resulted in differences in timing of clutch initiation among sites in the Flint Hills and Smoky Hills ecoregions of Kansas, with delayed initiation in annually burned and heavily grazed grasslands. Duration of incubation and age at fledging were similar for all populations. Egg-laying rates >1 egg per day indicate that intraspecific nest parasitism may be more common in the core range of Kansas than in relict populations elsewhere.

Timing of Lek Attendance and Nesting

Lek attendance by both male and female prairie-chickens in Kansas was highest during the second week of April, with no annual variation in seasonal timing during our 3–year study. Timing of lek attendance was earlier in Kansas than at northern study sites in Wisconsin and Minnesota (Hamerstrom and Hamerstrom 1973, Svedarsky 1988); a latitudinal trend reported for other species of prairie grouse (Connelly et al. 1998, Schroeder et al. 1999). Earlier breeding phenology at lower latitudes may be due to differences in photoperiod or local cues based on availability of resources (Schoech and Hahn 2008). Male attendance at leks was stable throughout March to May, although males were most active in display behaviors when females visited in mid-April (Nooker and Sandercock 2008). We did not observe seasonal declines in male lek attendance as previously described for prairie-chickens in Kansas (Robel 1970), and our results were more consistent with the stable lek attendance reported for other populations (Hamerstrom and Hamerstrom 1973, Svedarsky 1983). Sustained male attendance may be driven by a propensity of females to initiate multiple nests or by extended nesting periods in our populations.

Clutch initiation for prairie-chickens in Kansas (1 April) began earlier than populations in Minnesota and Wisconsin (20–27 April; Svedarsky 1983, Hamerstrom and Hamerstrom 1973), but later than a population of Attwater's prairie-chicken (*T. c. attwaterii*) in coastal Texas (12 Mar; Lutz and Silvy 1994). Latitudinal differences in the onset of clutch initiation may be due to variation in vegetation phenology across the species range, which likely results in earlier availability of suitable resources at lower latitudes. In addition, the nesting season was longer in Kansas than reported previously for both northern and southern populations of prairie-chickens, with active nests located during a 3–month period between 1 April and 4 July. Elsewhere, nests have been found during a 2-month period for both interior greater prairie-chickens (mid-April–early June; reviewed by Schroeder and Robb 1993) and Attwater's prairie-chicken (mid-March–early May; Lutz and Silvy 1994). Early nesting and a longer breeding season may allow prairie-chickens in Kansas to cope with nest failure due to initially poor nesting cover (McNew et al. 2010) with higher rates of renesting.

We observed site differences in the timing of clutch initiation, but unexpectedly, nests were initiated later at the most southerly study site in the Flint Hills. Differences in rangeland management and agricultural use may explain differences in timing of clutch initiation of about a week among our study sites in Kansas. Most of the native tallgrass pastures at the South (~90%) and North (~70%) sites were burned during March and April, whereas none of the native tallgrass pastures at the Smoky site were burned during our study. Spring burning may affect timing of nesting if female prairie-chickens delay egg-laying until vegetative cover is sufficient to conceal the clutch. Although delayed nesting in response to poor habitat conditions has not previously been reported for prairie-chickens, female prairie grouse tend to initiate clutches in areas with greater residual cover and visual obstruction (Pitman et al. 2005, Fields et al. 2006, L.B. McNew, unpubl. data.). Alternatively, variation in timing of clutch initiation could have been due to site differences in food availability or weather. Prairie-chickens and other grouse are income breeders that require exogenous nutritional resources for egg-laying (Meijer and Drent 1999), and site differences in rangeland quality or access to subsidies from agricultural crops could have affected variation in timing through effects on nutritional status. Cultivated agricultural fields comprised a higher proportion of the landscape at the Smoky site and prairie-chickens will utilize grain sorghum and other crops prior to nesting (Robel et al. 1970). Females were heavier at the Smoky site (mean ± SE = 929 ± 8.8 g) than at North (908 ± 8.7 g) or South (879 ± 7.9 g) sites. It is unclear whether females at the Smoky site were in better body condition but larger females tended to initiate clutches earlier than smaller females (McNew et al. 2010). Weather can influence the timing of clutch initiation in grouse as well (Martin et al. 2000, Martin and Wiebe 2004). However, warmer average daily temperatures (~2–3°C; Table 1) during the period when initiation of first clutches would be impacted (Mar-May) did not result in advanced reproductive phenology at the South site. In contrast, clutch initiation occurred later at this site. We found no differences in mean monthly precipitation ($F_{2,18} = 0.9$, $P = 0.42$) among study sites during the clutch initiation period (Table 2.1); suggesting that weather was not responsible for the observed variation in clutch initiation timing among study sites.

The influence of landscape composition and land use on prairie-chicken nesting behavior and demography is well documented. Habitat conditions like residual cover directly affect the selection of nest and brood sites and the resulting success of these vital parameters (McKee et al. 1998, Pitman et al. 2005, Fields et al. 2006). Therefore, land management practices which alter habitat conditions, such as prescribed burning, grazing, and row crop agriculture, can have significant impacts on prairie-chicken habitat use, reproductive success, and survival (Patten et al. 2007, McNew et al. 2010). Our data suggest that the effects of landscape alteration and management can influence not only vital rates directly through impacts on availability and quality of habitat, but through impacts on the effort and timing of reproduction as well. Although it is unclear whether nest initiation was delayed at the South site due to limited nesting cover or whether initiation was advanced at the Smoky site because females were in better condition, human manipulation of prairie-chicken habitats appears to be impacting the nesting phenology of prairie-chickens in Kansas. Given the effects of temporal variation on nest survival and renesting propensity (Hannon et al. 1988, Sandercock et al. 2005, Martin et al. 2010), human activities that alter prairie-chicken resources, such as range management practices, may have even greater influence on populations than previously recognized.

Egg-Laying and Incubation

The average egg-laying rate of female prairie-chickens in Kansas was one egg per 1.11 days, similar to published reports from other populations (Schroeder and Robb 1993). We estimated that 6–15% of the nests in our sample had egg-laying rates of >1 egg per day, with uncertainty due to the margins of error from our egg flotation technique. Given that egg-laying rates of >1 egg per day are unknown for large-bodied birds (Welty and Baptista 1988); we conclude that a subset of our nests were affected by conspecific nest parasitism by other prairie-chickens. Intraspecific nest parasitism has not been documented for prairie-chickens but has been reported in a few other species of grouse (willow ptarmigan [*Lagopus lagopus*], Martin 1984; sharp-tailed grouse [*T. phasianellus*], Gratson 1989, Yom-Tov 2001).

Duration of incubation for prairie-chicken nests in Kansas (25.0 ± 2.5 d) was similar to values reported for northern populations in Wisconsin and Minnesota (23–25 d; Hamerstrom and Hamerstrom 1973, Svedarsky 1988, Schroeder and Robb 1993). Age-specific mortality rates can influence patterns of nest attentiveness through effects on residual reproduction, leading to variation in duration of incubation for songbirds (Martin 2002). We found no regional variation in the duration of incubation in prairie-chickens, despite pronounced differences in nest survival and adult female mortality rates among our three study sites (McNew et al. 2010).

Female prairie-chickens renested readily if their first nest was destroyed. A minimum of 50% of female prairie-chickens renested after failure and the probability of renesting declined seasonally with the date of failure for first nesting attempts. Our reported estimates of renesting probability are conservative because our method of locating nests based on tracking of radio-marked females made it difficult to find nests during the laying period; possibly resulting in many undocumented first nests which failed before discovery. Nevertheless, renesting propensity is usually lower in other species of grouse (< 36%, but see Martin et al. 2010) and has been explained by other factors, including stage of loss during the nesting cycle and female age-class (Sopuck and Zwickel 1983, Robb et al. 1992, Connelly et al. 1993, Storaas et al. 2000, Martin et al. 2010). Prairie-chickens may have had high rates of renesting for three reasons. First, they are a relatively short-lived species that make a large investment in reproduction (Bergerud and Gratson 1988) and renests can contribute to the annual fecundity of single-brooded precocial birds (Martin et al. 1989, Milonoff 1991, Martin et al. 2010). Second, date of first nest failure impacted the probability of renesting and a large proportion of first nests failed early in the season (>80%; L. B. McNew, unpubl. data). Date of failure may have been more important than stage of loss because prairie-chickens breed at southerly latitudes and have a longer breeding season than forest and tundra grouse (Sandercock et al. 2005). Last, differences in habitat conditions among the study sites could have influenced the probability of renesting. Because prairie-chickens are income breeders, marked differences in landscape composition, fragmentation, and land management practices observed among study sites could have impacted the resources available for egg deposition. However, prairie-chickens shared similar abilities to initiate renesting attempts among the three sites, suggesting that exogenous resources for follicle development during renesting attempts were not limiting for any of our populations. The resource availability hypothesis has also been rejected for arctic grouse (Sandercock et al. 2005, Martin et al. 2010); suggesting alternate hypotheses may be more appropriate for explaining renesting abilities of Tetraoninae.

In summary, the reproductive chronology of prairie-chickens in Kansas started earlier and lasted longer than in other populations possibly due to a combination of longer summers at low latitudes and regional differences in landscape composition and rangeland management practices. Rangeland management practices that remove or reduce residual vegetative cover during March and April, such as annual spring burning and intensive early stocking of cattle, have the potential to negatively impact prairie-chickens by delaying onset of clutch initiation and reducing nesting success. A better understanding of the breeding chronology of prairie grouse and the duration of reproductive stages will assist management efforts and provide a foundation for intensive studies of population demography in the future. For example, wildlife biologists planning lek surveys for population monitoring or live-trapping of prairie-chickens for translocations or population studies would optimize field effort in Kansas by planning field work from late March to mid–April, the period of greatest lek attendance and activity. Likewise, land managers can reduce negative impacts on prairie-chicken populations by limiting haying, spraying, and other disturbances during early April–late July as this is the primary nesting and brood-rearing period in Kansas.

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Table 2.1. Comparison of southern Flint Hills (South), northern Flint Hills (North) and Smoky Hills (Smoky) study sites for population studies of greater prairie-chickens in Kansas, 2006-2009.

	South	North	Smoky
Area (km^2)	1,106	671	1,630
Prairie-chicken density index[a]	0.10	0.19	0.17
Proportion grassland	0.90	0.81	0.53
Proportion cropland	0.03	0.10	0.38
Road density (km/km^2)	0.32	0.57	1.04
Mean (SE) precipitation (cm)[b]	12.3 (2.0)	11.4 (2.4)	8.2 (2.4)
Mean daily temperature (°C)[c]	15.0 (0.4)	12.9 (0.4)	12.1 (0.4)
Land management[d]	IESB	IESB, SLSB	SLSU, RG&B

[a] Mean number of birds per lek × number of leks / study site size

[b] Mean monthly precipitation during March – May, 2006–2008.

[c] Mean daily temperature during March – May, 2006–2008

[d] Dominant land management at each study site: IESB = intensive early stocking, annual burning; SLSB = season long stock grazing, annual burning; SLSU = season long stocking, unburned; RG&B = rotational grazing and burning (after Smith and Owensby 1978, With et al. 2008).

Table 2.2. Model selection based on minimization of AICc for the estimation of renesting probabilities of greater prairie-chickens at three study sites in Kansas, 2006-2008.

Model[a]	K[b]	AIC_c	ΔAIC_c	w_i
Fail Day + First Nest Age	3	91.4	0	0.41
Site + Fail Day + TCL + First Nest Age	5	92.0	0.5	0.32
Fail Day + TCL + First Nest Age	4	92.4	1.0	0.25
Fail Day	2	100.7	9.3	0.0
Site + Fail Day	3	101.4	10.0	0.0
Fail Day + TCL	3	101.8	10.4	0.0
Site + Fail Day + TCL	4	105.1	11.2	0.0
TCL	2	128.4	37.0	0.0
Site	2	128.5	37.1	0.0

[a] Fail Day = date of failure for initial nesting attempt, First Nest Age = stage of development when initial attempt failed, Site = study site, TCL = clutch size of initial attempt.

[b] K = number of parameters, w_i = AIC_c weight or relative support for model i.

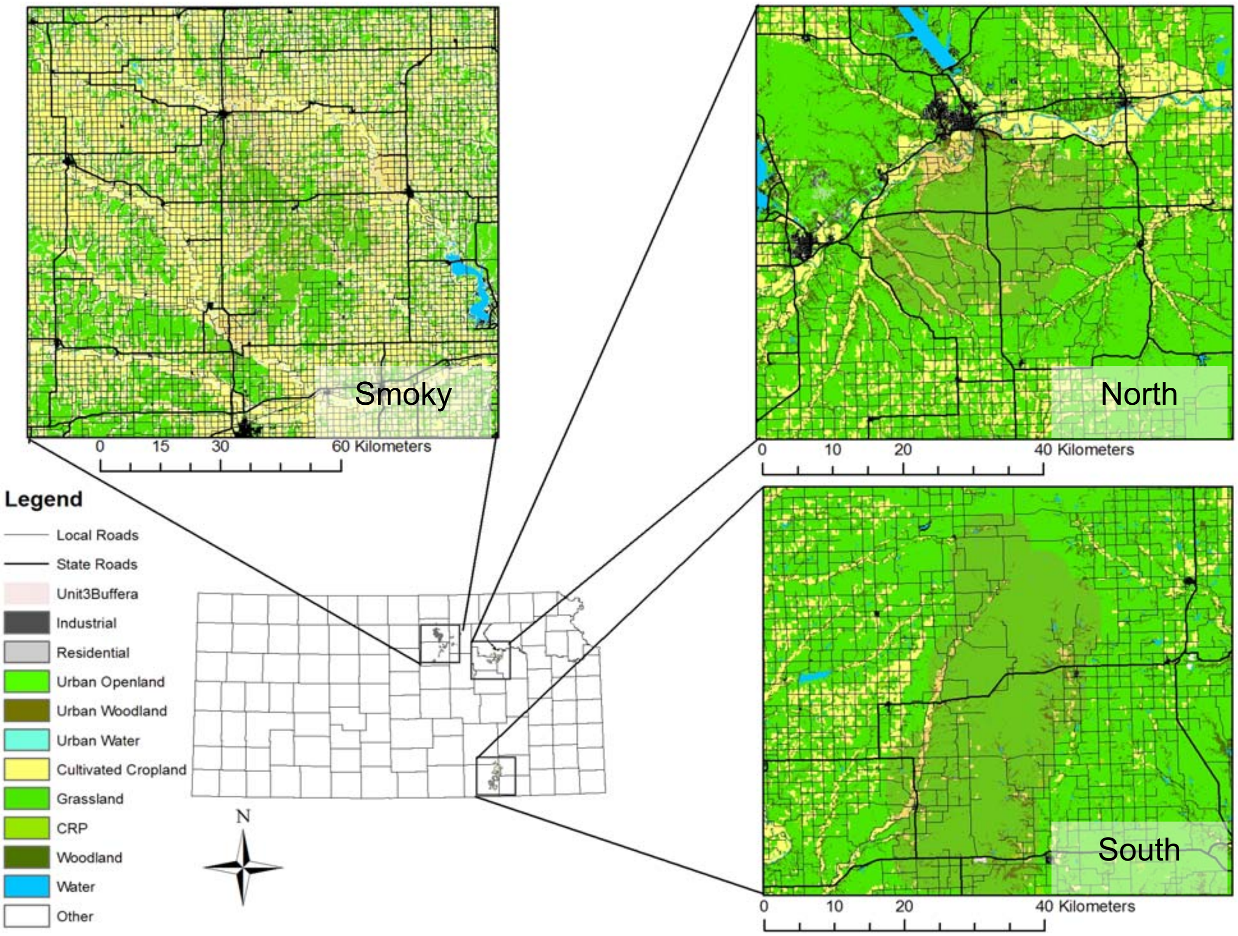

Figure 2.1. Locations and landscape composition of the Southern Flint Hills (South), Northern Flint Hills (North), and Smoky Hills (Smoky) sites for study of the population biology of greater prairie-chickens in eastern Kansas, 2006-2008.

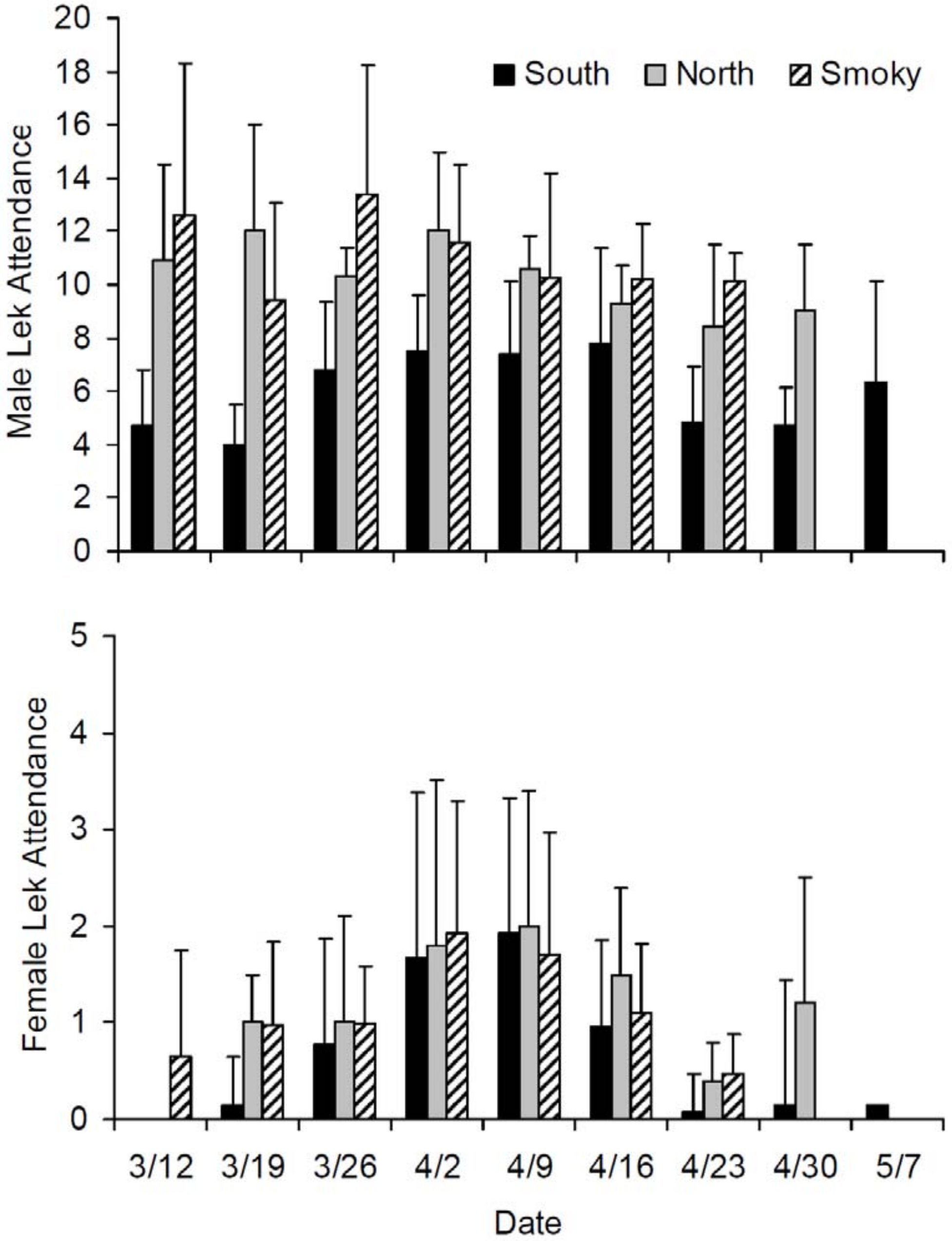

Figure 2.2. Mean daily lek attendance per week (birds per day ± SD) of (a) male and (b) female greater prairie-chickens in Kansas, 2006-2008.

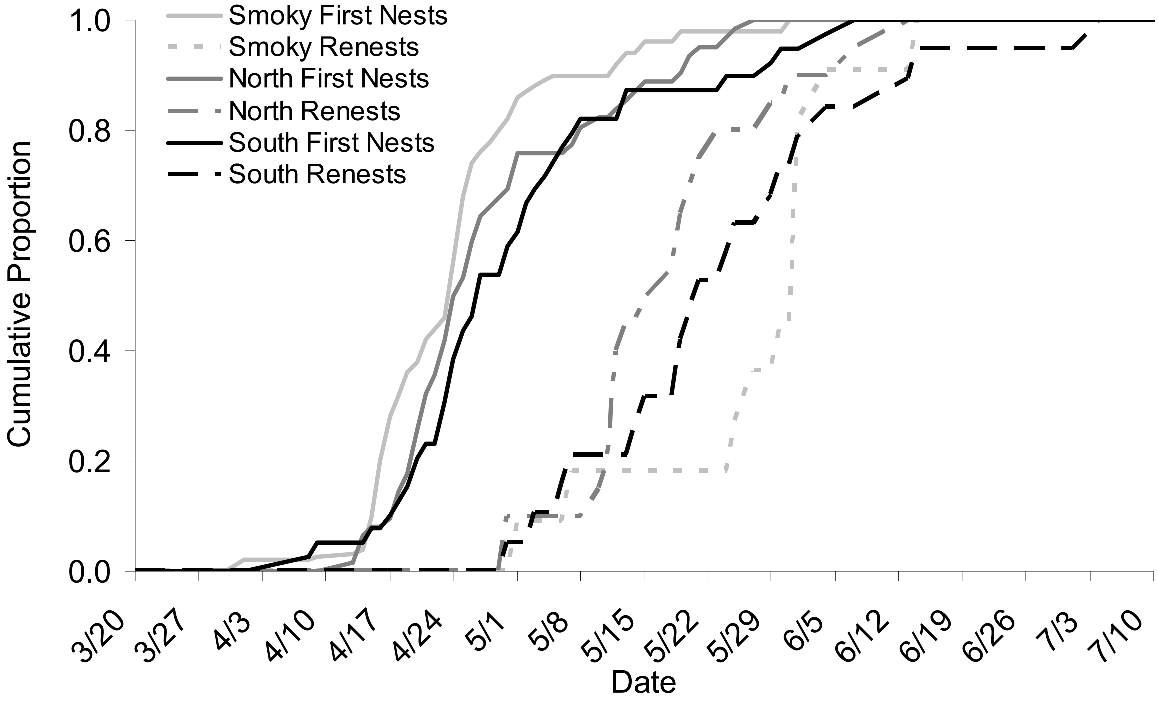

Figure 2.3. Cumulative clutch initiation dates for first nests and renests of female greater prairie-chickens at three study sites in Kansas, 2006-2008.

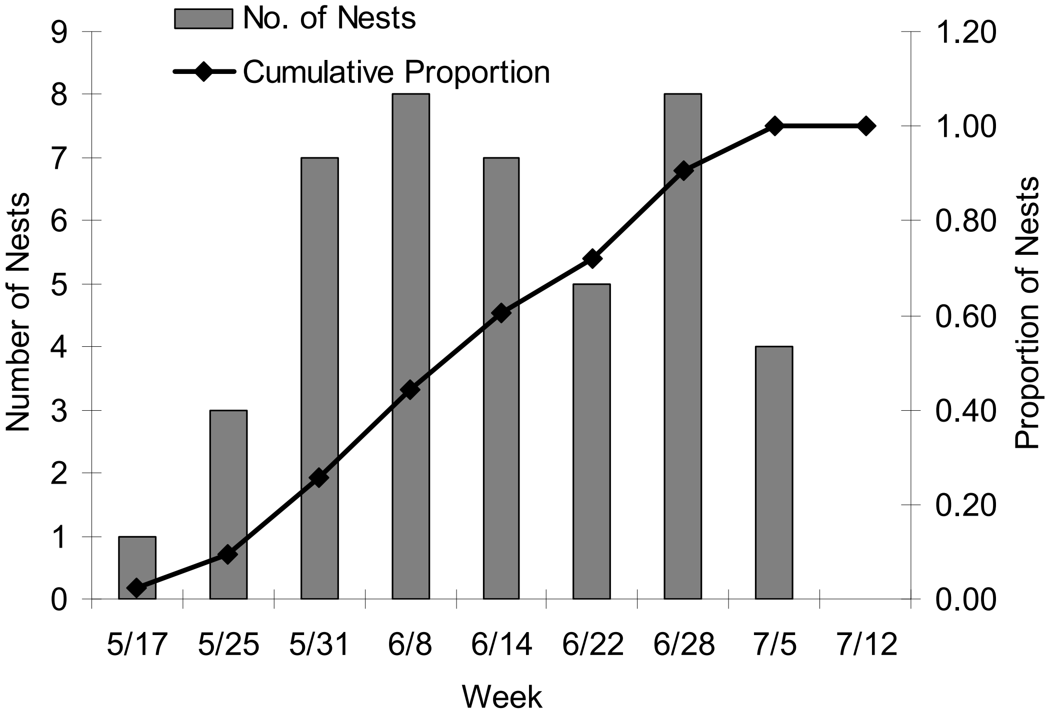

Figure 2.4. Weekly distribution of nest hatches and cumulative weekly hatch for female greater prairie-chickens in Kansas, 2006-2008.

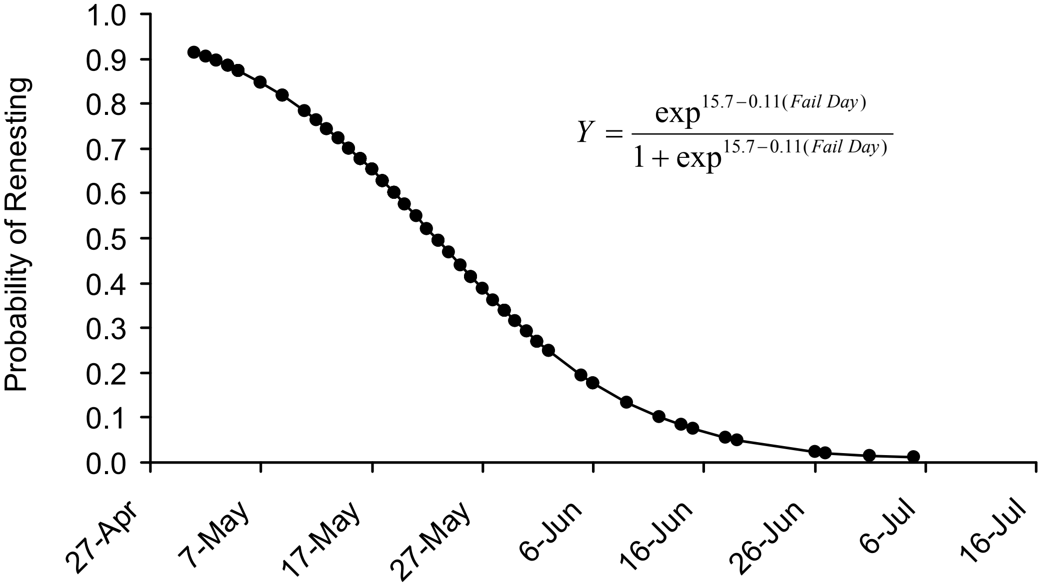

Figure 2.5. Probability of renesting for female greater prairie-chickens as a function of date of failure for the first nesting attempt. Probability of renesting was not influenced by stage of loss, clutch size or study site (see text).

CHAPTER 3 - EFFECTS OF EXPERIMENTAL RANGELAND MANAGEMENT AND LANDCOVER CHANGE ON THE OCCUPANCY OF GREATER PRAIRIE-CHICKENS

Abstract

We used multiseason occupancy models to evaluate the long-term occupancy of greater prairie-chickens at a tallgrass prairie preserve in northeastern Kansas over a 28-year period. Our objectives were to estimate trends in occupancy and detection probabilities, and evaluate whether habitat conditions and grassland management practices influenced the dynamic processes of site colonization and local extinction of greater prairie-chickens over the 28-year survey period. We conducted multiple surveys each spring (Mar-May) of 187 250-m^2 survey sites at Konza Prairie Biological Station. Detection probabilities were less than one and varied among years (range = 0.12–0.82), while occupancy per 250-m^2 site (± se) showed a linear decline from 0.18 ± 0.02 in 1981 to 0.11 ± 0.03 in 2008. The probability of an unoccupied site being colonized was negatively associated with the proportion of site occupied by woodland cover (β = -1.29, 95% CI = -2.13, -0.45) and was greater for ungrazed sites than those that were grazed by bison or cattle (β = -0.61, 95% CI = -1.06, -0.15). Parsimonious models suggested that the probability of local extinction was influenced by the interaction between grazing and average frequency of fire (β = -2.82, 95% CI = -5.27, -0.37). Our results suggest that (1) biologists should account for imperfect detection probabilities when conducting seasonal surveys of prairie-chickens, (2) prairie-chicken occupancy declined 39% over the 28-year period despite being protected from hunting in a natural reserve and provided with a diversity of habitat types, and (3) land managers should strive to eliminate and prevent woody encroachment using combinations of fire-return intervals of 3-4 years and grazing regimes that facilitate a heterogeneous mosaic of prairie-habitats.

Introduction

More than 95% of native tallgrass prairie has been lost to cultivation and urban development since European settlement, and > 80% of the remaining biome is located in the Flint Hills region of eastern Kansas and northeastern Oklahoma (Samson and Knopf 1994). Although the tallgrass prairie of the Flint Hills has not suffered wide-spread losses from cultivation, it has been impacted by intensive grazing regimes, planting of exotic grazing-tolerant grasses, and encroachment by woody plants (Vickery et al. 2000, Robbins et al. 2002, Briggs et al. 2005). More than 98% of grasslands in the Flint Hills is managed for cattle production and much of the region has suffered losses to structural and vegetational heterogeneity due to prescribed burning and grazing regimes designed to increase palatable forage for cattle production (Fuhlendorf and Engle 2001, With et al. 2008). The Flint Hills have also been degraded by deliberate planting of grazing-tolerant exotic grasses like tall fescue (*Festuca arundinaceae*), invasion of exotic plants like sericea lespedeza (*Lespedeza cuneata*), woody encroachment from eastern red cedar (*Juniperus virginiana*) and roughleaf dogwood (*Cornus drummondii*), and exurban development; all of which have resulted in the loss and fragmentation of tallgrass prairie (Briggs et al. 2002*a*, Johnson and Sandercock, in press). Eastern red cedar is of special concern because encroachment can convert tallgrass prairie to closed canopy forest in as little as 40 years without fire or grazing (Briggs et al. 2002*b*). In addition, deciduous trees of gallery forests can encroach into uplands from riparian areas by as much 2% per year if prairies are left unburned (Knight et al. 1994, Briggs et al. 2005).

The greater prairie-chicken (hereafter “prairie-chicken”) is a grassland obligate bird and an indicator species for tallgrass prairie ecosystems. Similar to other grassland birds, declines in the continental distribution and numbers of prairie-chickens have paralleled the extensive loss and fragmentation of prairie habitats (Knopf 1994, Peterjohn and Sauer 1999, Svedarsky et al. 1999). As a result, Partners in Flight have listed greater prairie-chickens as an extremely high priority species and recommended close monitoring of population numbers (Pashley et al. 2000). The Flint Hills has been considered a stronghold for prairie-chickens due to large expanses (> 1.6 million ha) of relatively intact grassland (Svedarsky et al. 1999, Johnsgard 2002). However, annual lek surveys conducted by the Kansas Department of Wildlife and Parks indicate that the Flint Hills population of greater prairie-chickens has declined by 60% over the last 30 years (Applegate and Horak 1999, Rodgers 2009). The demographic mechanisms of population declines of greater prairie-chickens in the Flint Hills remain unknown because long-term field studies of demography over large spatial extents are impractical. In addition, the traditional population monitoring technique of surveying leks is considered suboptimal in assessing population status because it assumes that all birds in the population attend leks as well as perfect detectability (Applegate 2000, Walsh et al. 2004, Clifton and Krementz 2006). Effective conservation requires efficient survey techniques that produce unbiased estimates of population status and assessments of the relationships between environmental conditions and species occurrence or use.

Recent advancements in the analysis of detection-nondetection data provide an alternative method of evaluating the distribution, population trends and ecological correlates of species occurrence. MacKenzie et al. (2003) described an approach for estimating the proportion of sites occupied by a species (i.e., occupancy) over time when the probability of detecting the species is <1. Similar to robust designs in capture-mark-recapture modeling (Pollock 1982), multiseason occupancy approaches assess detection probabilities and occupancy over closed periods among surveys within seasons and open periods between consecutive seasons or years. Multiseason occupancy models allow evaluation of how the occupancy of a species changes over time and how extrinsic factors affect occupancy rates and two components, the dynamic processes of colonization and local extinction (MacKenzie et al. 2003).

We used multiseason occupancy models to evaluate long-term occupancy rates, and the factors influencing changes in colonization and local extinction of areas by prairie-chickens at Konza Prairie Biological Station (hereafter, “Konza”) in northeastern Kansas during a 28-year period from 1981-2008. Konza is a tallgrass prairie preserve managed as a Long Term Ecological Research (LTER) site where experimental watersheds receive combinations of prescribed burning and grazing (Knapp et al. 1998). We expected that population declines at Konza would not be as great as private lands in the Flint Hills because the study area is protected from hunting, has limited public access, and is managed for conservation of natural resources with a diversity of grassland habitat types. A long-term data set of annual prairie-chicken surveys coupled with the experimental management of individual watersheds at Konza provided a unique opportunity to assess the utility of occupancy modeling in describing the trends and mechanisms of prairie-chicken persistence. Our objectives were to (1) estimate the long-term occupancy rates of prairie-chickens at Konza, (2) estimate the detection probabilities of prairie-chickens from roadside surveys, and (3) evaluate the habitat conditions that influence changes in occupancy for prairie-chickens.

Study Areas

Konza Prairie Biological Station is located in the Flint Hills ecoregion of northeast Kansas (39°05'N, 96°35'W; Fig. 3.1). Konza is a 3,487 ha native tallgrass prairie preserve owned by The Nature Conservancy and Kansas State University (KSU) and has been operated as a National Science Foundation long-term ecological research (LTER) station by the Division of Biology at KSU since 1981. The climate of Konza is characterized by warm, wet summers and dry, cold winters. Mean annual precipitation (83.5 cm) is adequate to support both grassland and woodland vegetation (Knapp et al. 1998). As an LTER site, Konza is managed in a replicated experimental design in which ~60 experimental units are subject to different prescribed burning and grazing treatments. Approximately 42% of the site is grazed by either bison (*Bos bison*; 27%) or by domestic cattle (*Bos primigenius*; 15%) with the remaining 58% of the site ungrazed. Stocking of bison and cattle is year- and season-long, respectively, at light-to-moderate rates that have varied over the 28-year study period (Gene Towne, pers. comm.). Prescribed fire-return intervals of watershed treatments vary from 1 to 20 years with some seasonal variations in timing of burns (i.e, spring, fall, winter) within return interval replicates. Overall, Konza is characterized by four structurally different habitat types: burned prairie, unburned prairie, attenuated forest, and gallery forest (Zimmerman 1993, Knapp et al. 1998). Although the majority of Konza (>85%) is composed of native prairie, succession to woody vegetation in watershed replicates with long fire-return intervals has increased overall woodland cover at Konza from 10% in 1983 to 13% in 2009 (T. Prebyl, unpublished data).

Methods

Prairie-Chicken Surveys

Konza was divided into a grid of 560 250 × 250-m cells (Fig. 3.1). Surveys of prairie-chickens were conducted during March – May of 1981-2008 by driving the 22-km circular access road and side roads between unit boundaries 2-4 times per spring, with the directions of surveys altering between clockwise and counterclockwise on successive visits to control for diurnal changes in lek activity after sunrise (Fig. 3.1). Surveys were not conducted in 1990. Only grid cells adjacent to the access road were surveyed (n = 186 sites). Surveys began at sunrise, lasted approximately two hours and were conducted under rainless and low wind (< 25 km/h) conditions to maximize detection of birds from calls and behavioral displays. Maintaining speeds of <20 km/h, surveyors counted birds and recorded all sites where prairie-chickens were observed. Counts of birds included leks and foraging birds encountered off leks.

Habitat Covariates

Land cover data were necessary to evaluate the impacts of land cover change on the colonization and local extinction probabilities of prairie-chickens over the 28-year study period. We used cloud-free Landsat 5 TM imagery (Path 28 / Row 33; 30×30 m pixels) from the USGS Global Visualization Viewer website in five year intervals from 1983 to 2009. We acquired three satellite images within the same growing season (March – August) for each year. However, due to a lack of cloud-free imagery in 1983 and 1984, one of the three Landsat images during this period was taken from the non-growing season (January). Landsat images were clipped to the extent of the Konza boundary and visually inspected to confirm that the images were spatially registered to each other. Next, we combined four Landsat bands 3 (blue), 4 (green), 5 (visible red), and 7 (near infrared) from each of the three time periods per year into a single 12-band image using ENVI 4.5 (ITT Visual Information Solutions, Boulder, CO, USA). The four spectral bands were selected because previous research showed them to be the most effective for identifying habitats in Kansas with multi-temporal landcover classification schemes (Price et al. 1997). To maintain consistency in classification, we created training sites that were suitable for all of the years of Landsat imagery and validated using aerial photographs of the area. We used a supervised maximum-likelihood classifier to assign each 30×30-m pixel (0.09 ha) in the 12-band Landsat composites to one of four land cover classes; grassland, woodland, cultivated agriculture, and water. It was not possible to discriminate between shrubland and forest cover types. To assess the accuracy of grassland and woodland classes, we compared the assigned land cover classes of 70 random points within the study boundary to aerial photographs. Our land cover classification technique correctly classified woodland and grassland pixels 70% and 98% of the time, respectively. Of pixels that were misclassified, 76% occurred in areas that contained both grass and woodland in the same 30×30-m pixel.

Land cover data were uploaded to ArcInfo 9.3 (Environmental Systems Research Institute, Redlands, CA). A vector of 560 250×250-m grids (6.25 ha) corresponding to prairie-chicken survey sites was overlaid on each land cover dataset. Prairie-chickens occupied uncultivated upland sites and survey sites were composed of only grassland and woodland habitats. Therefore, the proportion of a site occupied by grassland was inversely related to its woodland cover, and woodland cover was the only land cover metric considered in our occupancy analyses. We used the zonal statistics tool to summarize the number of pixels of woodland for each survey site (ca. 1,440 pixels per survey site). The proportion of woodland for each survey site was estimated directly from our land cover data at 5-year intervals in which land cover data were created (1983, 1988, 1993, 1998, 2003, and 2009). We interpolated the values of woodland cover for intervening years, resulting in estimated woodland cover for every survey site in every year from 1983–2008. Experimental fire-return intervals were set at 1, 2, 4, 10, or 20 years on burned watershed treatments, but actual fire return intervals were sometimes different for several reasons. A few sites occurred in areas not treated with fire in the entire 30-year history of Konza, unplanned wildfires occasionally burned study sites off schedule, and not all sites entered the experiment in 1981–1983. Therefore, we used actual fire-return intervals (i.e., years since last fire) and grazing regime of each site from historical records available at the Konza LTER website (http://www.konza.ksu.edu/). In preliminary analyses, we found that bison and cattle grazing had similar effects on prairie-chicken occupancy, therefore the two grazing treatments were pooled and a single dummy variable was used to indicate whether a site was grazed or ungrazed.

Data Analysis

We conducted two analyses to evaluate 1) long-term and yearly occupancy and detection probabilities of prairie-chickens at Konza, and 2) factors influencing the site colonization and local extinction of prairie-chickens. From each survey of a 250-m^2 site, counts of prairie-chickens were transformed into detection – nondetection data where birds were detected (1) or not detected (0). Detections included birds at lek sites and small flocks of foraging birds. For each survey occasion, prairie-chickens were either detected, $\psi \times p$, where ψ is the proportion of sites occupied and p is the probability of detection, conditional upon occupancy. Non-detection could occur when prairie-chickens were not present $(1 - \psi)$ or present but undetected $[\psi \times (1-p)]$. Failure to detect birds could be the result of disturbance by predators at lek sites or local movements of foraging birds.

Detection and annual occupancy.— All modeling was performed using Program Presence (version 3.0; Patuxent Wildlife Research Center, United States Geological Survey, Laurel, MD) to build and evaluate models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) in an information-theoretic framework (Burnham and Anderson 1998). We used an alternative parameterization of the unconditional multiseason approach developed by MacKenzie et al. (2003) to model seasonal occupancy (ψ) and local extinction (ε) corrected for the probability of detection (p) of prairie-chickens at Konza over the 28-year survey period from 1981–2008. Our primary objective was to determine how occupancy and local extinction probabilities changed over time. Therefore, we limited our analysis to include only sites where a prairie-chicken was detected at least once during any survey in the entire 28-year study (n = 112 sites). Conditioning on detection likely inflates overall estimates of annual occupancy at Konza, but better depicts trends in occupancy over time by discarding sites not used by prairie-chickens. We developed a suite of *a priori* models representing yearly and survey-specific effects as well as linear and non-linear time trends. For example, ψ_{linear}, $\varepsilon_{\text{year}}$, $p_{\text{season, survey}}$, represents a model where occupancy (ψ) varied linearly over the 28-year study, local extinction (ε) varied among years (but not in a trend), and detection probability (p) varied among sampling occasions for the entire study. We also included the survey-specific count data as a covariate to evaluate the effect of site abundance on detection probabilities and occupancy. We considered models with ΔAIC_c values ≤ 2 to have strong support. We were unable to assess goodness of fit because no formal test exists for multiseason models (MacKenzie et al. 2003). Occupancy, local extinction, and detection probabilities were estimated directly using the most parsimonious model and maximum likelihood integration (MacKenzie et al. 2006). In addition, we derived the finite rate of change in occupancy (λ_t) per year as

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}.$$

Analogous to the finite rate of population change, $\lambda_t < 1$ indicates declining occupancy, whereas $\lambda_t \geq 1$ indicates stable or increasing occupancy.

Correlates of colonization and local extinction.— We developed a second suite of multiseason occupancy models to evaluate the influences of habitat factors on the underlying dynamic processes of prairie-chicken occupancy at Konza. We used the original model parameterization described by MacKenzie et al. (2003) where ψ was held constant at the initial occupancy level in 1983 and the dynamic processes of occupancy, colonization (γ) and local extinction (ε) were then modeled and estimated. We fit a suite of candidate models in which γ and ε were modeled as a function of four site-specific habitat factors: fire-return intervals, average fire frequency, grazing treatment, proportion of the site occupied by woodland cover, and interactions among these factors. Fire-return intervals were the number of years since a site was burned at the time of each survey, whereas average fire frequency was the average rate of burning over the entire 28-year study period (e.g., fire frequency of 0.5 was burned every 2 years on average). Fire-return intervals evaluated short-term management actions, whereas average fire frequency described the long-term management for a site. Woodland proportion was arcsin-square-root transformed and then z-transformed. We also evaluated the second order polynomials of covariates to assess non-linear responses of γ and ε. Landcover data derived from Landsat 5 imagery were available only for the 1983–2008 period, and for analyses of covariates we discarded prairie-chicken survey data from 1981 and 1982. Maximum likelihood estimates of occupancy, detection probability, and local extinction were calculated using the most parsimonious model or model averaging when appropriate. We used the delta method to derive standard errors and confidence intervals for probabilities (MacKenzie et al. 2006:74).

Results

During March–May, 1981–2008, 2-4 surveys were conducted per year at each of the 187 survey sites. The peak count was 142 birds in 9 groups of $\geq$ 5 birds in 1981, and the lowest was 18 birds with no groups of $\geq$5 birds in 2008. The mean number of prairie-chickens observed decreased by 3.8% per year from 1.5 ± 0.4 birds per site in 1981 to 0.09 ± 0.03 birds per 250-m^2 site in 2008 (Fig. 3.2). Conversely, the mean proportion of woodland cover at survey sites increased from 0.05 ± 0.01 in 1983 to 0.08 ± 0.01 in 2008. Woodland cover increased at 42% of sites, decreased at 20% of sites, and did not change at 38% of the sites over the 28-year study period. During the study period, 79 (42%) sites were grazed by bison or cattle, and 108 (58%) were ungrazed.

Detection and Annual Occupancy

We found strong evidence that detection probabilities were year-specific (AIC_c weights for models with $p_{\text{year}} > 0.99$), ranging from $p = 0.12 \pm 0.05$ to 0.82 ± 0.07, but did not vary in an annual trend (Table 3.1). Two models were equally parsimonious ($\Delta AIC_c < 2$) and occupancy varied in linear annual trend in both (Table 3.1). Occupancy probabilities had a negative linear trend (*β* = -2.82, 95% CI = -4.98, -0.66; Table 3.2) with the probability ($\pm$ SE) of a 250×250-m (6.25-ha) site being occupied decreasing by 38% over a 28-year period from $\psi = 0.18 \pm 0.02$ in 1981 to 0.11 ± 0.03 in 2008 (Fig. 3.3). A model that allowed the local extinction probability to vary in positive linear manner was considered parsimonious and had 29% of the relative support of the data. We found no evidence that detection probabilities or occupancy were influenced by the prairie-chicken count values (AIC_c weights were < 0.01 for ψ_{count}, p_{count} models; Table 3.1). The annual probability of local extinction per site increased from $\varepsilon = 0.52$ per 250-m^2 site in 1981 to 0.68 in 2008 (Fig. 3.4). However the slope coefficient did not significantly differ from 0 (*β* = 2.7, 95% CI = -1.61 – 7.01). Derived estimates of site colonization showed a decreasing linear trend from $\gamma = 0.11 \pm 0.03$ in 1981 to 0.09 ± 0.03 in 2008. The average rate of change in occupancy derived from the top model was $\lambda = 0.97$ (95% CI = 0.96 – 0.99); indicating significantly decreasing occupancy at 3% per year over the 28-year period.

Ecological Correlates of Colonization and Local Extinction

Similar to the annual occupancy analysis, we found strong evidence that detection probabilities should be modeled as year-specific when evaluating colonization and local extinction (AIC_c weights for p_{season} models > 99%). We expected the proportion of a survey site occupied by woodland cover to be related to the fire-return interval. However, fire-return intervals explained only half of the variation in the proportion of forest cover across sites ($r^2 = 0.50$, df = 1, n = 150, $P < 0.001$). The 30-m spatial resolution of our landcover data prevented us from correctly classifying patches of woody vegetation < 0.045 ha in size (< half the pixel size). Woody plots < 0.045 ha were likely shrub patches associated with longer fire-return intervals (Briggs et al. 2002*a*). Therefore, the experimental treatments may account for additional variation in site occupancy and local extinction and we included both landcover data and fire-return interval in our analysis.

Three models were equally parsimonious ($\Delta AIC_c \leq 2$) and had 59% of the relative support of the data. All models indicated that probability of a site being colonized was influenced by the proportion of the site in woodland cover and the grazing treatment (Table 3.2). Site colonization (γ) was negatively associated with woodland cover (*β* = -1.29, 95% CI = -2.13, -0.45) and grazing (*β* = -0.61, 95% CI = -1.06, -0.15), and ungrazed sites were 1.8 times (95% CI

= 1.2 – 2.8) as likely to be colonized as grazed sites (Fig. 3.5). There was some uncertainty for local extinction models (Table 3.2). The top model included an interaction between grazing and the average frequency of fire; suggesting the effect of fire frequency on local extinction depends on whether the site was grazed (Table 3.3). Grazed sites were less likely to be abandoned as the frequency of fire increased (β = -2.26); whereas ungrazed sites were more likely to be abandoned at frequently burned sites (β = 0.56; Fig. 3.6). Models that included grazing treatment had >80% of the relative support; suggesting that grazed sites were more likely to be abandoned (β = 1.76, 95% CI = 0.49, 3.03). However, a model where extinction probability was constant over the study period was parsimonious (Table 3.2). We found no evidence that colonization or local extinction were explained by the actual fire-return interval of sites (i.e., years since last fire) or varied non-linearly in regard to woodland cover or fire (AIC_c weights were < 0.01 for γ_{season}, ε_{season} and $\gamma_{covariate}{}^2$, $\varepsilon_{covariate}{}^2$ models; Table 3.2).

Discussion

Our study is the first analysis to incorporate estimates of detectability to examine the long-term occupancy of greater prairie-chickens, and to evaluate the influence of environmental variables on dynamics of site occupancy by prairie-chickens. We found that detection probabilities were <1 and varied substantially among study seasons; suggesting that analyses of prairie-chicken population dynamics based on lek counts must account for varying rates of detection. Because Konza Prairie Biological Station is a tallgrass prairie preserve, we expected the prairie-chicken population to be stable compared to declines on private lands in the Flint Hills. Nevertheless, prairie-chicken occupancy at Konza declined 39% from 1981 to 2008. In addition, the ecological processes driving occupancy, colonization and local extinction, were influenced by fire and grazing regimes, and the relative amount of woodland cover in the survey area.

Detection and Annual Occupancy

The probability of detecting prairie grouse can be influenced by factors within and among seasons such as sex and age of birds, time of day and time of season, as well as variability in habitat conditions among survey sites (Walsh et al. 2004, Clifton and Krementz 2006). We used protocols similar to previous studies and conducted prairie-chicken surveys within three hours of sunrise on fair-weather days during the spring lekking season when detection should be high.

However, detection probabilities were always p <0.82 per 250 m^2 site and were highly variable among years. In addition, the probability of detecting a prairie-chicken was not influenced by the number of birds counted at a site; suggesting that the detection of prairie-chickens was not influenced by abundance. Variable detection probabilities unrelated to abundance may be typical for prairie-chickens, which are cryptic when loafing or roosting but highly visible during breeding displays and flight (Hamerstrom et al. 1957). Naïve estimates of occupancy, in which detection probabilities were assumed to be perfect, were less than modeled estimates but also indicated population declines similar to the trend estimated by our top model. However, naïve estimates were much more variable (ranging from 0.04 – 0.24) than were estimates adjusted for imperfect detectability (Fig. 3.2) and sometimes indicated increasing occupancy during shorter time series (e.g., from 1990 – 2000). Anderson (2001) argued that controlling for detection probabilities is necessary if point counts or transect surveys are to be related to population trends, and we recommend that researchers and managers conducting roadside surveys for prairie-chickens incorporate detection probabilities into estimates of occupancy and population surveys.

Our results generally agree with previous reports of declining numbers of prairie-chickens at Konza during the 1990's (Zimmerman 1993, Kauffman et al. 1998). Zimmerman (1993) reported more than 200 males attending 13 active leks at Konza in 1981. Only 12 birds and 0 leks were observed during surveys in 2008. Our data indicate that the annual rate of decline in prairie-chicken occupancy was 3% per year over the 28-year survey period and was similar to the observed annual decline in the annual count data at Konza (3.5%; Fig. 3.2). In contrast, the annual decline in prairie-chicken densities estimated from annual lek surveys for the entire Flint Hills region in the same 28-year period was lower at ~2% (Rodgers 2008). Two factors may be contributing to greater rates of decline in occupancy at Konza compared to regional trends in lek counts for the Flint Hills region. First, it is possible that the assumption of perfect detectability in traditional lek surveys may have underestimated the rate of population decline in the Flint Hills region. The utility of lek counts to monitor the status and trend in prairie grouse populations has been questioned due to the variability in daily and seasonal attendance and observer bias (Applegate 2000, Walsh et al. 2004). Second, if trends in lek counts are a good index of prairie-chicken decline in the region, greater rates of decline might be explained by the effects of experimental treatments on habitat suitability for prairie-chickens at Konza. Manipulations of fire and grazing have provided important insights into the ecosystem function of tallgrass prairie (Knapp et al. 1998). However, we found experimental fire-return treatments up to 20 years have resulted in a greater increase in woody cover on Konza (~60%) compared to that of the surrounding area (~40%; T. Prebyl, unpublished data), and encroachment of woodland cover significantly decreased the probability of establishment by prairie-chickens. Protocols of the LTER program allowing for fire-return intervals to exceed 10 years on more than a third of Konza may have led to more rapid population declines than in the surrounding Flint Hills, despite the status of Konza as a protected natural reserve.

Colonization and Local Extinction

Lek attendance by prairie-chickens is a tradeoff between the benefits of mating opportunity and the potential cost of an increased risk of predation (Gibson et al. 2002, Boyko et al. 2004). Therefore, prairie-chickens should initiate leks in areas that minimize predation risk. Our results agree with previous studies that have found prairie grouse avoid forested landscapes when settling to form new lek sites (Merrill et al. 1999, Niemuth 2003, Gregory et al. 2010). Trees and other tall structures may be avoided if they serve as hunting perches for avian predators (Gratson 1988). Encroachment of forests into prairie habitats increases travel and hunting opportunities for mammalian predators by increasing the amount of habitat edge (Kuehl and Clark 2002). Survival of prairie-chickens in fragmented grasslands is lower than that in contiguous grasslands (McNew et al. 2010), and prairie-chickens may minimize their risk of predation by selecting areas unfragmented by woody encroachment. Site colonization was also influenced by grazing regime with prairie-chickens nearly twice as likely to colonize ungrazed sites as grazed sites. Ungrazed areas provide taller grasses and more forbs during the late spring and early summer (Fuhlendorf et al. 2001, Robbins et al. 2002) and higher colonization of ungrazed areas may be associated with greater recruitment in areas with better cover for nesting, brood-rearing, and loafing. For example, McNew et al. (2010) found variation in prairie-chicken productivity was related to variation in nest and brood cover caused by differences in burning and grazing regimes among study sites at large spatial scales.

A different set of ecological factors influenced local extinctions of 250-m^2 survey sites. Prairie-chickens may abandon grassland sites with extensive woody encroachment due to increased risk of predation. However, abandonment of sites likely occurred more quickly than our method of determining changes in woodland cover allowed us to assess. Abandonment of sites by prairie-chickens was influenced by changes in habitat conditions occurring over shorter time frames related to fire and grazing regimes. We found a significant interaction between the average fire frequency and grazing treatment; indicating that the influence of fire frequency was conditional upon whether the site was grazed (Fig. 3.6). Frequent burning reduced the probability that a site would be abandoned if it was grazed, but not if it was ungrazed, and grazed sites that were burned often had lower probabilities of local extinction than ungrazed sites regardless of their fire frequency.

Due to the selective nature of grazers, fire and grazing have significant interactive effects on the plant communities and vegetative structure of grasslands (Shaw and Carter 1990, Vinton et al. 1993). Burning typically reduces plant species diversity on ungrazed prairie while moderate grazing increases diversity on burned prairies (Coppedge et al. 1998, Collins 1987, Vinton et al. 1993). Fire-return intervals of 3–4 years result in diverse grassland plant communities and structural heterogeneity, whereas intervals >4 years favor woody encroachment (Briggs et al. 2005, Fuhlendorf et al. 2006). Greater prairie-chickens require a diversity of grassland habitats for different portions of their life-cycle. Open areas with little residual vegetation are preferred for lekking arenas (Hamerstrom et al. 1957, Patten et al. 2007) whereas areas with ample vertical and horizontal cover are selected for nesting and brood-rearing (Patten et al. 2007, L.B. McNew, unpublished data). Nest and brood survival is often significantly reduced in areas where residual cover has been reduced by annual spring burning and intensive early cattle grazing (McKee et al. 1998, McNew et al. 2010). Because female prairie-chickens generally initiate nests within 3 km of leks, the proximity and configuration of a variety of habitat types is likely vital to the long-term viability of populations (Schroeder and Robb 1993, Patten et al. 2007). We predicted but did not find evidence of a non-linear response of local extinction to fire in which prairie-chickens are less likely to abandon sites that are burned every 3–4 years than those that are burned more or less frequently. Finally, the average fire frequency per site over the 28-year study period had a significant effect on extinction, whereas the actual fire-return interval, or years since a site was last burned, did not. Overall, our results suggest that the long-term fire management of a site is more important to prairie-chicken persistence than short-term or singular management actions; especially in grazed areas.

Our results from occupancy modeling suggest that the long-term decline of prairie-chickens at Konza may have been caused by poor recruitment, low adult survival, or a combination of these factors. Over the 28-year study period, the probability of site abandonment was 5.9 times higher than colonization. Moreover, colonization declined while abandonment of sites increased over the study period. Prairie-chickens have high fidelity to lek sites (Nooker 2007), and increased abandonment coupled with decreasing colonization suggests that recruitment of prairie-chickens did not offset annual mortality of established birds. Research results from occupancy modeling are consistent with population studies based on radio-marked birds that show that population growth in Kansas is limited by depressed nest and brood survival due to high rates of predation (Nooker 2007, McNew et al. 2010). Although Konza is a protected prairie preserve at the core of its range, the prairie-chicken population is as demographically limited, if not more so, as the surrounding unprotected population. Experimental grassland management at the site, which has allowed for increased grassland fragmentation by woody vegetation, may be exacerbating the regional decline of prairie-chickens by facilitating numerical or functional increases of nest and brood predators (McKee et al. 1998, Ryan et al. 1998, Kuehl and Clarke 2002).

Management Implications

Multiseason occupancy models require a minimum of data (detection – nondetection) that are easily collected and are robust to variable sampling effort, which make their application easily incorporated into most wildlife monitoring programs. Assumptions of multiseason occupancy models are easily satisfied and include (1) the population of interest must be closed to additions or losses within each season, (2) detection of prairie-chickens at each site is independent, (3) a site is never classified as occupied when it is not, and (4) there is no unmodeled heterogeneity in occupancy or underlying dynamic processes. The first assumption can be satisfied by allowing only a short interval between surveys within a season during the spring when prairie-chicken movements are limited (Robel et al. 1970). Assumptions 2 and 3 are likely satisfied for prairie-chicken surveys because no other bird in the area has the same behavior or calls, which minimizes classification errors. Detection at one site could be biased if flushed birds move among survey units, and precautions should be taken to avoid double counting. Assumption 4 can be tested by assessing the influence of covariates on the probabilities of interest, and such modeling is often the primary interest in occupancy studies. Incorporation of occupancy modeling into monitoring protocols requires little alteration of current upland bird surveys, and previously-collected data can be incorporated by simplifying point or transect counts to detection/nondetection data. Similar to robust mark-recapture studies, occupancy models require ≥ 2 surveys of the same area or transect. However, this requirement can be relaxed in some cases (MacKenzie et al. 2006). Moreover, habitat covariates (e.g., habitat conditions, weather, observer) should be incorporated to document seasonal occupancy and rates of decline and to identify the likely mechanisms of observed declines, resulting in more justifiable management recommendations. At the scale of our survey grids (250 m^2; 6.25 ha), the probability that prairie-chickens colonized a site was significantly reduced in areas with >20% woodland cover; regardless of fire-return interval. Therefore, increasing the burn frequency in areas where forest has exceeded this threshold may do little to increase the colonization and occupancy of prairie-chickens, and we recommend average fire-return intervals of ≤ 4 years to minimize woody encroachment.

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Table 3.1. Model selection results for occupancy (ψ), local extinction (ε), and detection probability (*p*) of greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1981-2008.

ψ	ε	*p*	K	AIC_c	ΔAIC_c	w_i
linear	constant	year	30	3000.2	0.00	0.567
linear	linear	year	31	3001.5	1.34	0.290
quadratic	constant	year	30	3004.3	4.14	0.071
constant	constant	year	29	3004.4	4.16	0.000
constant	constant	constant	3	3016.4	16.2	0.000
linear	constant	year, survey	83	3170.5	170	0.000
year	year	year	80	3171.3	171	0.000
count	constant	year	31	4188.3	1188	0.000
linear	constant	count	5	4450.3	1450	0.000

Table 3.2. Model selection results for colonization (γ) and local extinction (ε) of greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1983-2008. Occupancy (ψ) was held constant at 1983 levels and detection probability (*p*) was allowed to vary among seasons.

Colonization	Local Extinction	K	AIC_c	ΔAIC_c	w_i
%woodland + graze	graze × fire freq	33	2623.2	0.00	0.258
%woodland + graze	graze	31	2624.0	0.81	0.172
%woodland + graze	constant	30	2624.1	1.00	0.158
%woodland + graze + fire freq	graze × fire freq	34	2625.4	2.26	0.083
%woodland + graze	graze + fire freq	32	2626.2	3.07	0.056
%woodland + graze	%woodland + graze	32	2626.2	3.08	0.055
%woodland + graze × fire-return	graze × fire-return	34	2626.7	3.53	0.054
%woodland + graze	graze × fire freq^2	33	2628.4	5.22	0.047
%woodland + fire + graze	%woodland + fire + graze	34	2626.5	4.01	0.044
%woodland^2 + graze	graze + fire return^2	34	2628.5	5.38	0.020
graze	graze	30	2633.1	9.98	0.002
%woodland^2 + fire-return^2 + graze	%woodland^2 + fire-return^2 + graze	38	2637.2	14.00	0.001
%woodland × fire-return × graze	%woodland × fire-return × graze	42	2636.1	13.54	0.000
constant	constant	28	2645.5	22.80	0.000

Table 3.3. Parameter estimates, standard errors, and 95% confidence intervals for the top models for occupancy, colonization, and local extinction for greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1981-2008.

Variable	Estimate	SE	95% CI
Occupancy			
Intercept	-1.41	0.17	-1.74, -1.08
Linear Time	-2.82	1.06	-4.98, -0.66
Colonization			
Intercept	-3.30	0.15	-3.60, -3.02
%woodland	-1.29	0.43	-2.13, -0.45
Grazing	-0.61	0.23	-1.06, -0.15
Local Extinction			
Intercept	-0.95	0.33	-1.60, -0.30
Fire frequency	0.56	0.60	-0.62, 1.74
Grazing	1.76	0.65	0.49, 3.03
Fire frequency × Grazing	-2.82	1.25	-5.27, -0.37

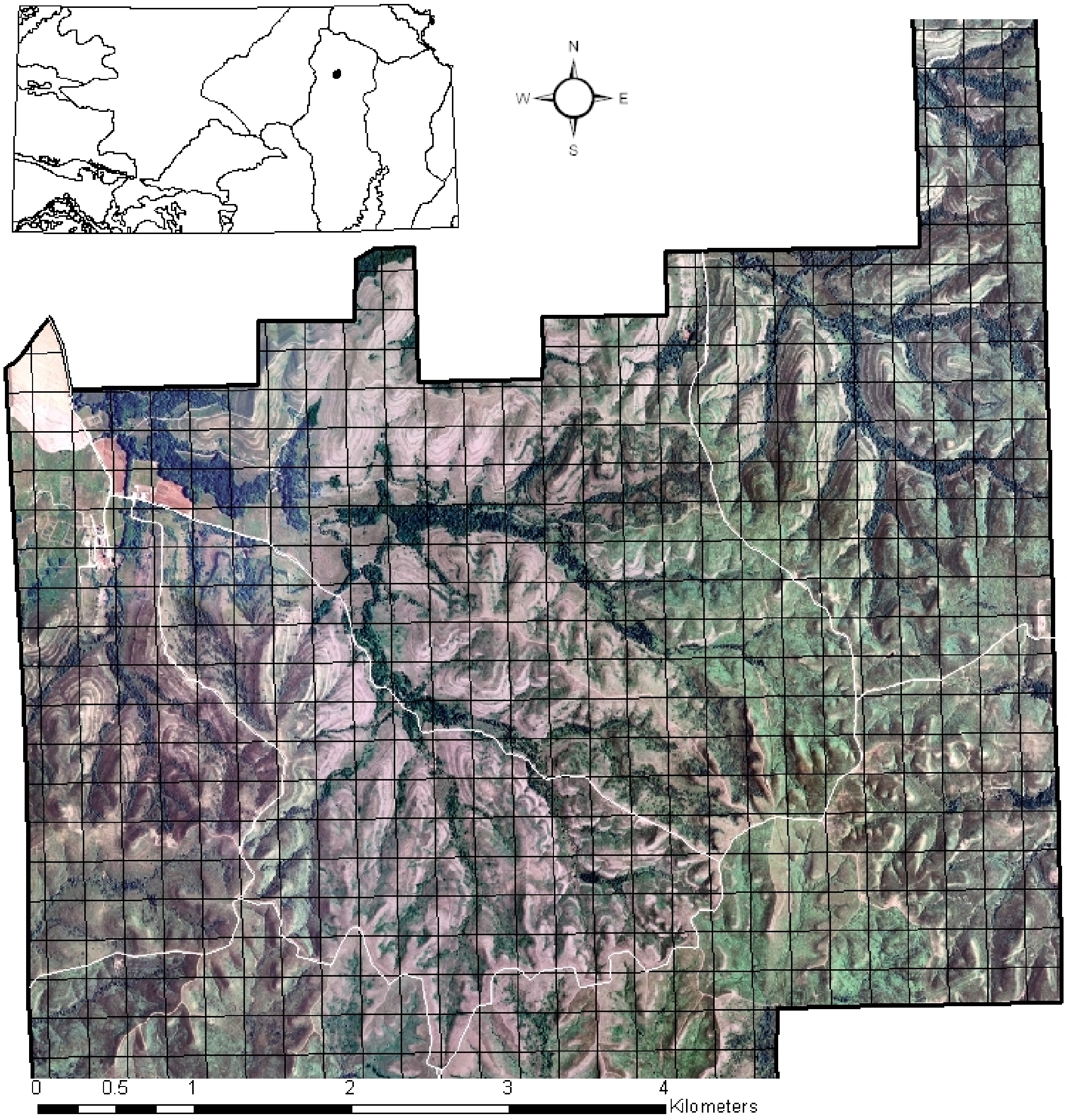

Figure 3.1. Study of greater prairie-chicken occupancy occurred at Konza Prairie Biological Station (black spot on inset) in the north-central Flint Hills region of Kansas, USA, 1981-2008.

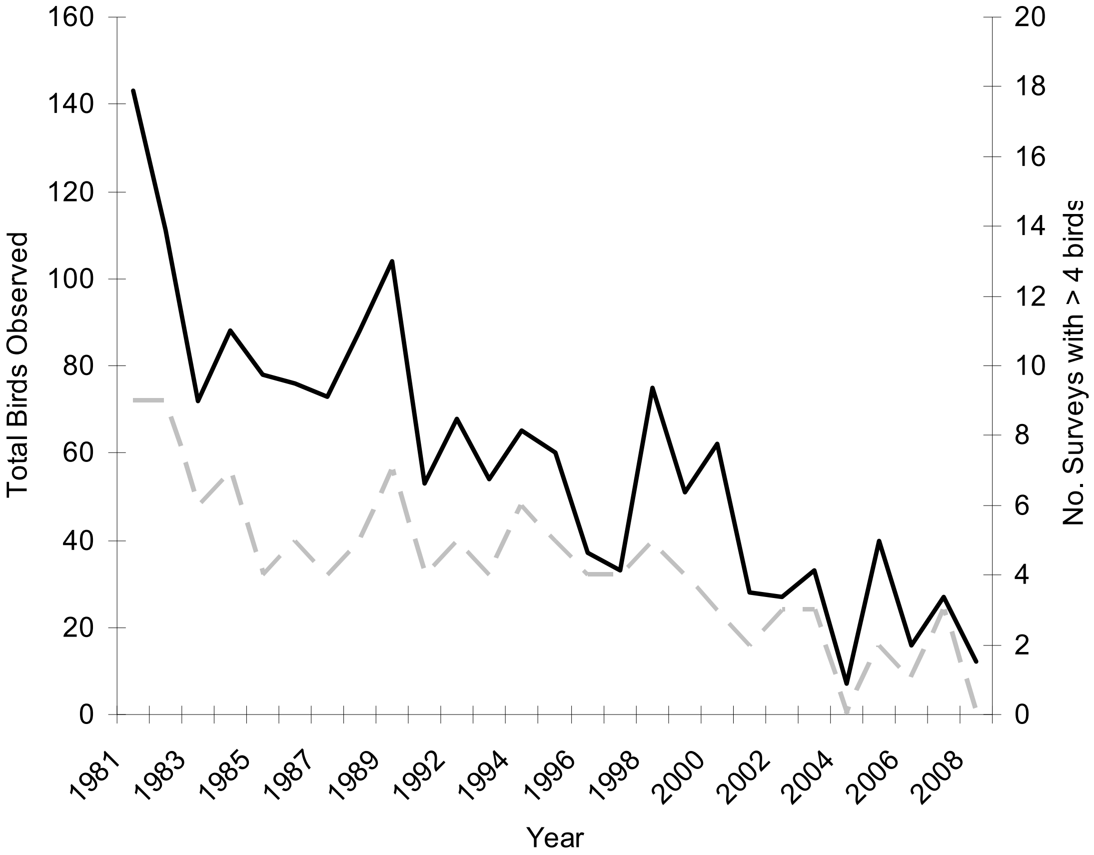

Figure 3.2. Maximum number of greater prairie-chickens observed (solid line) and the number of surveys in which ≥5 birds were observed together (dashed line) per survey year at Konza Prairie Biological Station, Kansas, 1981–2008.

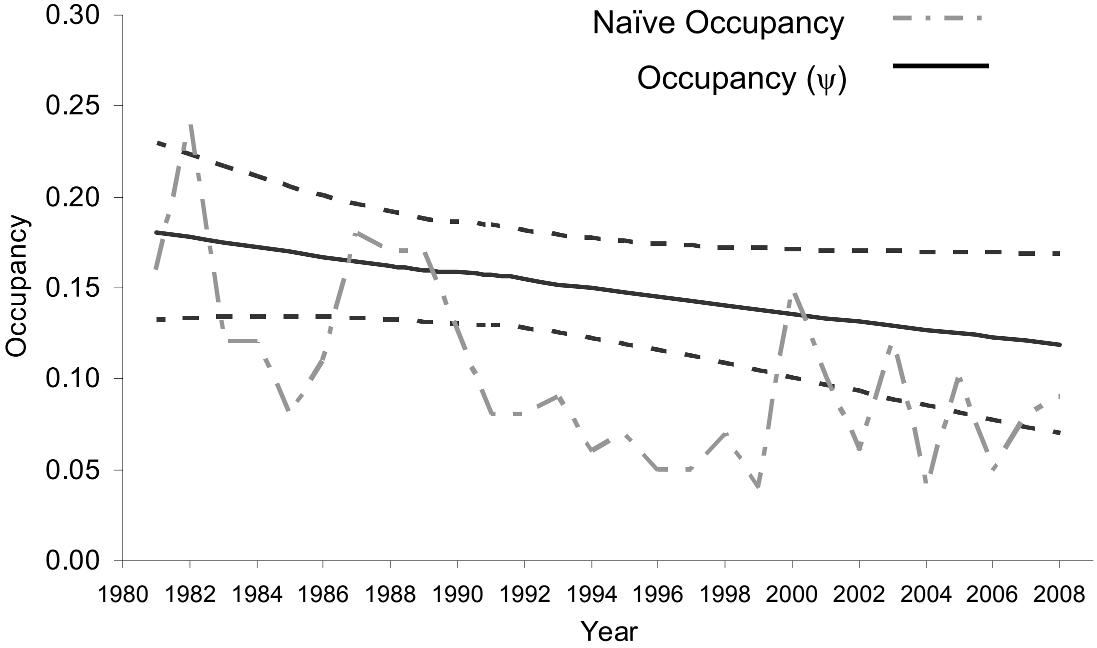

Figure 3.3. Year-specific proportions of sites with greater prairie-chickens present (naïve occupancy) and occupancy (± 95% CI) estimated from the parsimonious model (ψ_{linear}, $\varepsilon_{\text{linear}}$, p_{season}) for prairie-chickens at Konza Prairie Biological Station, Kansas, 1981-2008.

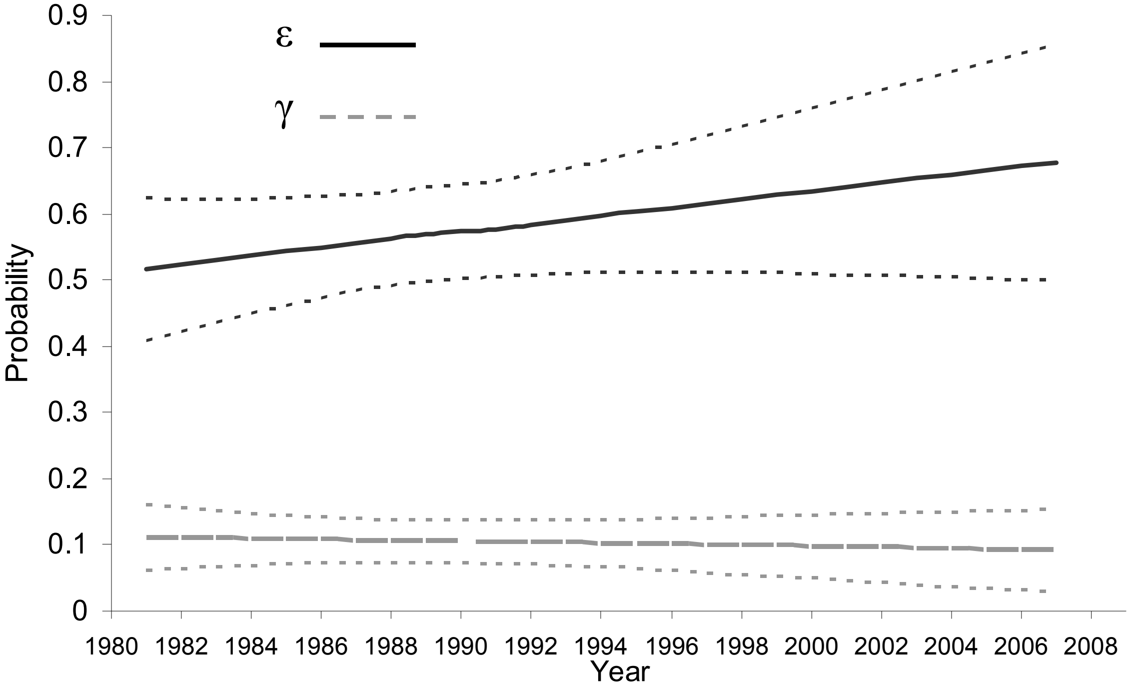

Figure 3.4. Estimated probabilities of local extinction (ε ± 95% CI) and derived colonization (γ + 95% CI) of greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1981-2008. Maximum likelihood estimates calculated using the parsimonious model, ψ_{linear}, $\varepsilon_{\text{linear}}$, p_{season}.

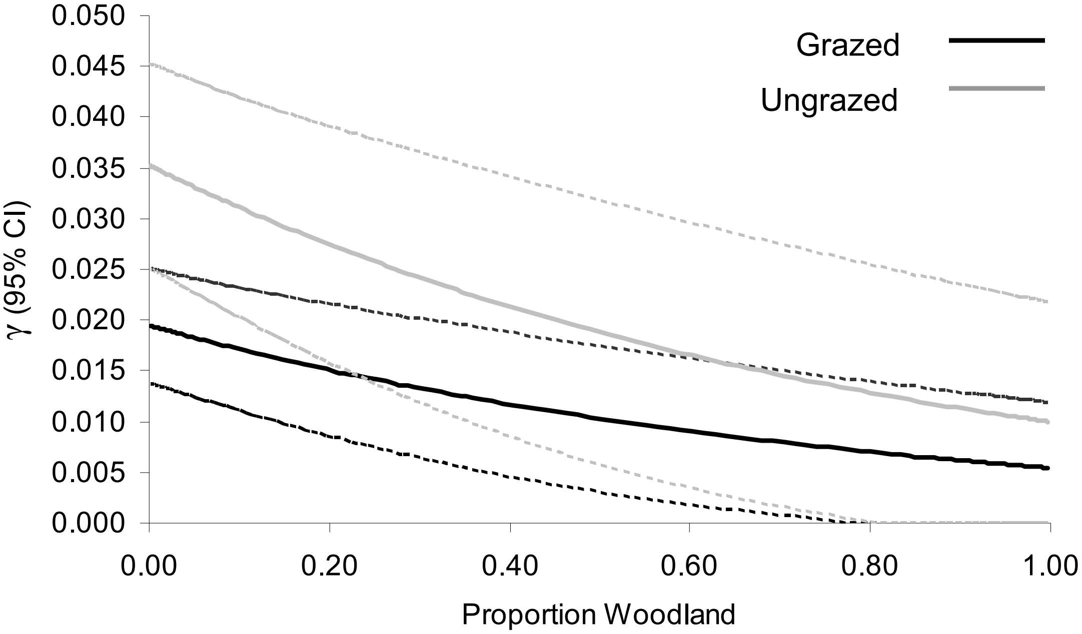

Figure 3.5. Relationship between the probability of colonization (γ) and the proportion of a site classified as woodland for grazed and ungrazed sites at Konza Prairie Biological Station, Kansas, 1983–2008.

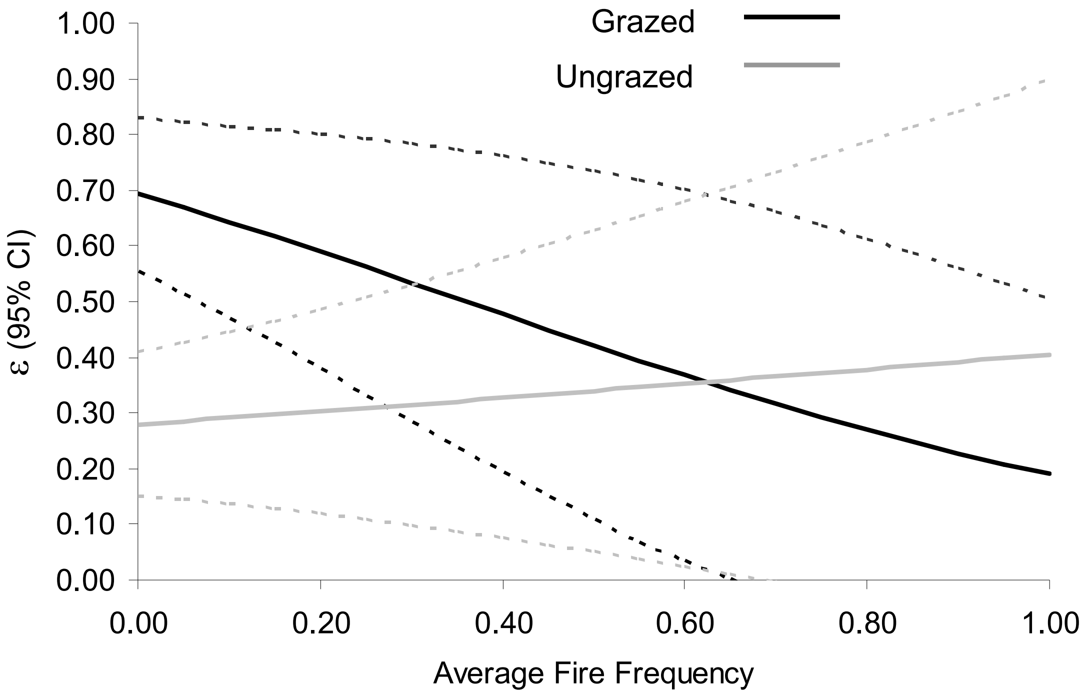

Figure 3.6. Relationship between the probability of local extinction (ε) and average frequency of fires for grazed and ungrazed sites at Konza Prairie Biological Station, Kansas, 1983–2008.

CHAPTER 4 - EVIDENCE OF HUMAN-MEDIATED SELECTION FOR VARIATION IN LIFE-HISTORY TRAITS IN GREATER PRAIRIE-CHICKENS

Abstract

Predation, food, climate and other environmental factors have a significant influence on selection processes and evolution of vertebrate life history traits. Growing evidence indicates that human activities can also affect evolutionary processes by a range of mechanisms, including impacts on life history traits mediated by the effects of habitat management on survival of nests and adults. We tested for anthropogenic effects on the life-history evolution of greater prairie-chickens (*Tympanuchus cupido*) breeding at three sites across a gradient of landscape alteration in eastern Kansas, USA. Female prairie-chickens breeding in an area heavily fragmented by rowcrop agriculture and roads had low annual survival probabilities (0.32 ± 0.001 SE), and higher survival of nests (0.16 ± 0.04) and broods (0.48 ± 0.12) than the other two study areas. In contrast, two populations breeding in areas with large tracts of contiguous heavily-grazed tallgrass prairie had higher annual survival (0.47 ± 0.002 and 0.68 ± 0.01), and lower survival of nests (0.07 ± 0.02 and 0.12 + 0.03) and broods (0.29 ± 0.09 and 0.38 ± 0.09, respectively). Consistent with life-history theory predictions, the population in the fragmented area with higher adult mortality also had greater reproductive effort, and egg and clutch volumes were 5% and 9% larger than at the other study areas. Reproductive effort was not influenced by other explanatory variables, including residual female body mass. Overall, variation in the life history traits of prairie-chickens was most consistent with site differences in predation rates and mortality of adult females. Impacts of predation on breeding females were apparently mediated by the anthropogenic effects of road development and conversion of grasslands to cropland. Our results indicate that land use and land cover change can influence selection on life-history traits for a short-lived species at small spatial and short temporal scales, even after adjusting for potential phenotypic plasticity.

Introduction

Life-history theory predicts that the diversity of life-history strategies in vertebrates can be explained by tradeoffs among demographic traits that maximize lifetime reproductive success and fitness. Species with low adult survival should invest heavily in components of reproduction whereas longer-lived organisms should invest less in current reproduction, at least early in their lives, to maximize benefits from residual reproductive value in future breeding attempts (Roff 1992, Martin 2002). Interspecific comparisons of variation in avian life history traits have provided evidence for tradeoffs between annual survival and the components of reproductive effort, including the probabilities of breeding and renesting, clutch size, and egg mass (Martin 1995, Ricklefs 2000, Sæther and Bakke 2000, Martin et al. 2006). Studies seeking ecological correlates of patterns of avian life history variation have usually focused on four major factors: predation, food limitation, climatic conditions, and duration of the breeding season (Badyaev 1997, Conway and Martin 2000, Sandercock et al. 2005). Of these four factors, predation may be most important for explaining life history variation within and among different species of birds because most demographic losses are caused by predator activity (Ricklefs 1969, Martin 1995, Ricklefs 2008).

High rates of nest predation are predicted to favor reductions in reproductive effort (Martin 2004). In songbirds, high levels of nest predation are associated with reductions in egg size, clutch mass, and nest attentiveness, and increases in nestling growth rates (Conway and Martin 2000, Fontaine and Martin 2006, Remeš and Martin 2002, Martin et al. 2006). Reductions in reproductive effort may be mediated by tradeoffs among the different components of fecundity if finite resources must be partitioned between the number and size of offspring (Smith and Fretwell 1974, Winkler and Wallin 1987). Juvenile survival may place thresholds on the minimum size of offspring, and large eggs tend to produce large chicks that have higher survival rates in birds with precocial young (Myrberget 1977, Moss et al. 1981). Intraspecific tradeoffs between clutch and egg size are rarely observed in birds, in part because egg size is highly heritable (Christians 2002). Nevertheless, egg mass decreased with increased clutch size in an interspecific comparison of songbird demography (Martin et al. 2006), and egg mass increased in response to removals of nest predators (Fontaine and Martin 2006).

In contrast to the effects of nest predation, low rates of adult mortality are predicted to favor reduced reproductive effort (Martin 2004). In songbirds, species with low adult mortality exhibit reduced rates of nest attendance, and lower attentiveness is associated with longer incubation periods (Martin 2002). Tradeoffs between survival and reproductive effort have been documented for precocial species as well, with females suffering lower annual survival laying larger clutches (Patten et al. 2007) or exhibiting a higher propensity to renest (Martin et al. in press). The effects of predators on juvenile survival may also play a critical role in shaping avian life histories, with low rates of juvenile mortality favoring increased reproductive effort (Russell 2000, Martin 2002). Life history studies that address juvenile survival are fairly limited, primarily because of logistical difficulties in tracking and monitoring mobile young during natal dispersal (Hannon and Martin 2006).

Differences in resource acquisition among females can confound the detection of life history trade-offs if life-history traits are phenotypically plastic (van Noordwijk and de Jong 1986). For example, tradeoffs between realized fecundity and annual survival can be produced by resource limitations (Ricklefs 2000). For example, clutch size, nesting propensity, and the interval between nesting attempts were associated with the spring body condition of female Mallards (*Anas platyrhynchos*; Devries et al. 2008), and plasma protein and female age were significant predictors of renesting probability in greater sage-grouse (*Centrocercus urophasianus*; Gregg et al. 2006). In addition, egg size has been found to vary among species in relation to residual body mass, an index of condition (Rahn et al. 1985, Sæther 1987). Indeed, the positive relationships between food resources and clutch and egg size have been invoked often to explain observations that do not support the clutch size:egg mass trade-off (Lack 1968, Sæther 1987, Martin et al. in press).

Comparative studies of grouse (Tetraoninae) have played an important role in the development and testing of life-history theory. Interspecific studies have demonstrated that grouse exhibit the same fast-slow continuum in life-history strategies that is found in other groups of vertebrates, including tradeoffs between clutch size and adult survival (Zammuto 1986, Arnold 1988, Jönsson et al. 1991). Demographic studies of ptarmigan (*Lagopus* spp.) have shown that alpine populations at southern latitudes have lower fecundity and higher adult survival than arctic populations at northern latitudes, and that predation is important as an environmental factor (Sandercock et al. 2005, Novoa et al. 2008). To date, most studies of life-history variation in birds have focused on the impacts of environmental factors under relatively undisturbed or natural conditions (Bears et al. 2009, Martin et al. 2009, Martin et al. in press).

However, mounting evidence now indicates that human activities can affect evolutionary processes through a variety of mechanisms, including habitat modification, selective harvest, captive breeding, and translocations (Carroll et al. 2007, Smith and Bernatchez 2008). Anthropogenic effects on land use and habitat fragmentation may have led to the observed changes in the demographic traits of lesser prairie-chickens (*Tympanuchus pallidicinctus*, Patten et al. 2005). Historic differences in land tenure created major differences in the extent of fencing, power lines and roads in rural areas of Oklahoma and New Mexico. Collisions with fences are a major cause of mortality of female prairie-chickens in Oklahoma (Wolfe et al. 2007), and higher adult mortality due to collisions was correlated with larger clutch sizes and higher renesting rates in Oklahoma as compared to New Mexico (Patten et al. 2005). However, the indirect impacts of nest failure and adult mortality due to human-caused habitat alteration on the selection for demographic traits have not been assessed.

In this study, we compare the demographic traits of three independent populations of greater prairie-chickens across a gradient of human landscape alteration. The landscapes of Kansas provide a unique opportunity to evaluate whether alteration of habitats impact the selection life-history traits of greater prairie-chickens (*T. cupido*) because land use and range management practices vary significantly within the state. In the Flint Hills, large contiguous tracts of grassland are intensively managed for cattle production, whereas in the Smoky Hills smaller tracts of less heavily grazed grassland are fragmented by row crop agriculture (McNew et al. 2010). Habitat conditions impact the seasonal availability of lekking, nesting, and brood-rearing habitat (Patten et al. 2007), the phenology of breeding events (McNew et al. 2010), and variation in reproductive success and survival (McKee et al. 1998, Matthews et al. 2010). If anthropogenic changes lead to rapid selection for avian life history traits, we expected that greater prairie-chickens might be good candidates to investigate these effects because this species has large clutch sizes, low adult survival, and presumably shorter generation times than tundra or forest grouse (Patten 2009). We also expected that changes in vital rates might be mediated by nest predation because greater prairie-chickens experience considerable variation in nest survival among different populations (0–72%), and nest predation is the primary cause of reproductive losses (Schroeder and Robb 1993, Peterson and Silvy 1996). If large variations in habitat conditions influence demographic rates, we expected greater reproductive effort in populations experiencing higher reproductive success or lower adult survival. Finally, our analyses were strengthened by use of standardized field protocols to investigate a suite of demographic traits among multiple populations of a single species. Our approach controls for differences in methodology and phylogenetic relationships that can be an issue for interspecific comparisons of life-history traits (Martin 1995, Sandercock et al. 2005, Martin et al. 2006).

Study Species and Study Sites

Greater prairie-chickens (hereafter ‘prairie-chickens’) are endemic to the native grasslands of the central United States. Prior to European settlement, prairie-chickens were distributed across all areas occupied by tallgrass prairie in North America (Schroeder and Robb 1993). Large-scale conversions of native prairies to rowcrop agriculture during the last century are thought to be the major cause of declines in both the distribution and number of prairie-chickens that have led to population bottlenecks (Johnson and Dunn 2008, Westemeier et al. 1998). The core of the extant range of prairie-chickens occurs in Kansas and adjacent states (Schroeder and Robb 1993). In Kansas, prairie-chickens primarily occur in areas that are dominated by native grasslands, such as the Flint Hills ecoregion. Nevertheless, prairie-chickens can tolerate moderate amounts of cultivated agriculture (<40% of total area), and populations of prairie-chickens are also found in more developed regions of Kansas. Elsewhere, cultivation, grazing, and other types of human land use have reduced the population viability of prairie-chickens, but the potential role of land use and land cover change as drivers of natural selection have not been investigated (Svedarsky et al. 2003).

Our study occurred at three discrete study sites; two sites located in the southern and northern Flint Hills (South and North, respectively) and one site in the Smoky Hills (Smoky; Fig. 4.1). The three study areas were $\geq$ 112 km apart and differed in landscape composition and pattern, as well as rangeland management practices (Table 2.1). The South site (635 km^2) had landcover of 90% grassland and 3% cropland, a mean grassland patch size of 185 ha, and a road density of 0.32 km of roads per km^2. The majority of the site was managed with range management practice of intensive early stocking and burned annually each spring (IESB, 1 head/0.8 ha for 90 days; Smith and Owensby 1978, With et al. 2008). The North site (533 km^2) had landcover of 81% grassland and 10% cropland, a mean grassland patch size of 51 ha, and a road density of 0.57 km per km^2. Annual spring burning was common and lands were managed with a mixture of IESB and season-long stock grazing and annual burning (SLSB; 1 head/1.6 ha for 180 days). The Smoky site (1,295 km^2) was more fragmented with landcover of 53% grassland and 38% cropland, a mean grassland patch size of 15 ha, and a higher road density of 1.4 km per km^2. Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at study area 3 were burned infrequently at fire return intervals >1 year, grazed at low intensity (1 head / >2 ha for 90 days), and cattle stocking occurred later in the season than at the other two study sites. Indices of prairie-chicken densities for years of study, calculated as: mean number of prairie-chickens per lek × number of leks per study area size, were 0.10, 0.19, and 0.17 birds/km^2 for the South, North, and Smoky sites, respectively.

Methods

Field Methods

Prairie-chickens were captured at lek sites during the spring with walk-in traps and drop-nets (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage characteristics (Henderson et al. 1967). We determined age-class as yearling or adult from the shape, coloration and wear of the outermost two primaries (numbers 9 and 10; Schroeder and Robb 1993). Morphometrics of adults, including total mass and length of the tarsus-metatarsus, were measured at the time of capture. All birds were individually marked with color leg bands and females were fitted with 11-g necklace-style VHF radio transmitters, equipped with mortality switches and an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). Radio-marked females were monitored $\geq$3 times per week from vehicles during the nesting and brood-rearing period (Apr–Aug) and $\geq$1 time per week during the rest of the year (Sep–Mar). Once a female localized in an area for three successive days, we used a portable radio receiver and handheld Yagi antenna to locate the nest. We flushed the female once in early incubation to count the eggs, to determine the stage of incubation, and to record the nest location. Females with nests were monitored daily at a distance $\geq$ 100 m by triangulation of the radio signal. Once it was determined that the female was no longer tending the nest, we classified nest fate as successful ($\geq$ 1 chick produced) or failed.

Body Mass of Females

Reproductive effort of female prairie-chickens at the different study sites could be influenced by site differences in food resources if females with heavier body mass were in better nutritional condition and laid larger eggs. Alternatively, site differences in body mass could be a result of seasonal differences in ovarian development among females at capture. We evaluated the first possibility by regressing female mass at capture on length of the tarsus–metatarsus as an index of body size. Residual body mass of females was used as an index of spring body condition before egg-laying. Assessment of ovarian development was difficult because we were unable to determine if females were gravid at capture. We used the interval between the day of capture and the day of nest initiation as a covariate (McNew et al. 2010, Chapter 2). Mass of female grouse increases before the onset of egg-laying (Hannon and Roland 1984), and we expected that females with shorter intervals between capture and nest initiation were more likely to be gravid. We used analysis of covariance to test whether regional differences in female mass at capture were influenced by the length of time between capture and nest initiation. We tested factorial models with main effects and interaction terms, and all parametric statistics were calculated using procedures of Program SAS (ver. 9.1, SAS Institute, Cary, NC).

Clutch Size and Egg Volume

Clutch size was calculated as the maximum number of eggs recorded per clutch once egg-laying was completed and a female had started incubation. We floated all eggs from clutches determined to be in incubation to assess stage of development from egg buoyancy adjusting for cases where egg laying rates exceeded one egg per day (McNew et al. 2009, McNew et al. 2010). We measured egg volume only once during incubation to minimize the impacts of nest visits. Egg length (L) and breadth (B) was measured to the nearest 0.1 mm using calipers, and linear measurements were converted to an estimated egg volume (V) with the following equation (Narushin 2005):

$$V = (0.6057 - 0.0018B)LB^2$$

Mean clutch size and egg volumes were compared among study areas using analysis of variance. We also compared egg volume and clutch size relative to residual body mass of females. Analysis of covariance was used to test whether site differences in clutch size and egg volume could be explained by potential variation in the nutritional condition or the age of females.

Nest and Brood Survival

Nest survival was the probability of a nest producing $\geq$1 hatched chick, whereas brood survival was defined as the probability that $\geq$ 1 chick survives to fledging at 14 days after hatching. We calculated daily rates of nest and brood survival for each study area with the nest survival model of Program Mark (ver. 4.3, White and Burnham 1999, Dinsmore et al. 2002). Multiple model selection and inference was used to evaluate the importance of three factors on daily nest survival (Burnham and Anderson 1998). The three factors included in the global model for nest survival included: nesting attempt (first or renest), female age, and study site. We estimated a corrected probability of nest survival by raising the daily nest survival probabilities to a power equal to the duration of the nest exposure period (37-d; Dinsmore et al. 2002, Sandercock et al. 2005). This method assumes that daily nest survival is similar across the nest exposure period within a study site. Duration of the nesting cycle was calculated assuming an egg-laying rate of one egg per day and an average incubation period of 25 d (Nooker 2007, Chapter 2). To estimate brood survival prior to fledging, we conducted early-morning flush counts of females attending broods at 14-d post hatch. (Hubbard et al. 1999, Fields et al. 2006). If no chicks were counted, we used subsequent flush counts at 10-d intervals to confirm presence or absence of chicks. We updated 14-d flush counts for 5% of cases from zero to the maximum number of observed chicks at later flush counts. The probability of brood survival to fledging was calculated as the product of the estimates of daily brood survival from top model for a 14-d period from hatching until fledging. Variances of derived parameters were calculated using the delta method (Powell 2007).

Survival of Females

We estimated monthly survival of female prairie-chickens during a 2-year period between March 2007 and February 2009 with the nest survival procedure of Program Mark. The nest survival model is a general procedure for known-fate data and is useful for estimating survival from ‘ragged’ telemetry data from radio-marked birds (Hartke et al. 2006, Mong and Sandercock 2007). Multiple model selection and inference was used to evaluate the importance several factors on monthly adult survival (Burnham and Anderson 1998), including female age, study area, residual body mass adjusted for tarsus-metatarsus length, and linear and quadratic time trends. We used the most parsimonious model to derive monthly survival probabilities, and then extrapolated annual survival rates at each study area as the product of monthly survival rates during the entire study period. Variances of derived parameters were calculated using the delta method (Powell 2007).

Results

Body Mass of Females

A total of 203 individual female prairie-chickens were captured before egg-laying at our three study areas in Kansas. Reproductive data were available for 159 females. We excluded females for which the capture to clutch initiation interval was less than zero (N = 8). Analysis of covariance showed there was no interaction between the effects of study site and the interval between capture and egg-laying ($F_{2,124} = 0.93$, $P = 0.40$). Body mass of female prairie-chickens differed significantly among the three study sites ($F_{2,124} = 7.7$, $P < 0.001$), and females were heaviest at the Smoky site (929 ± 8.8 g), intermediate at the North site (908 ± 8.7 g), and lightest at the South site (879 ± 7.9 g, Table 4.1). The interval between capture and egg-laying was unrelated to female mass ($F_{1,124} = 1.7$, $P = 0.20$). Mass did not differ between age classes ($F_{1,124} = 0.39$, $P = 0.54$) and the interaction between female age and study site was not significant ($F_{1,124} = 0.88$, $P = 0.42$). In addition, the interval between female capture and clutch initiation did not differ among age classes ($F_{1,136} = 1.6$, $P = 0.21$). We found no significant relationship between female mass and tarsus-metatarsus length ($r^2 < 0.01$, df = 1, $P = 0.64$).

Clutch Size and Egg Volume

Analysis of covariance showed there was no interaction between the effects of study area or nesting attempt on clutch size ($F_{2,151} = 0.13$, $P = 0.88$). First nests were consistently larger than renests ($F_{1,151} = 39.1$, $P < 0.001$), and the number of eggs per clutch averaged 12.5 to 13.1 eggs for first nesting attempts and 10.2 to 10.9 eggs for renests (Table 4.1). First nests at the Smoky site tended to be larger by about 0.5 eggs per clutch, but overall, clutch size did not differ significantly among study areas ($F_{1,151} = 0.44$, $P = 0.65$). Clutch size did not differ between female age classes (mean ± SE = 12.7 ± 0.25 for both groups; $F_{1,141} = 0.98$, $P = 0.32$) and there was no interaction between age class and study site ($F_{2,141} = 0.28$, $P = 0.75$). Analysis of covariance showed that there was no interaction between the effects of residual female mass and study area on egg volume ($F_{2,143} = 1.07$, $P = 0.35$). Egg volume differed among the three study areas ($F_{2,142} = 3.2$, $P = 0.04$), with the largest eggs laid at the Smoky site (24.7 ± 0.2 ml) and the smallest eggs at the South site (23.7 ± 0.2 ml, Table 1). Egg volume did not differ between female age classes ($F_{1,140} = 2.8$, $P = 0.09$) and there was no interaction between age class and study site ($F_{2,140} = 2.5$, $P = 0.08$). Egg volume was not related to clutch size ($r^2 = 0.01$, $P = 0.20$).

Nest Survival and Brood Survival

During the breeding seasons of 2006–2008, 231 nests of 155 female prairie-chickens were located and monitored, of which 44 were successful, for an apparent nest success rate of 19%. Daily nest survival was modeled for a 37-day exposure period during a 103-day nesting season from 23 April to 19 July. The most parsimonious model ($\Delta AIC_c = 0$) included a group effect for study area. Models where nest survival varied among study areas were 9.9 times more likely than models where nest survival was constant ($w_i/w_j = 0.79/0.08$). Variation in survival among study areas accounted for 79% of the relative support of the data. Nest survival was lower at the South site (0.07 ± 0.02) compared to the North (0.12 ± 0.03) and Smoky sites (0.16 ± 0.04, Table 4.1). Overall nest survival for all sites and nesting attempts combined was 0.12 ± 0.04 SE. Evidence at failed nests indicated that predation was the primary cause of nest mortality, accounting for 94% of all losses.

Forty-three broods were monitored from hatch until fledging at 14-d of age. Daily brood survival during this period was modeled for a 69-day brood-rearing period from 17 May to 24 July. A model that contained an effect of study area was considered parsimonious ($\Delta AIC_c = 0.37$). Models where brood survival varied among study areas had 44% of the relative support. Site differences in brood survival were similar to patterns of nest survival: survival of broods was highest at the Smoky site (0.45 ± 0.11), intermediate at the North site (0.32 ± 0.12), and lowest at the South site (0.24 ± 0.10, Table 4.1). Overall, the model-averaged estimate of brood survival until fledging across all study areas was 0.35 ± 0.07.

Female Annual Survival

Monthly survival probabilities were estimated for 203 females. Model selection based on AIC_c indicated that variation in survival among study sites was strongly supported by the data, accounting for more than 99% of the relative support. Estimates of annual survival extrapolated from monthly rates were greater at the South site (0.68 ± 0.01) than at the North (0.47 ± 0.002) and Smoky sites (0.32 ± 0.001; Table 4.1). Overall annual survival of females during the 12-month period from March to February for all sites pooled was 0.48 (± 0.001).

Discussion

Female greater prairie-chickens breeding at three sites across a gradient of human landscape alteration and use in the Flint Hills and Smoky Hills of Kansas exhibited variation in a suite of eight life-history traits. Females breeding at a study site consisting of large, contiguous blocks of heavily-grazed native prairie (South) had the lightest body mass, laid the smallest eggs, and had the lowest clutch volume. Nest and brood survival were low but annual survival was high for prairie-chickens breeding in large tracts of heavily-grazed and intensively burned prairie. In contrast, females breeding at a highly fragmented, moderately-grazed and infrequently burned site (Smoky) had the heaviest body mass, laid the largest eggs, and had the greatest clutch volume. The Smoky site had the highest rates of nest and brood survival, although our estimates were depressed compared to values compiled for other populations (Peterson and Silvy 1996). In fact, our estimates of annual survival for females at the fragmented Smoky site are among the lowest values ever reported for a field study of prairie-chickens. The study site in the northern Flint Hills (North) had intermediate amounts of habitat fragmentation and grazing intensity, and the vital rates of female prairie-chickens were intermediate as well. We evaluate the potential roles of phenotypic plasticity and evolutionary processes as potential explanations for the results of our demographic analyses.

Tradeoffs between realized fecundity and annual survival are often interpreted as resulting from evolutionary processes, but tradeoffs can also be produced by phenotypic plasticity and resource limitations (Ricklefs 2000). For example, site differences in female mass in our study could have been an artifact of differences in date of capture and the degree of gravidity among females before egg-laying. Timing of lek attendance did not differ among the three study areas but clutch initiation was delayed at the South site, and females at Smoky could have been closer to egg-laying at capture (Chapter 2). Alternately, variation in female mass could have been the result of site differences in female age structure provided there are differences in mass between yearling and adult females. We reject differences in seasonal phenology as an explanation for variation in female mass at capture, because body mass was not related to the interval between capture and date of nest initiation, and reproductive effort still differed among areas after adjustment for the covariate. Likewise, we reject the latter explanation because the age structure of captured females was similar among sites (~50% yearlings, 50% adults) and female mass did not differ between the age classes.

Phenotypic plasticity (i.e., the ability of females to alter their reproductive effort based on body condition) could also be relevant if site differences in body mass, clutch size and egg volume were due to regional differences in food availability that impacted the nutritional body condition of egg-laying females. Females had the highest body mass, and laid the largest clutches and eggs at the Smoky site; a site fragmented by agricultural development. Cultivated agricultural fields comprised a higher proportion of the landscape at the Smoky site and prairie-chickens will utilize grain sorghum and other crops during winter and early spring (Robel et al. 1970). Two lines of evidence suggest that body condition cannot explain regional variation in reproductive effort of prairie-chickens in Kansas. First, residual female mass did not explain variation in egg volume among our three study areas. Food supplementation usually has little impact on egg size of birds, but can have larger effects on timing of laying and clutch size (Christians 2002). Estimates of heritability for egg size are often high in birds, suggesting that egg size may be under selective pressures unrelated to the nutritional status of laying females. Second, egg volume of prairie-chickens was not related to clutch size. Life-history theory predicts a negative relationship between egg size and clutch size if female resources must be partitioned (Roff 1992), but a positive association would be expected if both traits are impacted by nutritional condition, which we did not observe.

Lower reproductive effort among prairie-chickens breeding in heavily-grazed contiguous grasslands and higher reproductive effort among prairie-chickens in moderately-grazed and fragmented grasslands was consistent with life-history theory, which predicts that high nest predation and high adult survival should select for reductions in reproductive effort (Roff 1992). Mortality of female prairie-chickens was almost entirely the result of predation (90%; L. B. McNew, unpubl. data). Thus, the most important environmental factor leading to divergence in the life-history traits of prairie-chickens appears to be the impacts of predators on the survival of adults and nests. We lacked estimates of predator abundance for our three study areas but fragmentation by agricultural development and road density were ranked Smoky > North > South. Known predators of prairie-chickens, such as coyotes (*Canis latrans*), use edge habitats and roads for travel and foraging (Kuehl and Clark 2002, Tigas et al. 2002). Higher quality nesting and brood-rearing habitat as a result of greater residual cover due to infrequent burning and lower cattle grazing intensity (Table 2.1) could explain greater reproductive success at the Smoky site. Thus, anthropogenic changes in land use and habitat fragmentation may have led to differential rates of exposure to predators. Limited data from prior to large-scale implementation of IESB suggest that nest success of prairie-chickens in the Flint Hills were similar (35%) to our estimates from the Smoky Hills (Robel 1970). Therefore, it appears that the direct effects of human activities on grassland ecosystems and the indirect impacts of habitat modification upon predator-prey interactions have influenced the selection of life-history traits of greater prairie-chickens in Kansas over a relatively short time period. Notwithstanding, our results should be viewed in the context of a relatively short-term field study.

There is mounting evidence that human activities have led to ecologically significant evolutionary change in a variety of taxa, and at range of temporal and spatial scales, contributing to growing interest in the study of contemporary evolution (Carroll et al. 2007, Smith and Bernatchez 2008). Relatively few studies have evaluated the impacts of habitat loss and degradation on the life-history evolution of terrestrial vertebrates. Cutting of grasslands for hay production destroys nests of grassland songbirds, including Savannah Sparrows (*Passerculus sandwichensis*) breeding in dairy pastures in Vermont. Perlut et al. (2008) showed that timing of hay cutting altered mating strategies and the occurrence of extra-pair copulations, as well as the strength of selection on morphological traits. Fencing of pastures for livestock is a landscape modification that poses a risk of collision mortality for female lesser prairie-chickens (Wolfe et al. 2007), and Patten et al. (2005) presented evidence that female prairie-chickens subject to higher fence collision mortality laid larger clutches and had a greater probability of renesting than birds at less heavily fenced sites. Our study extends these previous results by showing that landscape modification by humans may lead to differential rates of predation that affect the life-history traits of greater prairie-chickens. Mammalian predators play an important role in structuring terrestrial ecosystems (Pace et al. 1999), but previous studies investigating trophic dynamics have primarily focused on the ecological consequences of the removal of top predators and mesopredator release (Elmhagen and Rushton 2007, Berger et al. 2008). Changes in predator abundance and diversity can also drive evolutionary change in the life-history strategies in lower trophic levels. For example, predators can determine the life-history evolution of guppies (*Poecilia reticulata*) in captivity and natural environments (Reznick et al. 2008).

Selective removal of top predators is one way that humans influence life-history evolution, but our results suggest that indirect effects of landscape modification on predation risk can also be important.

Our analysis is one of the first studies to assess the influence of human landscape alteration on the life-history evolution of grouse, and our work could be extended in two ways. First, we observed the impacts of predation on the demographic parameters of prairie-chickens but were unable to determine whether variation in predation rates were due to a numerical or a functional response. We lacked estimates of predator abundance, and the identity of major predators was surmised by inspecting the remains of depredated nests and carcasses. Our analyses would be informed by a better understanding of predator abundance and activity in relation to land use and land cover changes. Second, our analyses were based on retrospective comparisons of demographic data for prairie-chickens at three study sites over a short time, and life-history traits could have covaried with an environmental factor that we failed to consider (Ricklefs 2000). Experimental protocols are a stronger approach to testing for local adaptation but would require raising birds in a common environment or reciprocal transplants among different populations (James 1983, Rhymer 1992, Bears et al. 2008). Experimental tests will be logistically difficult for prairie-chickens because of their large home range requirements, vagility and conservation status. Wildlife management activities are rarely considered from an evolutionary perspective but could have potential for analyses of contemporary life-history evolution in prairie-chickens. For example, comparisons of performance between wild prairie-chickens and pen-reared Attwater's prairie-chickens (*T.c. attwateri*) might yield insights into the selection conditions of captive-rearing environments (Peterson and Silvy 1996, Hess et al. 2005). Finally, ongoing translocations of prairie-chickens from Kansas to relict populations in Illinois and Missouri (Westemeier et al. 1998, J.C. Pitman, Kansas Department of Wildlife and Parks, pers. comm.) will provide future opportunities for investigating adaptation in wild populations in new environments.

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Table 4.1. Mean estimates (± SE) for body mass and demographic traits of female greater prairie-chickens breeding at three study areas in eastern Kansas, 2006-08. Statistical analyses are described in text.

Parameter	South	N	North	N	Smoky	N	Statistics[a]
Body mass of females (g)	879 (7.9)	61	908 (8.7)	51	929 (8.8)	50	$F = 6.8, P < 0.01$
Clutch size of first nests	12.5 (0.3)	41	12.6 (0.3)	43	13.1 (0.3)	40	$F = 1.6, P = 0.21$
Clutch size of renests	10.4 (0.4)	21	10.9 (0.5)	14	10.2 (0.5)	10	$F = 0.5, P = 0.62$
Egg volume (ml)	23.7 (0.2)	62	24.2 (0.2)	58	24.7 (0.2)	51	$F = 2.3, P = 0.05$
Clutch volume (ml)	278 (6.8)	62	290 (7.1)	58	304 (7.5)	51	$F = 2.8, P = 0.06$
Nest survival	0.07 (0.02)	83	0.12 (0.03)	85	0.16 (0.04)	63	$\Delta AIC_c = 0.0$, $w_i/w_j = 7.3$[a]
Brood survival	0.29 (0.09)	15	0.38 (0.09)	12	0.48 (0.12)	16	$\Delta AIC_c = 0.37$, $w_i/w_j = 1.2$[a]
Annual survival of females	0.68 (0.01)	55	0.47 (0.002)	84	0.32 (0.001)	69	$\Delta AIC_c = 0.0$, $w_i/w_j = 99.0$[a]

[a] Parametric statistics were based on analysis of variance. Analyses of survival were based on model selection with AIC_c, where ΔAIC_c = difference in AIC_c between a model where survival differs among the three study areas and the minimum AIC_c model, and w_i/w_j = evidence ratios calculated as the ratio of relative support for the pooled weights of models where survival rates differed among the three study areas versus models where survival did not differ among areas.

CHAPTER 5 - COMPARATIVE DEMOGRAPHY OF GREATER PRAIRIE-CHICKEN POPULATIONS IN KANSAS: REGIONAL VARIATION IN POPULATION DYNAMICS AND VITAL RATE CONTRIBUTIONS

Abstract

We modeled population dynamics and conducted sensitivity analyses from field data collected during a 4-year study that examined demographic parameters of components of reproductive effort and success, juvenile survival, and annual adult female survival for three populations of greater prairie-chickens occurring across a gradient of human landscape alteration and land use in east-central Kansas, USA. The primary differences among study sites were in degree of grassland fragmentation and livestock grazing / rangeland management practices. We estimated demographic rates for the three populations, synthesized them in stage-based matrix models, and evaluated their relative influences on population growth using elasticity analyses and variance-scaled sensitivities. We observed regional differences in reproductive success, survival, and population dynamics among our three study areas. A prospective analysis of population growth revealed that all populations of prairie-chickens are projected to decline steeply given observed vital rates, and that declines across the gradient of landscape alteration and use were dissimilar ($\lambda_{South} = 0.74$; 95% CI = 0.71–0.78), $\lambda_{North} = 0.54$; 95% CI = 0.52–0.59, $\lambda_{Smoky} = 0.49$; 95% CI = 0.46–0.53). Finite rates of population decline were more sensitive to changes in adult survival than to other demographic parameters, including reproductive rates; suggesting that adult survival may be more important than previously thought for prairie-chickens, especially for declining populations. However, population change was more sensitive to reproductive rates at the most fragmented and least intensively grazed study site; suggesting that patterns of landscape fragmentation and land use may be impacting the relative influences of underlying vital rates on rates of population growth. Our results indicate that (1) populations of prairie-chickens in Kansas are not viable without immigration, (2) rates of population decline vary among areas under different land management practices, (3) human land-use patterns may impact the relative influences of vital rates on population trajectories, and (4) anthropogenic

effects on population demography may influence the regional life history strategies of a short-lived game bird.

Introduction

Populations of greater prairie-chickens (*Tympanuchus cupido*; hereafter "prairie-chickens") have declined more than 50% over the last 40 years (Svedarsky et al. 2000). Large-scale declines in both the distribution and numbers of prairie-chickens have paralleled the large-scale loss of native tallgrass prairie, and prairie-chickens currently occupy a fraction of their pre-European settlement range (Schroeder and Robb 1993, Johnsgard 2002). Eastern Kansas is often regarded as a stronghold for prairie-chickens because large tracts of grasslands remain relatively intact (Johnsgard 2002). However, the best available data suggest that populations of prairie-chickens in the most contiguous tallgrass prairie in North America have been declining for the last 30 years (Rodgers 2009, Fig. 1.2). Relatively little is known about the vital population processes of prairie-chickens in this region, and mechanisms linking grassland fragmentation and rangeland management with population declines are unknown. Vital rates of greater prairie-chicken populations have been studied extensively in auxiliary or fragmented portions of their range (Svedarsky 1988, McKee et al. 1998, Ryan et al. 1998), but few demographic data exist in areas considered to be at the core of their native range (Robel 1970, Horak 1985).

Conservation efforts for greater prairie-chickens require baseline data representing vital rates and their respective influence on population fluctuations in native habitats. Based on a small sample of nests (n = 34) from a single study site, Nooker (2007) found that nest success of greater prairie-chickens (7.5%) in the north-central Flint Hills ecoregion of Kansas was significantly lower than what was reported for the same area more than 30 years previously (35%; Robel 1970), and suggested that changes in range management practices in the last 30 years were the cause (Robbins et al. 1998). It is unclear whether results from these studies can be extrapolated to other areas if landscape composition and patterning and rangeland management practices vary across the range of prairie-chickens. Prairie-chickens can occupy habitats ranging from relatively unfragmented and intensively-grazed rangeland in the southern Flint Hills to moderately fragmented and lightly to moderately-grazed grassland in the Smoky Hills (McNew et al. 2010*a*). Variation in important vital rates such as nest survival and adult survival appear to be influenced by variation in prescribed burning and grazing regimes and landscape patterning (Robbins et al. 2002, Patten et al. 2007, McNew et al. 2010*b*). However, it is unknown how human-induced variations in vital rates impact population growth rates or viability of prairie-chickens at the core of their extant distribution, or which vital rates are driving regional population dynamics. Wisdom and Mills (1997) explored the influences of vital rates with elasticity analyses using input variables taken from across the range of greater prairie-chickens and suggested that a composite measure of fecundity (nest survival and brood survival) was most important to projected population changes. Population models for other species of grouse sometime identify juvenile or adult survival as important vital rates (Hagen et al. 2009). Given large differences in the landscapes over which greater prairie-chickens occur, it is unclear whether universal management recommendations are appropriate for stabilizing or increasing regional greater prairie-chicken populations.

In this study, we estimated demographic rates for the three populations of greater prairie-chickens, applied them to stage-based matrix models to estimate regional rates of population change, and evaluated impacts of demographic parameters on population growth. First, we assess the population status of greater prairie-chickens by estimating the finite rate of population change (λ) and 95% confidence intervals to assess whether populations were viable ($\lambda \geq 1.0$) or predicted to decline ($\lambda < 1.0$). Second, we conduct prospective elasticity and variance-scaled sensitivity analyses to identify the vital rates predicted to have the greatest influence on λ, and whether proportional vital rate sensitivities were similar among populations with significantly different demographies. Last, we performed a retrospective life-table response experiment to examine the relative contribution of vital rates to the variation in population growth rates among the three populations in different landscapes. We hypothesized that site differences in grassland fragmentation and rangeland management would result in significant variation in population growth rates, as well as population responses to vital rate manipulation. We posit that large differences in landscape patterns and rangeland management practices will require regionally specific management strategies to stabilize populations. We conclude with region-specific recommendations aimed at improving important demographic parameters and conserving greater prairie-chickens in Kansas.

Study Areas

Our study occurred at three study sites in two ecoregions of eastern Kansas; two sites located in the southern and northern Flint Hills (South and North, respectively) and one site in the Smoky Hills (Smoky; Fig. 2.1). The three study areas were >100 km apart and differed in grassland fragmentation, as well as rangeland management practices (McNew et al. 2010*a,b*). The South site (635 km^2) had landcover of 90% grassland and 3% cropland, a mean grassland patch size of 185 ha, and a road density of 0.32 km of roads per km^2. The majority of the site was managed with range management practices of annual spring burning and intensive early stocking with cattle (IESB, 1 head per 0.8 ha for 90 days; Smith and Owensby 1978, With et al. 2008) with pastures stocked in late March – early April. The North site (533 km^2) had landcover of 81% grassland and 10% cropland, a mean grassland patch size of 51 ha, and a road density of 0.57 km per km^2. Annual spring burning was common and lands were managed with a mixture of IESB and season-long stock grazing and annual burning (SLSB; 1 head per 1.6 ha for 180 days). The Smoky site (1,295 km^2) was more fragmented with landcover of 53% grassland and 38% cropland, a mean grassland patch size of 15 ha, and a higher road density of 1.4 km per km^2. Cultivated crops include wheat, sorghum, soybeans, and corn. Native grass pastures at the Smoky site were burned infrequently at fire return intervals $\geq$2 years, grazed at low to moderate intensities (1 head per >2 ha for 180 days), and cattle stocking occurred later in the season (ca. 1 May) than at the other two study sites.

Methods

Capture and Monitoring of Prairie-chickens

We were able to make direct comparisons among our three study populations because standardized field methods were used at all sites. Prairie-chickens were captured with walk-in traps and drop-nets at lek sites during the springs of 2006-2009 (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage characteristics (Henderson et al. 1967). We determined age-class as yearling or adult from the shape, coloration and wear of the outermost two primaries (numbers 9 and 10; Schroeder and Robb 1993). All captured prairie-chickens were individually marked with a numbered metal leg band and three colored leg bands. Females were fitted with 11-g necklace-style VHF radio transmitters, equipped with mortality switches and an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). Radio-marked females were monitored ≥3 times per week during the breeding, nesting and brood-rearing seasons (March – August) and weekly during the post-breeding and winter periods (September – February). Once a female localized in an area for three successive days, we used a portable radio receiver and handheld Yagi antenna to locate the nest. We flushed the female once in early incubation to count the eggs, to determine the stage of incubation, and to record the nest location. To minimize disturbance, females with nests were monitored daily at distances ≥100 m by triangulation of the radio signal. Once it was determined that the female was no longer tending the nest, we revisited nests to determine nest fate. We classified nest fate as successful (≥1 chick produced) or failed if no chicks hatched.

For broods that successfully hatched, we conducted systematic brood flushes within one hour of sunrise at 14, 24, 34, and 60-d post-hatch by radio-tracking the brood female (Fields et al. 2006, Pitman et al. 2006). If the female flushed, the area was carefully searched to be sure all chicks were flushed and the maximum number of flushing chicks was recorded. If no chicks were counted, we conducted a second flush count two days later to confirm presence or absence of chicks.

Dipnets and spotlights were used to capture ≥25 day old chicks by locating radio-marked females at night. We collected 20 μL of blood, recorded morphometrics and attached radio-transmitters to their backs with surgical sutures (Burkepile et al. 2002). The 3-g transmitters (modified model A4300, Advanced Telemetry Systems, Isanti, MN) were <5% of juvenile mass and had an expected battery life of 400 days.

Radio-marked prairie-chickens were monitored ≥3 per week during March – August and ≥1 time per week during September – February until they died or were censored from the study due to transmitter failure or leaving the study area. Field investigations of transmitter locations were used to determined whether the bird died or if the transmitter was lost (Hagen et al. 2007). Field methods were approved by Kansas State University's Institutional Animal Care and Use Committee (Protocol numbers 2474 and 2781).

Demographic Rates

We estimated ten demographic parameters for prairie-chickens.

1) Nesting Rate: (NEST); the probability of a female initiating a nest.

2) Total Clutch Laid (TCL); the maximum number of eggs laid per nest. The sample was restricted to nests found during incubation.

3) Nest Survival (NSURV); the probability of a nest producing ≥ 1 hatched chick. Estimates were calculated separately for both first ($NSURV_1$) and renesting ($NSURV_2$) attempts.

4) Renesting Rate (RENEST); the probability of a female producing a replacement clutch conditional upon failure of her first clutch.

5) Chicks per Egg Laid (C/E); the proportion of eggs laid that hatched and produced chicks. We calculated C/E for nests that survived incubation and hatched at least one egg. Values of C/E < 1 included partial clutch losses due to eggs that disappeared during incubation and eggs that survived incubation but failed to hatch.

6) Brood Survival (BSURV); the probability that ≥ 1 chick survived to 24-d of age, conditional upon at least one chick leaving the nest. Brood survival has been previously reported from hatch until fledging at 14-d of age (Pitman et al. 2006). We estimated brood survival to 24-d because juveniles could not be fitted with transmitters until 25-d of age. Values of BSURV < 1 were due to total brood failure which was readily determined by behavior and movements of females. Females without broods flushed long distances >400 m or joined small groups of failed breeders.

7) Fledglings per Chick Hatched (F/C); the proportion of hatched chicks that survived until 24-d of age conditional upon ≥ 1 chick surviving to 24-d of age.

Fecundity (F), or the number of female chicks produced per female was calculated as a function of these seven parameters as follows:

$$F = [(\mathrm{NEST} \times \mathrm{TCL}_1 \times \mathrm{NSURV}_1) + \\ [(1\text{-}\mathrm{NSURV1}) \times \mathrm{RENEST}_1 \times \mathrm{TCL}_2 \times \mathrm{NSURV}_2]] \\ \times \mathrm{C/E} \times \mathrm{BSURV} \times \mathrm{F/C} \times 0.5$$

Bootstrapping procedures were used to calculate 95% confidence intervals for fecundity estimates by randomly drawing from the underlying distributions of input parameters (e.g., normal distribution for clutch size, beta distributions for probabilities). Bootstrapped means of F were similar to observed means (<0.01). Therefore confidence intervals derived from bootstrapping were unbiased and did not require adjustment (Caswell 2001).

8) Survival of Juveniles (S_j); The 8-month probability that juvenile prairie-chickens survived from 24-d of age until their first breeding season.

9) Survival of Yearling Females (S_y); The annual probability that a female prairie-chicken aged ~ 8 mo survived from its first breeding season to the next.

10) Survival of Adult Females (S_a); The probability that a female prairie-chicken $\geq$20 months of age survived the year.

Estimation of Demographic Parameters

Nesting Statistics. – Nesting frequency (NEST) was calculated as the percentage of females that attempted a nest. Renesting rates (RENEST) were calculated as the percentage of radio-marked females that initiated a second nest conditional on loss of first nest and availability. A female was considered unavailable for renesting if she was killed while incubating a first nest or was unable to be located during the renesting period. Estimates of demographic variance (Var(p)) for nesting frequencies were calculated as:

$$\mathrm{Var}(p) = p(1-p)/\mathrm{N}$$

where p is the frequency and N is the sample size (Akcakaya 2002, Sandercock et al. 2005).

Nest and Brood Survival. – Nest survival (NSURV) was the proportion of nests that produce $\geq$1 hatched chick, whereas brood survival (BSURV) was the proportion of hatched clutches that produce $\geq$ 1 24-d old chick. We used the nest survival model in Program Mark 4.3 to generate maximum likelihood estimates of daily nest survival corrected for exposure before discovery, as well as daily brood survival from hatch to 24-d of age. Multiple model selection and inference based on minimization of Akaike's Information Criterion adjusted for small sample size (AIC_c) was used to evaluate the importance of four factors on daily nest survival: nesting attempt (first or renest denoted by subscripts 1 and 2), female age, year and study site (Burnham and Anderson 1998). We evaluated the effect of three factors on daily brood survival: female age, year, and study site. We used the most parsimonious model to estimate daily survival probabilities, and then extrapolated the overall nest survival probability as the product of daily survival probabilities. Similarly, brood survival from hatch to 24-d of age was calculated as the product of the estimates of daily brood survival. Variances of extrapolated nest survival were calculated using the delta method (Powell 2007).

Juvenile and Female Survival. — We monitored radio-marked prairie-chickens weekly during a four-year period between March 2006 – February 2010 until death, transmitter failure, or until birds left the study area and could not be located for one month. We estimated juvenile and mature female (yearling and adult) survival using nest survival procedure, a general model for known-fate data (Hartke et al. 2006, Mong and Sandercock 2007) in Program MARK to estimate monthly probability of survival at each study site. Survival of females were evaluated for the entire year (Mar – Feb), but juvenile survival was evaluated from 25-d of age until recruitment into the breeding population the following spring (8 months; Aug – Feb). Multiple model selection and inference based on minimization of AIC_c was used to evaluate the importance of female age (female survival only) and study site on monthly survival (Burnham and Anderson 1998). For each independent analysis of juvenile and female survival, we used the most parsimonious model to derive monthly survival probabilities, and then extrapolated annual survival rates (mature females) or 8-month survival rates (juveniles) at each study area as the product of monthly survival rates during the entire study period.

Prospective Analysis

Development of the population model.— To describe the dynamics of greater prairie-chicken populations, we developed a deterministic density-independent matrix population model for each of the three study areas using demographic data collected during the study. We first developed and parameterized a stochastic model to calculate the finite growth rates (λ) for each of the three populations. We then calculated the elasticities and variance-scaled sensitivities of λ to changes in the values of the demographic parameters.

For each population, we developed and parameterized a Leslie matrix model (Caswell 2001) with vital rates for three stage-classes of female prairie-chickens: juveniles (<1 year old), yearlings (1-2 years old), and adults (>2 years old). Because females were captured during the spring lekking season, we used a pre-breeding birth-pulse model. Greater prairie-chickens breed as yearlings, but generally have lower fecundity than adults (Schroeder and Robb 1993, Wisdom and Mills 1997). Survival also appears to be age-specific for prairie grouse (Pitman et al. 2006, Hagen et al. 2007), therefore the matrix model took the form:

$$\mathbf{A} = \begin{bmatrix} F_Y S_J & F_A S_J \\ S_Y & S_A \end{bmatrix},$$

where F_i is stage-class specific fecundity, S_i is stage-specific survival probability, and subscripts include J = juvenile, Y = yearling, and A = adult.

Analytical Procedures.— We analyzed matrix population models in program Matlab 6.5 (Mathworks Inc. 2003) to estimate the finite rates of population change (λ), the stable age distributions (**w**), and the reproductive values (**v**) of prairie-chicken populations. The finite or asymptotic rate of population change (λ), the stable stage structure (**w**), and the reproductive value (**v**) of any population matrix (**A**) are given by the dominant eigenvalue, and right and left eigenvectors, respectively (Caswell 2001). Bootstrapping procedures were used to calculate 95% confidence intervals for derived estimates such as λ by randomly drawing from the underlying distributions of input parameters (e.g., normal distribution for clutch sizes, beta distribution for probabilities). If 95% CI (λ) included 1, then λ was not considered significantly different than a stationary population. Likewise, λ was not considered to differ among study populations if means were within 95% CIs of another population's distribution.

Sensitivity Analysis.—The sensitivities of λ with respect to changes in matrix elements (a_{ij}) predict which demographic parameters will have the greatest impacts on population change (Lande 1988, Caswell 2001). Sensitivities can be assessed in both absolute ('sensitivity') and/or proportional ('elasticity') terms (Caswell 2001). We calculated the sensitivities of λ to changes in the elements a_{ij} of **A** according to Caswell (2001):

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_i}{\langle w, v \rangle},$$

where '$\langle \ \rangle$' denotes the scalar product. The elasticities, or proportional sensitivities, of λ to changes in a_{ij} of **A** are given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}.$$

The elasticities of the lower-level vital rates (x_{ij}) that compose F_1 and F_2 were evaluated by taking the partial derivatives of the matrix elements (Caswell 2001),

$$e_{x_{ij}} = \frac{x}{\lambda} \frac{\partial \lambda}{\partial x_{ij}},$$

where

$$\frac{\partial \lambda}{\partial x_{ij}} = \sum \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_{ij}}.$$

Elasticities of lower-level vital rates do not sum to 1 like those of the matrix elements, but may still be summed to determine the relative net effect of management actions on λ (Caswell 1989, Mills et al. 1999). Thus we summed elasticities across stage-classes and nesting attempts to evaluate the relative effectiveness management actions for improving λ. Because the variance of vital rates can influence their elasticities, we also used variance-scaled sensitivities (VSS) to assess vital rate sensitivities (Link and Doherty 2002). We calculated the VSS for a given vital rate probability ($\hat{\theta}$) as

$$VSS = \left(\frac{\sqrt{\hat{\theta}(1-\hat{\theta})}}{\lambda} \right) \frac{\partial \lambda}{\partial \hat{\theta}},$$

We converted clutch size, a normally-distributed demographic rate, to a proportion prior to estimating VSS (Hagen et al. 2009):

$$q(\hat{\theta}) = \ln(\hat{\theta}) \,/\, k_{\max},$$

where $\hat{\theta}$ = mean clutch size and $k_{\max}$ was the maximum clutch size observed for a specific age class and nesting attempt (Link and Doherty 2002). We report both standard elasticities and VSSs for comparison.

Retrospective Analysis

We used a life-table response experiment (LTRE) to assess the contribution of variation of vital rates on the variability in λ among study sites (Caswell 1996, Caswell 2000). Differences in landscape or habitat conditions may be complex, impacting many demographic parameters simultaneously. LTRE decomposes treatment effects into contributions (*c*) from each of the vital rates in the model by comparing each population's matrix to a reference population, in which vital rates are averaged over all three study sites ($\mathbf{A}^{R}$). The effect of each of the study sites on λ were decomposed from each matrix element by,

$$\Delta\lambda \approx \sum_{i,j} (x_{ij}^{I} - x_{ij}^{R}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \bigg|_{A^{+}},$$

Error! Bookmark not defined.where "I" represents one of the three study sites, a_{ij} represents matrix elements, x_{ij} represents lower-level matrix elements or vital rates. The partial derivatives are evaluated from a mean matrix (Caswell 1996),

$$\mathbf{A}^{R} = (\mathbf{A}^{1} + \mathbf{A}^{2} + \mathbf{A}^{3}) / 3$$

where

$$\mathbf{A}^{+} = (\mathbf{A}^{R} + \mathbf{A}^{I}) / 2$$

All analyses were conducted using the Program Matlab 6.5 (Mathworks Inc. 2003).

Results

Demographic Rates

We captured 287 yearling and adult female prairie-chickens at the three study sites during 2006–2009. Eight females were released without radio-marking. Therefore, 279 female prairie-chickens (n = 56, 107, and 116 at South, North and Smoky sites, respectively) were monitored for reproduction and survival from time of capture until death or until transmitters were lost or failed.

Fecundity.— Apparent nest initiation rates (± SE) were 0.88 ± 0.04, 0.81 ± 0.04, and 0.86 ± 0.04 at the South, North and Smoky sites, respectively. Renesting rates were 0.67 ± 0.06, 0.40 ± 0.06, and 0.40 ± 0.06, respectively, and did not differ between female age-classes (Chapter 2, Table 5.1). Hatch rate of eggs in successful nests that survived incubation was high at 0.82 (0.03) chicks per egg. Average clutch size (± SD) of first nests was 12.4 ± 2.3 eggs was significantly larger than renests (10.5 ± 2.5; $F_{1,168}$ = 47.1, $P < 0.001$). Clutch sizes did not differ significantly among study sites ($F_{2,168}$ = 1.13, $P = 0.33$; Table 5.1).

During the breeding seasons of 2006–2009, 283 nests of 189 radio-marked female prairie-chickens were located and monitored. In addition, we found three nests of unmarked females to bring the total number of nests to 286; of which 63 were successful. Nest survival was modeled for a 103-day nesting period (23 April – 19 July). The most parsimonious model ($\Delta AIC_c = 0$) included the effects of study site and nesting attempt. Models in which nest survival varied among study sites were strongly supported and were 70 times more likely than a model where nest survival was constant among sites (w_i/w_j = 0.981/0.014; Table 5.2). Models in which nest survival differed between first and renesting attempts were considered parsimonious and had 60% of the relative support of the data (Table 5.2). Nest survival of first attempts was low at the South site (0.05 ± 0.03), intermediate at the North site (0.09 ± 0.03) and higher at the Smoky site (0.17 ± 0.05). Survival of renests was significantly higher than first attempts and showed a similar pattern among sites: South (0.11 ± 0.05), North (0.17 ± 0.05), and Smoky (0.29 ± 0.08; Table 2). There was moderate support ($w_{female\ age}$ = 0.26/0.74) that adults were more successful than yearlings at producing successful nests (Table 5.1).

Sixty-six broods were monitored from hatch until 24-d of age or failure. Brood survival to 24-d of age was modeled for an 80-day brood-rearing period (17 May – 4 August). The top model indicated that brood survival was constant among study sites and had 42% of the relative support (Table 5.3). However, a model that contained a study site effect was parsimonious ($\Delta AIC_c = 1.72$), and models where brood survival varied among sites had 35% of the relative support. Models where brood survival varied between female age-classes and among years were not supported ($\Delta AIC_c > 2$; Table 5.3). Model averaged estimates of brood survival from hatch to 24-d were 0.29 ± 0.08, 0.27 ± 0.08, and 0.34 ± 0.07 at the South, North, and Smoky study sites, respectively (Table 5.1).

Fecundity, or the number of 24-d old female chicks produced per breeding female, was low across all sites (0.14 ± 0.06 chicks per female). However, fecundity was more than twice as great at the Smoky site (yearling $F_{\mathrm{Smoky}} = 0.21 \pm 0.05$, adult $F_{\mathrm{Smoky}} = 0.23 \pm 0.05$) than either of the Flint Hills sites ($F = 0.06 \pm 0.04$ for both yearlings and adults at the South site, and $F = 0.09 \pm 0.04$ and 0.10 ± 0.04 for yearlings and adults at the North site, respectively), although 95% confidence intervals overlapped in all cases (Table 5.1).

Juvenile Survival.— During 2007 – 2009, 23 juveniles from 11 broods (n = 5 at North, n = 18 at Smoky) were radio-marked and monitored until death or until they lost their transmitters. Due to low production, we were unable to fit transmitters to any juveniles at the South site. The top model ($\Delta AIC_c = 0$) indicated that monthly survival probabilities were similar between the study sites. A model in which monthly survival rates varied between study sites was considered equally parsimonious ($\Delta AIC_c = 1.9$; Table 5.4). However the beta estimate for the effect of site did not differ significantly from 0 (95% CI: -0.02, 0.14). Therefore, monthly juvenile survival for the North and Smoky sites estimated from the constant model was 0.895 ± 0.033, and overall juvenile survival from 25-d of age to first breeding was 0.41 ± 0.001 (Table 5.1).

Yearling and Adult Survival.— We monitored 279 radio-marked yearling and adult female prairie-chickens during March 2006 – January 2010. Differences in survival among study sites were strongly supported by the data, and models with a site effect accounted for more than 99% of the relative support (Table 5.5). A model that included both study site and female age was parsimonious ($\Delta AIC_c = 0.65$) and suggested higher survival among adults than yearlings (Table 5.1). Survival was ranked across the three sites: Smoky site (yearlings = 0.34 ± 0.001, adults = 0.42 + 0.002), North site (yearlings = 0.42 $\pm$ 0.001, adults = 0.50 $\pm$ 0.003) and South site (yearlings = 0.64 $\pm$ 0.01, adults = 0.71 $\pm$ 0.01; Table 5.1).

Prospective Analyses

The asymptotic rates of population change for the three populations were: $\lambda_{\mathrm{South}} = 0.74$ (95% CI = 0.71, 0.78), $\lambda_{\mathrm{North}} = 0.54$ (95% CI = 0.52, 0.59), and $\lambda_{\mathrm{Smoky}} = 0.49$ (95% CI = 0.46, 0.53); projecting different rates of decline for all populations. Damping ratios were high ($\rho > 72$) and all populations would be expected to converge rapidly to a stable age distribution ($t_{20} < 0.7$ yrs). Stable-age distributions were skewed toward adults at all sites ($\mathbf{w}_{\mathrm{A}} = 0.96$, 0.90, and 0.83 at South, North, and Smoky, respectively), and reproductive values were greater for adults ($\mathbf{v}_{\mathrm{A}} = 1.11 – 1.22$) than yearlings ($\mathbf{v}_{\mathrm{Y}} = 1.0$) for all populations. Yearling females at all sites had a low net reproductive rates but, despite short generation times ($T < 2.2$ yr), the likelihood of a female replacing herself was greater at the Smoky site ($R_0 < 0.13$) than at the South and North sites ($R_0 = 0.06$ and 0.08, respectively; Table 5.6).

Elasticity values for the vital rates suggested λ was most sensitive to future changes in adult survival (S_{A}) at all study sites. Elasticities and VSSs were ranked second for the cumulative influence of nest survival of both stage-classes and all nesting attempts. Other components of fecundity, such as nest initiation rates (NEST, RENEST) and clutch size (TCL) had lower elasticities and VSSs than adult survival at all sites. Nevertheless, λ was sensitive to components of fecundity, especially NSURV at the Smoky site (Fig. 5.1). Variance-scaled sensitivities generally agreed with elasticities and indicated that changes in adult survival would have the largest impacts on λ at all sites.

Retrospective Analysis

Using a mean matrix of all three populations as a reference population, the effect of study site on λ was $\lambda_{\mathrm{South}} - \lambda_{\mathrm{Reference}} = 0.15$, $\lambda_{\mathrm{North}} - \lambda_{\mathrm{Reference}} = -0.05$, and $\lambda_{\mathrm{Smoky}} - \lambda_{\mathrm{Reference}} = -0.10$. The effect of study site was relatively large and affected adult survival (S_{A}) the most. Contributions of S_{A} accounted for most ($\geq 52\%$) of variation in λ at all sites. There were positive contributions from advantages in adult survival for the South and North study sites but contributions were negative for the Smoky site (Fig. 5.2). Large improvements in reproductive success at the Smoky site contributed little to the variation in λ. Thus, it appears that large differences in adult female survival rates are responsible for observed differences in rates of population change among the study areas. Differences in reproductive success among the study sites had relatively little effect on observed differences in rates of population decline.

Discussion

This study provides demographic data for three populations of greater prairie-chickens in Kansas, and provides evidence for the demographic mechanisms driving population declines in the core of the extant range of a sensitive grassland bird. Nest initiation rates were high, clutch sizes large, and hatchability of eggs high; indicating high reproductive potential for all three populations. However, estimates of fecundities, which were driven by low nest survival, were among the lowest ever reported for prairie-chickens, while survival rates of yearlings and adults were highly variable among study sites. Depressed nest and brood survival resulted in projected population declines at all three sites, and rates of decline were not similar among populations. Population growth rates were more sensitive to changes in adult survival at all sites, highlighting the importance of survival for declining populations of upland game birds. However, the relative influence of fecundity parameters was not similar among the study populations. The relative importance of vital rates was not influenced by the type of sensitivity analysis applied. Finally, our data indicate that differences in the rates of population decline among study sites were largely due to variation in adult survival; which was likely mediated by human landscape alteration. Our results suggest that conservation actions aimed at recovering declining populations of prairie-chickens must be aimed at local conditions rather than general practices across the species range.

Demography

Despite high reproductive potential, low nest and brood survival resulted in depressed productivity; especially at the South and North sites in the intensively-grazed Flint Hills ecoregion. Indeed, our estimates of nest survival are among the lowest reported for prairie-chickens and significantly less than the 0.50 threshold suggested by Westemeier (1979) for maintaining stable populations. Reported nest survival for 22 studies of greater prairie-chickens averaged 49% (Bergerud and Gratson1988), and previous work suggests that nest survival is likely greater in more isolated and auxiliary populations than our populations which occurred at the core of the species range. Reported nest survival ranged from 31-39% in the fragmented prairie of southwestern Missouri (McKee et al. 1998, Ryan et al. 1998) to 80% in relatively contiguous grasslands of North and South Dakota (Svedarsky 1988, Norton 2005). In fact, nest survival at our study sites was less than that reported for the endangered Attwater's prairie-chicken in Texas (32%; Peterson and Silvy 1996) and is not sufficient to maintain viable populations. Brood survival to 24-d post hatch ranged from 27-34% at our study sites and was lower than previously reported for greater prairie-chickens in the privately managed grasslands of southeast Nebraska (59%; Matthews et al., in press) and Ft. Pierre National Grasslands of South Dakota (83%; Norton 2005). Our estimates of 24-d brood survival rate were also lower than those reported for 60-d survival of lesser prairie-chicken broods in the sand sagebrush prairie (50%; Pitman et al. 2006) and short-grass prairie (53%; Fields et al. 2006) of western Kansas. Survival of lesser prairie-chicken broods is influenced by habitat conditions, especially overhead cover, and differences in rangeland management of grasslands are likely responsible for regional differences in nest and brood survival (Pitman et al. 2005, Fields et al. 2006).

The three populations of greater prairie-chickens had markedly different demographic rates that corresponded to gradients of grassland fragmentation and prescribed burning and grazing intensity. Rangeland management appears to be influencing reproductive success, whereas landscape composition and pattern accounts for variation in regional survival rates of prairie-chickens in Kansas. Though depressed at all sites, nest and brood survival were significantly greater in the less intensively grazed and more fragmented prairie of the Smoky Hills site than in the more contiguous and intensively-grazed Flint Hills sites. These results are contrary to previous reports that nests occurring in a fragmented prairie-agricultural mosaic had lower survival than nests in state-managed contiguous prairie in southwestern Missouri (Ryan et al. 1998). In addition, previous work has shown a general correlation between fragmentation and predation of grassland bird nests (Winter et al. 2000, Herkert et al. 2003). However, grassland management was likely similar between fragmented and contiguous sites in the Missouri study; whereas grassland management differed significantly among our study sites (Table 2.1). Our low estimates of nest and brood survival in large unfragmented Kansas prairie are consistent with Nooker (2007), who suggested that the prevalent grassland practice of annual burning and intensive early stocking of cattle (IESB) results in limited nesting cover for prairie-chickens in the Flint Hills. The amount and quality of residual cover limits nest and brood survival for prairie-chickens (McKee et al. 1998, Pitman et al. 2005, Fields et al. 2006), and annual burning and intensive early cattle grazing greatly reduces residual vegetation (Fuhlendorf et al. 2001, With et al. 2008). Indeed, nest survival in the northern Flint Hills was found to be 2-3 times greater than our estimates before large-scale implementation of IESB was introduced 30 years ago (Robel 1970, Smith and Owensby 1978). We do not have brood survival estimates for the Flint Hills prior to IESB implementation, but brood survival at our annually burned and intensively grazed Flint Hills sites were significantly less than at the fragmented and less intensively managed Smoky site. Our data suggest that large-scale implementation of annual spring burning and intensive cattle grazing of contiguous tallgrass prairie is more limiting to nest and brood survival than moderate fragmentation by agriculture and roads.

In contrast to regional patterns of nest and brood survival, survival probabilities of juveniles, yearlings and adults were higher in the least fragmented and most intensively-grazed South site and lowest in the most fragmented and least intensively-grazed Smoky site (Table 5.1). In fact, our estimates of annual survival for females at the Smoky site ($S_Y = 0.34$, $S_A = 0.42$) are among the lowest and our estimates for the South site ($S_Y = 0.64$, $S_A = 0.71$) among the highest values ever reported for a field study of prairie-chickens (Hammerstrom and Hammerstrom 1975, Schroeder and Robb 1993). The North site had intermediate amounts of habitat fragmentation and grazing intensity, and the survival rates of prairie-chickens were intermediate as well. Higher rates of mortality at the Smoky site may be the result of a combination of higher predator densities in fragmented grasslands and tradeoffs between female survival and nest survival. More than 90% of mortality events were due to predation, and greater predation rates at the Smoky site could be due to numerical or functional predator responses to habitat fragmentation. Known predators of prairie-chickens, such as coyotes (*Canis latrans*), use edge habitats and roads for travel and foraging (Kuehl and Clark 2002, Tigas et al. 2002), and preliminary data suggest that predator densities were higher at the fragmented Smoky site than Flint Hills sites (A.J. Gregory, unpublished data). In addition, higher predation rates of females in fragmented areas with greater residual vegetation agrees with previous research that found mortality rates of female grouse to be correlated with vertical structure during the incubation period (Wiebe and Martin 1998, Hagen et al. 2007). Because the vertical cover sought by females to protect nests also limits their own ability to detect predators, there is likely a tradeoff between nest and female survival mediated by the amount of cover at a nest site (Wiebe and Martin 1998). Although our results suggest that large differences in the rangeland management and human landscape alteration among study sites appeared to influence the variation in population vital rates, future analyses will be required to evaluate the relationships between vital rates and manageable multi-scale habitat conditions.

Projected Population Declines and Vital Rate Sensitivities

Bootstrapped confidence intervals for λ were <1; indicating that all three populations are projected to decline without immigration. High damping ratios ($\rho \geq 72.1$) and rapid convergence to a stable age distribution ($t_{20} < 0.7$ yr) indicate that asymptotic matrix properties accurately describe current population demographics (Caswell 2001). All three populations were short-lived ($T \leq 2.2$ yrs) with low net reproductive rates ($R_0 \leq 0.13$). However, higher adult survival and lower reproductive success at the South site resulted in a longer generation time, a lower net reproductive rate, and a stable age distribution more heavily skewed toward adult females. Depressed female survival coupled with higher, albeit still depressed, fecundity resulted in a shorter generation time and a higher net reproductive rate. Intermediate vital rates resulted in an intermediate demography of prairie-chickens at the North site. Non-overlapping confidence intervals of λ among study sites indicate that the rates of population declines were not similar. Projected annual population declines without immigration were 26%, 46%, and 51% at the South, North, and Smoky sites, respectively. Variation in local and large-scale habitat conditions and predation risk due to human land use may account for differences in rates of population decline (Table 2.1). Poor nest and brood survival likely facilitated population declines at the Flint Hills sites that were predominantly managed with annual burning and intensive early cattle grazing. Despite having higher reproductive success than the Flint Hills populations, low survival of mature prairie-chickens coupled with low fecundity resulted in the greatest projected population declines at the highly fragmented and moderately grazed Smoky site.

An assumption of Leslie population models is that populations are closed to emigration and immigration or at least movements into and out of the population are offsetting (Caswell 2001). Therefore projected rates of population change will not reflect observed annual population trends at a site if effective immigration is ≥ 0. Our results generally agree with an independent data set of annual lek surveys collected during our spring trapping efforts, as well as annual lek counts conducted for the entire region by the Kansas Department of Wildlife and Parks, which indicate 30-50% declines in lek attendance at our Flint Hill sites during the study period (Rodgers 2009, L.B. McNew, unpublished data). However, annual male lek attendance did not decline significantly over the study period at the Smoky site, which had the greatest projected population declines; suggesting that either demographic parameters were biased or that immigration was supplementing the Smoky population.

We exclude the possibility that our demographic rates were significantly biased for three reasons. First, previous work has shown that estimates of survival from radio-marked juvenile and female prairie-chickens are unbiased (Pitman et al. 2006, Hagen et al. 2006). We are also confident in our estimates of nest survival because nest visitations (≤ 2 per nest) occurred under dry conditions with researchers wearing rubber boots and latex gloves to minimize scent. Moreover, females never abandoned nests due to visits, and only four of 286 nests were abandoned during the entire study. Finally, brood flushes were conducted soon after sunrise when chicks are brooded by females; resulting in high detection probabilities of broods and accurate estimates of brood survival. Notwithstanding, we believe that our estimates of nest initiation (NEST) and renesting (RENEST) rates were likely biased low because they assume 100% detection of nests. Our protocol for locating nests based on incubation behavior of radio-marked females likely prevented us from locating nests that failed during the laying period when females are not attending nests regularly. However, projected population declines were not significantly altered when we adjusted NEST and RENEST to 100%; indicating that potential biases in these vital rates did not impact model inferences.

A more likely explanation that lek counts did not agree with model projections is that immigration into the Smoky population was prevalent. Annual lek surveys conducted by the Kansas Department of Wildlife and Parks suggest that the greater regional population of prairie-chickens in the Smoky Hills ecoregion was stationary or increasing during the last 12 years (1997-2009; Rodgers 2009). The grassland-dominated landscapes on which prairie-chickens occur are highly fragmented in the Smoky Hills. Therefore, sub-populations of prairie-chickens in the Smoky Hills may be relatively isolated, or closed to movements, within a breeding season but not among breeding seasons. For instance, preliminary genetic data suggest that prairie-chickens captured at the Smoky site and an adjacent Smoky Hill sub-population are functionally linked and a high number of migrants is predicted (A.J. Gregory, unpublished data). Due to size and arrangement of suitable grassland habitat in a matrix of cultivated farmland, the population dynamics of prairie-chickens in the Smoky Hills may be better explained as a metapopulation, and four years of demographic data suggest that the Smoky study site may be an ecological sink.

Our high elasticities and VSSs for adult survival probabilities differ from previous work noting that prairie-chicken populations were more sensitive to changes in nest and chick survival than adult survival (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). Female prairie-chickens reach sexual maturity early (ca. 1 year), lay large clutches, and have a high propensity for renesting (McNew et al. 2010*a*). High reproductive potential and relatively short life expectancies ($\leq$ 3 yrs; Robel and Ballard 1974, Schroder and Robb 1993, this study) suggest that fecundity should have the greatest influence on prairie-chicken population fluctuations (Bergerud and Gratson 1988, Morrow et al. 1996, Sæther and Bakke 2000). However, changes in nest and chick survival had relatively little influence on changes in asymptotic λ for populations suffering high rates of reproductive failure, and suggest that management actions directed at improving adult survival would be more effective at mitigating population declines for all populations. Nevertheless, λ appeared to be less sensitive to adult survival and more sensitive to fecundity parameters at the Smoky site than the two Flint Hill sites (Fig. 3); suggesting that human land use patterns impact not only vital rates themselves but the relative influences of vital rates on population dynamics.

Because they quantify the relative importance of vital rates to population growth rates, elasticities are a popular tool in conservation biology (de Kroon et al. 2000, Hagen et al. 2009). However, it is wise to discuss the caveats of elasticities prior to making management recommendations based upon them. First, elasticity solutions are only valid for populations with stable age distributions (de Kroon et al. 2000) and should not be used to make management prescriptions if matrix models take a long time to converge (Caswell 2001, Fefferman and Reed 2006). Our populations converged to stable age distributions rapidly ($t_{20} < 0.7$ years); suggesting that elasticities accurately predict the impacts of management prescriptions in the short term (Fefferman and Reed 2006). Second, elasticities vary with projected population growth rates (de Kroon et al. 2000); suggesting that differences in the relative importance of vital rates for a population depend on whether the population is increasing or decreasing. Our results of higher elasticities for adult survival are typical of game bird populations with $\lambda < 1$, and highlight the importance of adult survival for declining populations (Sandercock et al. 2008). Third, elasticities may be related to the variances of their respective vital rates (Mills et al. 1999) and vital rates with high variances tend to have low elasticities (Pfister 1998). We addressed the functional relationship between the mean and variance of vital rates by calculating variance-scaled sensitivities and comparing them to elasticities (Link and Doherty 2002, Hagen et al. 2009), and found that the relative influence of vital rates on λ were generally unaffected by differences in observed variance among rates. Finally, elasticities change in relation to the values of their respective vital rates. Because they are local, or calculated for infinitesimally small changes around observed demographic estimates, they will change systematically with vital rate estimates (Drechsler 1998, Mills et al. 1999, de Kroon et al. 2000). A combination of λ < 1 and significantly depressed fecundities at all sites may explain why our elasticities suggest that management actions aimed at increasing adult survival would be most effective at increasing λ, whereas previous studies have prescribed actions to increase reproductive success or juvenile survival parameters (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). While elasticities identify key vital rates, logistics and economics may constrain management actions (Mills et al. 1999, Link and Doherty 2002). For example, high elasticities for adult survival at the South site are not particularly informative, because survival is already higher than most populations and improvement is likely impossible. Therefore, elasticity analyses should not be the only tool used to evaluate potential management actions for declining populations such as ours (Ehrlén and van Groenendael 1998, Mills et al. 2001, de Kroon et al. 2000; see below).

Life Table Response Experiment

Retrospective analyses, such as life-table response experiments (LTREs), describe how observed variation in the vital rates affects the observed variation in λ among populations (Caswell 1989, 1996). Many of the vital rates differed among our populations of greater prairie-chickens due to large differences in habitat conditions among study sites. By assessing the contributions of vital rates to differences in λ, we found that the effect of study site on the rate of population decline was primarily caused by large differences in adult survival. Indeed, variation in adult survival accounted for 52-68% of the variation in λ among study sites, and contributions were positive in the nearly unfragmented South site, while negative in the moderately and highly fragmented North and Smoky sites. Because variation in predation rates among sites were positively associated with the degree of habitat fragmentation (McNew et al. 2010*b*), variation in the regional rates of population declines are more appropriately explained by landscape composition and pattern than by differences in rangeland management practices of grasslands.

Management Implications

Populations of greater prairie-chickens at our study sites in the Flint Hills and Smoky Hills of Kansas are not viable with current rates of reproductive output. Results of sensitivity analyses suggest that management actions aimed at increasing adult survival will have the greatest benefit to declining populations. However, actions focused solely on improving adult survival rates would likely be unsuccessful at stabilizing populations, especially in the annually burned and intensively grazed Flint Hills region, as adult survival is already near a biological maximum. At current levels of nest and brood survival, adult survival would need to exceed 95% to curb population declines at our study sites in the Flint Hills. Management efforts aimed at increasing nest and brood survival are likely more realistic. Provided adult survival remains unchanged, nest and brood survival would need to exceed 55% and 63% for populations to stabilize at the South and North sites, respectively. Moreover, these rates are likely overestimates since management actions that improve brood survival may improve chick survival as well (Pitman et al. 2006). We believe that reproductive performance can be improved in the Flint Hills by implementation of burning and grazing regimes that provide adequate residual vertical and overhead herbaceous cover for successful nesting and brood-rearing while preventing encroachment and fragmentation of native prairie by woody vegetation (McKee et al. 1998, Robbins et al. 2002, Patten et al. 2007, Chapter 3). Rotational grassland management regimes such as patch-burn grazing may provide adequate nesting and brood rearing habitat without reducing revenues for cattle ranchers (Fuhlendorf et al. 2006, Rensink 2009), and future research should address the potential of patch-burn grazing for mitigating declines of prairie-chickens and other grassland birds in the Flint Hills.

Although nest and brood survival were higher for the Smoky Hills population than the Flint Hills, fecundity was still significantly less than levels required for a self-sustaining population. In addition, the population at the highly fragmented Smoky site experienced higher rates of predation on yearling and adults than populations in relatively unfragmented prairie. At current levels of nest and brood survival, annual survival would need to exceed 92% for the population to stabilize. Alternately, nest and brood survival would need to exceed 80% for $\lambda \geq 1$ at the Smoky site, given current survival rates. Thus, mitigating population declines will likely be more difficult in areas suffering significant loss (> 40%) and fragmentation of prairie than in low quality but contiguous prairies, because actions that improve both reproductive and survival rates simultaneously, such as predator removals or prairie restoration, will be required. Predator removals may potentially increase both fecundity and adult survival of ground-nesting game birds (Garrettson and Rohwer 2001, Frey et al. 2003). However, predator removals are expensive and time consuming and are likely only short-term solutions over small spatial extents (Côté and Sutherland 1996). Management actions aimed at reducing the negative impacts of edge effects by increasing the number, sizes, and proximity of tallgrass prairie fragments will likely be more effective at increasing vital rates, and improving population viability over the long term. However, the effects of landscape composition and arrangement, rangeland management regimes, and their interaction on prairie-chicken productivity and survival need to be quantified for more effective management of prairie-chickens.

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Table 5.1. Vital rates of yearling and adult greater prairie-chickens from three study areas in Kansas, 2006–2009.

Parameter[a]	South				North				Smoky			
	Yearling		Adult		Yearling		Adult		Yearling		Adult	
	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)
NEST	66	0.88 (0.04)			102	0.81 (0.04)			136	0.86 (0.04)		
TCL$_1$	19	12.7 (0.36)	22	10.8 (0.56)	30	11.7 (0.33)	46	12.5 (0.24)	33	13.1 (0.33)	32	13.7 (0.33)
NSURV$_1$	22	0.04 (0.02)	30	0.05 (0.03)	36	0.08 (0.03)	48	0.09 (0.03)	37	0.16 (0.05)	35	0.18 (0.05)
C/E$_1$	13	0.77 (0.04)			18	0.87 (0.04)			28	0.83 (0.03)		
RENEST	47	0.67 (0.06)			62	0.40 (0.06)			62	0.40 (0.06)		
TCL$_2$	8	12.2 (0.38)	9	11.1 (0.61)	9	11.0 (0.61)	12	10.9 (0.47)	11	11.2 (0.56)	7	10.4 (0.71)
NSURV$_2$	15	0.10 (0.04)	15	0.12 (0.05)	10	0.16 (0.05)	15	0.18 (0.05)	12	0.28 (0.07)	8	0.31 (0.08)
C/E$_2$	13	0.77 (0.04)			18	0.87 (0.04)			28	0.83 (0.03)		
BSURV	8	0.29 (0.08)	6	0.29 (0.08)	4	0.27 (0.08)	13	0.27 (0.08)	15	0.34 (0.07)	20	0.34 (0.07)
F/C	3	0.41 (0.08)			4	0.56 (0.06)			16	0.51 (0.02)		
Fecundity (F)		0.06		0.06		0.09		0.11		0.21		0.23
95% CI (F)		0.02 - 0.12		0.02 - 0.14		0.04 - 0.18		0.04 - 0.21		0.10 - 0.35		0.12 - 0.38
S_J	0	--			5	0.50 (0.002)			18	0.38 (0.002)		
S_F	31	0.64 (0.01)	25	0.71 (0.01)	54	0.42 (0.001)	53	0.50 (0.003)	53	0.34 (0.001)	63	0.42 (0.002)

[a] Parameters defined in text

Table 5.2. Candidate models and model statistics for daily nest survival (n = 286 nests) of greater prairie-chickens at three sites in Kansas, USA, 2006-2009.

	Model statistics[a]				
Model structure	*K*	Dev	AIC_c	ΔAIC_c	w_i
site + attempt	4	1265.7	1273.7	0.0	0.423
site	3	1269.2	1275.2	1.5	0.206
site + attempt + female age	5	1265.4	1275.5	1.8	0.179
site + female age	4	1268.9	1277.0	3.3	0.085
site + year	4	1269.1	1277.1	3.4	0.078
constant	1	1278.6	1280.6	6.9	0.014
year	2	1277.3	1281.3	7.6	0.010

[a] Model fit is described by the number of parameters (*K*), deviance (Dev), Akaike's Information Criterion corrected for small sample size (AIC_c), and AIC weights (w_i).

Table 5.3. Candidate models and model statistics for daily brood survival to 24-d post-hatch of greater prairie-chickens (n = 66 broods) at three sites in Kansas, USA, 2006-2009.

	Model statistics[a]				
Model structure	*K*	Dev	AIC_c	ΔAIC_c	w_i
constant	1	86.5	88.5	0.0	0.416
site	3	84.2	90.3	1.7	0.176
year	2	86.4	90.4	1.9	0.162
site + female age	4	83.9	91.9	3.4	0.076
year + female age	3	86.0	92.1	3.5	0.071
site + year	4	84.0	92.1	3.6	0.069
site + female age + year	5	83.8	93.9	5.4	0.029

[a] Model fit is described by the number of parameters (*K*), deviance (Dev), Akaike's Information Criterion corrected for small sample size (AIC_c), and AIC weights (w_i).

Table 5.4. Candidate models and model statistics for monthly (Sep-Mar) survival of juvenile greater prairie-chickens (n = 23) from 25-d of age to first breeding at the North and Smoky study sites in Kansas, USA, 2007-2009.

	Model statistics[a]				
Model structure	*K*	Dev	AIC_c	ΔAIC_c	w_i
constant	1	57.7	59.7	0.0	0.421
year	2	56.5	60.6	1.0	0.262
site	2	57.5	61.6	1.9	0.160
site + year	3	55.8	62.1	2.4	0.129
month	7	49.7	65.2	5.5	0.027
month × site	14	40.4	74.3	14.6	0.000

[a] Model fit is described by the number of parameters (*K*), deviance (Dev), Akaike's Information Criterion corrected for small sample size (AIC_c), and AIC weights (w_i).

Table 5.5. Candidate models and model statistics for monthly (Mar-Feb) survival of yearling and adult greater prairie-chickens (n = 279) at three study sites in Kansas, USA, 2006-2009.

	Model statistics[a]				
Model structure	K	Dev	AIC$_c$	ΔAIC$_c$	w_i
site	3	793.5	799.5	0.0	0.535
site + female age	4	792.2	800.2	0.7	0.386
time	46	209.4	803.9	4.8	0.060
constant	1	805.5	807.5	8.0	0.010
female age	2	803.7	807.7	8.2	0.009
time*site	101	656.7	871.0	71.4	0.000

[a] Model fit is described by the number of parameters (K), deviance (Dev), Akaike's Information Criterion corrected for small sample size (AIC$_c$), and AIC weights (w_i).

Table 5.6. Asymptotic properties of projection matrices for three populations of greater prairie-chickens in Kansas, USA, 2006-2009.

Matrix properties[a]	South		North		Smoky	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
λ	0.74	0.71 – 0.78	0.54	0.52 – 0.59	0.49	0.46 – 0.53
$\mathbf{w}_Y$	0.04	0.01 – 0.09	0.10	0.04 – 0.17	0.17	0.10 – 0.25
$\mathbf{w}_A$	0.96	0.91 – 0.99	0.90	0.83 – 0.96	0.83	0.75 – 0.90
$\mathbf{v}_Y$	1.00	1.00 – 1.00	1.00	1.00 – 1.00	1.00	1.00 – 1.00
$\mathbf{v}_A$	1.11	1.05 – 1.17	1.18	1.11 – 1.25	1.22	1.10 – 1.31
ρ	324	22 – 2,566	211	16 – 1,685	72.1	10 – 935
t_{20}	0.52	0.38 – 0.97	0.56	0.40 – 1.09	0.70	0.43 – 1.28
R_0	0.06	0.03 – 0.14	0.08	0.04 – 0.16	0.13	0.07 – 0.20
T	2.16	1.67 – 2.42	1.77	1.48 – 1.96	1.50	1.37 – 1.76

[a] λ = finite rate of population change, **w** = stable age distribution, **v** = reproductive value, ρ = damping ratio, t_{20} = time to model convergence, R_0 = net reproductive rate, T = generation time (years).

Table 5.7. Elasticities (e) and variance-scaled sensitivities (VSSs) for lower-level demographic rates (x) of matrices for 3 populations of greater prairie-chickens in Kansas, USA, 2006-2009. BSURV has been combined for both stage classes and NSURV has been combined for stage classes and attempts. The top three ranked models are in bold.

Rate	South ($\lambda = 0.74$)		North ($\lambda = 0.54$)		Smoky ($\lambda = 0.49$)	
	e_x	VSS	e_x	VSS	e_x	VSS
NEST	0.027	0.005	0.062	0.022	0.096	0.039
RENEST	0.025	0.016	0.05	0.045	0.051	0.063
TCL	0.028	0.002	0.067	0.008	0.104	0.016
NSURV	**0.129**	**0.113**	**0.276**	**0.270**	**0.366**	**0.443**
C/E	**0.053**	0.020	**0.112**	0.032	**0.147**	0.067
BSURV	0.052	**0.098**	0.107	**0.098**	0.138	**0.204**
F/C	**0.053**	0.045	0.102	0.073	**0.147**	0.145
S_J	**0.053**	0.037	**0.112**	0.082	**0.147**	0.188
S_Y	0.051	0.027	0.102	0.088	0.124	0.173
S_A	**0.897**	**0.592**	**0.786**	**0.843**	**0.729**	**0.856**

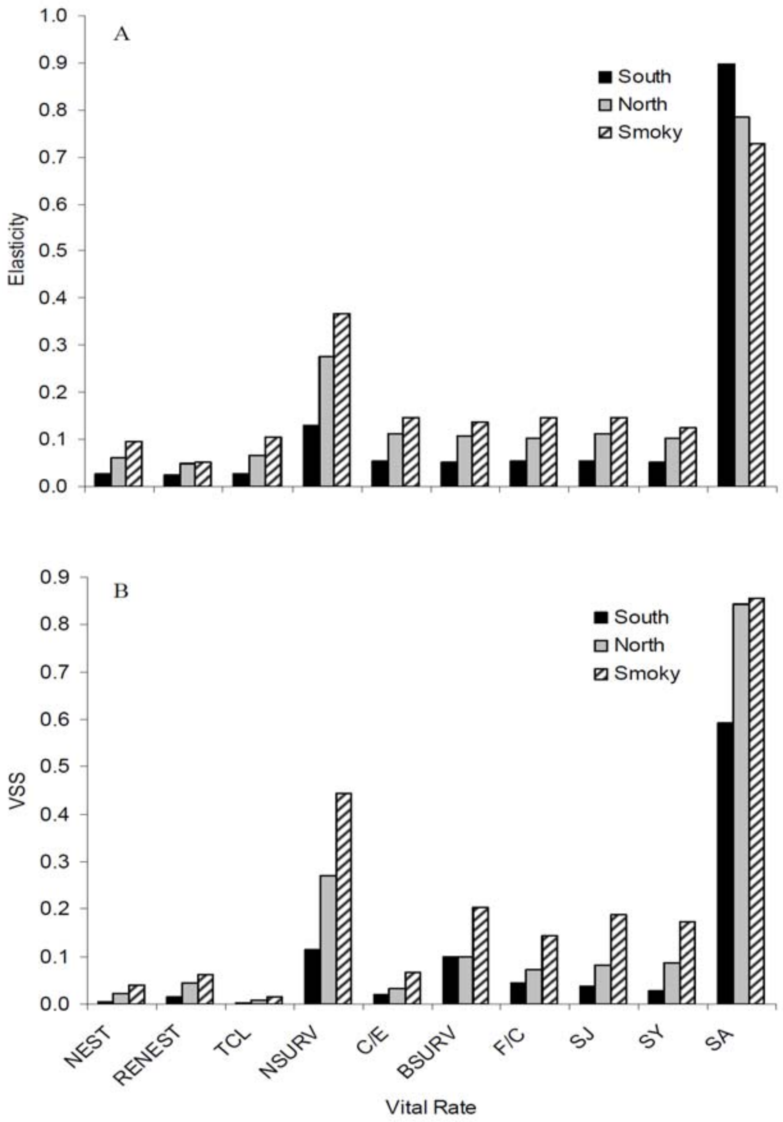

Figure 5.1. (A) Elasticities and (B) variance-scaled sensitivities (VSS) of demographic rates of three populations of greater prairie-chickens in Kansas, 2006-2009. Because management actions would influence stage-specific reproductive parameters similarly, elasticities and VSSs have been summed across female age classes and nesting attempts. NEST and RENEST = initiation rates of first and renests, TCL = clutch sizes, NSURV = nest survival probabilities, C/E = chicks hatched per eggs laid for successful nests, BSURV = brood survival probabilities, F/C = fledglings produced per chick hatched, SJ = 8-mo survival of juveniles to recruitment, SY and SA = annual survival probabilities for yearling and adult females, respectively.

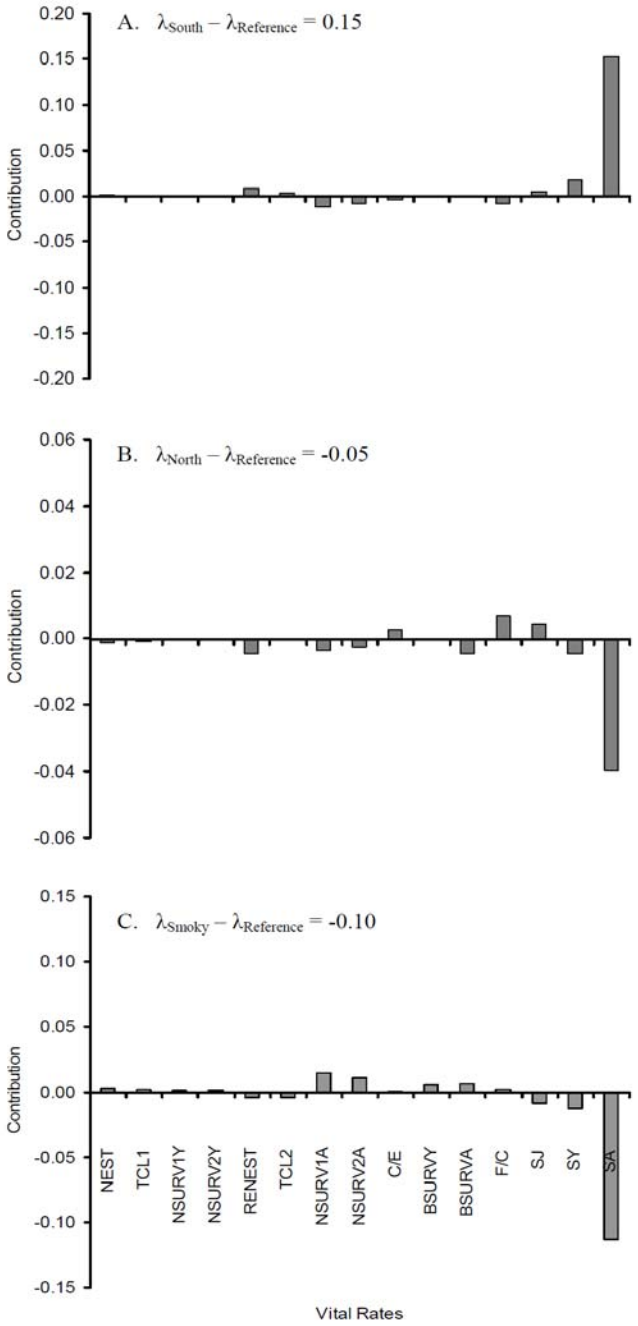

Figure 5.2. Contributions of each of the stage-specific vital rates to the differences between each population's growth rate and a mean reference population. NEST and RENEST = initiation rates of first and renests, TCL1,2 = clutch sizes for first and renests, NSURV1,2= nest survival probabilities of first and renests for yearlings (Y) and adults (A), C/E = chicks hatched per eggs laid for successful nests, BSURV = brood survival probabilities for broods raised by yearling (Y) and adults (A), F/C = fledglings produced per chick hatched, and SY and SA = annual survival probabilities for yearling and adult females, respectively.

CHAPTER 6 - CONCLUSIONS AND RECOMMENDATIONS

The greater prairie-chicken (*Tympanuchus cupido pinnatus*) is an obligate grassland bird and indicator species for tallgrass prairie ecosystems. Few species have suffered more severe loss and degradation of native habitat over the last 100 years, and populations are thought to be only 10-25% of their former size. Although most tallgrass ecosystems that were suitable for cultivation have already been lost, those that remain are still being degraded by invasive and exotic plants, intensive grazing by livestock, unnatural fire regimes, and energy development. One subspecies, the heath hen (*T. c. cupido*) is extinct and another, Attwater's prairie-chicken (*T. c. attwaterii*) is endangered, primarily due to habitat loss and degradation. Kansas contains the largest remaining tracts of native tallgrass prairie and is considered to be vital for the long-term viability of the species. Given the area's importance, it is critical to understand the demography and dynamics of the range-wide and regional populations for effective conservation and management to proceed. However, prior to this study, little information on the population demography and viability of greater prairie-chickens was available for greater prairie-chickens in Kansas.

My research provides the first comprehensive analysis of the complete demography of three populations of prairie-chickens occurring across the species' primary range in Kansas, and is the first to evaluate how regional variation in landscape composition and land use practices impact the demography and viability of prairie-chickens. My specific objectives were to 1) assess how variation in human land use and habitat alteration impacts the phenology and demography (e.g., fecundity, survival) of greater prairie-chickens, 2) use stochastic population models to evaluate variation in the rate of population change across a gradient of human landscape alteration, 3) evaluate how human manipulations of habitats have influenced the long term dynamics of greater prairie-chicken populations, 4) describe how human land management mediates selection for life-history traits, and 5) combine various quantitative methods to evaluate the efficacy of various conservation strategies in reducing or reversing population declines of greater prairie-chickens.

Results of this study indicate 1) populations of prairie-chickens in Kansas are not viable without immigration, 2) demographic rates and rates of population decline vary among areas under different land management practices, 3) human land-use patterns may impact the relative influences of vital rates on population trajectories, 4) anthropogenic effects on population demography may influence the regional life history strategies of a short-lived game bird, and 5) human-driven alterations to habitat conditions, landscape composition and patterning, and range management regimes influence nearly every aspect of greater prairie-chicken population ecology and dynamics. First, my collaborators and I found that variation in landscape composition and pattern and land use practices among three study sites impacted the reproductive phenology and demography of prairie-chickens. Females delayed initiation of first nests at the most southerly study site by more than a week due to a lack of suitable nesting cover early in the season as a result of range management practices that eliminated residual nesting cover (Chapter 2). Moreover, prairie-chicken vital rates were highly variable as a result of site differences in land management and habitat conditions (Chapters 4 and 5). Females breeding at a site heavily fragmented by row crop agriculture and roads had low annual survival probabilities (0.34–0.42), and higher survival of nests (0.16–0.31) and broods (0.34) than the other two study sites. In contrast, two populations which were breeding at sites with large tracts of contiguous heavily-grazed tallgrass prairie had higher annual survival (0.42–0.50 and 0.64–0.71), and lower survival of nests (0.08–0.18 and 0.04–0.12) and broods (0.27 and 0.29 for the North and South sites, respectively). Consistent with life-history theory predictions, the population in the fragmented area with higher adult mortality also had greater reproductive effort, and egg and clutch volumes were 5% and 9% larger than at the other study areas; suggesting that human-mediated changes in predator abundance not only impacts the demography of prey populations, but can also drive evolutionary change in the life-history strategies of lower trophic levels (Chapter 4). Overall, variation in the life history traits of prairie-chickens was most consistent with site differences in predation rates and mortality of adult females. The anthropogenic effects of road development and conversion of grasslands to cropland appear to facilitate increased predation on breeding females, whereas grazing and burning practices appear to determine reproductive success (Chapter 5).

Depressed fecundity at all sites ($\leq$ 0.22 female chicks produced per breeding female) resulted in significant projected annual population declines ranging from 26% at the contiguous and intensively-grazed South site to 51% at the fragmented and moderately-grazed Smoky site. Variation in predation likely due to human land use accounted for observed differences in rates of population decline among populations. Poor nest and brood survival led to population declines at the Flint Hills sites that were predominantly managed with annual burning and intensive early cattle grazing, whereas a combination of low survival of mature prairie-chickens coupled with low fecundity resulted in the greatest projected population declines at the highly-fragmented and moderately-grazed Smoky site. Projected rates of population declines were generally supported by long-term lek count data collected by the Kansas Department of Wildlife and Parks for the Flint Hills populations. However, annual lek surveys indicating a stationary population did not agree with the projected rates of population decline at the Smoky site; suggesting that immigration may be supporting our study population in the fragmented Smoky Hills.

Contrary to previous analyses of prairie grouse populations, results of two independent sensitivity analyses showed that the finite rates of change for all populations were most influenced by changes in adult survival (Wisdom and Mills 1997, Hagen et al. 2009, Chapter 5). Changes in nest and chick survival had relatively little influence on changes in asymptotic λ for populations suffering high rates of reproductive failure. Under the standard interpretation, high elasticity values for adult survival would suggest that management actions directed at improving adult survival would be most effective at mitigating population declines for all populations. However, the results of sensitivity analyses may not be biologically meaningful because adult survival at the South site is near a biological maximum, and increases of depressed fecundity parameters like nest and brood survival are more realistic. Although the finite rates of population change were most sensitive to adult survival at all populations, λ appeared to be less sensitive to adult survival and more sensitive to fecundity parameters at the Smoky site than the two Flint Hill sites; suggesting that human land use patterns impact not only vital rates themselves but may impact the relative influences of vital rates on population dynamics. Limitations of elasticity analyses notwithstanding (Chapter 5), future research should address how covariation in vital rates impacts the priority rankings derived from common sensitivity analyses as managing habitats for increases of a single vital rate will most likely impact other non-target vital rates. For example, managing for increases in nesting cover to improve nest survival will likely impact the survival rates of broods or the nesting female (Hagen et al. 2009). Therefore, sensitivity analyses would be more realistic in evaluating the future responses of populations to management actions by incorporating relationships among vital rates as well as their joint response to actual management actions.

The results of this study provide circumstantial evidence that a shift in rangeland management of grasslands from irregular burning and traditional grazing to annual burning and intensive early stocking limits the reproductive success of prairie-chickens and is the likely cause for the observed populations declines since wide-spread implementation some 30 years ago (Robbins et al. 1998, Nooker 2007). Nest and brood survival were significantly lower at our annually burned and intensively-grazed sites in the Flint Hills than in the irregularly burned and moderately-grazed grasslands of the Smoky Hills. However, this interpretation would be better informed by experimental evidence from multiple sites under different combinations of burning and grazing. Rotational grassland management regimes such as patch-burn grazing may provide adequate nesting and brood rearing habitat to increase fecundity (Fuhlendorf et al. 2006, Rensink 2009), and future research should address the potential of patch-burn grazing for mitigating declines of prairie-chickens in the Flint Hills.

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APPENDIX A - ESTIMATING THE STAGE OF INCUBATION FOR NESTS OF GREATER PRAIRIE-CHICKENS USING EGG FLOTATION

Researchers often require accurate estimates of incubation stage for back-calculating the timing of nest initiation or predicting the date of hatching to capture young, to determine the durations of egg-laying, incubation and the construction of breeding phenologies, and to calculate nest productivity. Estimates of nest age are also critical for assessment of the influence of temporal variation in nest survival, and to model daily nest survival as a function of individual- or time-specific covariates (Dinsmore et al. 2002). For example, the timing of nest losses is often related to nest success and the probability of renesting (Schroeder 1997, Pitman et al. 2006, Chapter 2). Egg flotation is one of the most common methods employed for estimating stage of embryo development with egg flotation-development relationships documented for many species of birds (Hays and LeCroy 1971, Dunn et al. 1979, Fisher and Sengel 1991, Custer et al. 1992, Brua and Machin 2000, Liebezeit et al. 2007). To our knowledge, there are no published techniques to estimate stage of incubation for nests of grouse. Field biologists estimating stage of incubation for eggs of grouse nests have often used a modified version of an egg flotation technique developed for captive ring-neck pheasants (*Phasianus colchicus*) and gray partridges (*Perdix perdix*; Westerskov 1950; Martin and Cooke 1987). It is unknown whether egg flotation can be used to accurately assess age of grouse nests under field conditions. As part of a larger study on the breeding ecology of greater prairie-chickens (*Tympanuchus cupido;* hereafter 'prairie-chickens'), we developed a regression model to accurately predict the stage of incubation for nests from egg flotation angles and egg buoyancy.

Methods

Prairie-chickens were captured with walk-in traps and drop-nets at leks during March–May of 2006–2008 at three study sites in eastern Kansas, USA (Schroeder and Braun 1991, Silvy et al. 1990). Females were fitted with radio transmitters and located via triangulation ≥ 4 times/week during the nesting period (April–July), and daily once it was determined from movement patterns that a female was nesting. Once a female had localized in an area for 3 successive days, we located and flushed the bird so that the eggs could be counted and the nest location recorded with a GPS unit. Females with nests were monitored daily from a distance of ≥100 m. Nest sites were revisited during incubation to assess clutch size and incubation stage.

To evaluate the relationship between egg buoyancy and stage of incubation, we restricted our analysis to nests of known age. Known-age nests included nests discovered during egg-laying and nests that successfully hatched. We collected the clutch from the nestbowl and retreated to a distance of >100 m to float the eggs in a small, clear container of lukewarm water (Fig. A.1). If an egg touched the bottom of the container, the angle between the bottom of the container and the center axis of the egg was measured. If the eggs floated freely in the water, the distance between the top of the egg and the surface of the water was measured. We used linear regression to evaluate the relationship between float angle and the age of the clutch in days (after Liebezeit et al. 2007). We converted egg angles to proportions (*P* = angle/90°) before transforming them to the logit scale. Values of 0 and 1 cannot be logit transformed, and we set angles of 0° and 90° to 1° and 89°, respectively, before transformation. Proportional angles were transformed to logits by:

Error! Bookmark not defined.Error! Bookmark not defined.logit $P = \ln [P / 1\text{-}P]$.

We then used linear regression to assess the relationship between the logit-transformed proportional float angles and days of incubation. For nests where eggs floated above the bottom of the cup, linear regression was used to predict the day of incubation from float height; measured as the distance between the surface of the water and the top of the egg (in mm). The predictive ability of regression equations was assessed by subtracting the nest age in days of incubation from the predicted age for each nest on a given day. The absolute mean deviation ± SE was used as the statistic of model error. Deviations were plotted against embryo age to illustrate model precision. Finally, interspecific error was compared between float curves developed for prairie-chickens and curves developed for ringed-neck pheasants by Westerskov (1950). All statistical analyses were conducted using Program SAS (ver. 9.1, SAS Institute Inc., Cary, NC).

Results

We collected float data from 68 clutches of known age. Mean float angle was estimated for eggs of 62 clutches found early in incubation. Average float height between the top of the egg and the water surface was measured for six clutches where eggs were floated above the cup bottom. Logit-transformed egg angle was a significant predictor of embryo age in early incubation (< 14-d old; $r^2 = 0.56$, $P < 0.001$; Fig. A.2):

$$Day\ of\ Incubation = 3.25 + 1.19\ (logit\ P).$$

The mean deviation (± SE) between actual embryo age and predicted embryo age was 0 ± 0.24 days and the 90th percentile of the predicted error for the early-mid incubation period was <9% (± 2 days). Model error was greater for clutches floated during mid-incubation (10-14 days) and was ± 4 days from predicted values. For clutches floated late in incubation (>14 d), linear regression analysis revealed a significant relationship between egg buoyancy and stage of incubation ($r^2 = 0.86$, $P = 0.007$; Fig. A.2):

$$Day\ of\ Incubation = 12.0 + 0.73\ (Float\ Height)$$

Mean deviation of model predictions for the late incubation period was ± 1 day.

Discussion

Egg floatation was an accurate indicator of stage of incubation for prairie-chicken clutches and had good levels of predictive power. Using data on egg angle and egg buoyancy and regression techniques described by Liebezeit et al. (2007), we found that 90% of prairie-chicken nests could be aged to ±1-2 days if the clutch was floated early or late in incubation (<10 or >14 d). Error was greater (± 4 d) for clutches floated during mid-incubation (10-14 d), due to greater variability in egg buoyancy in a smaller sample of clutches. This study is the first evaluation of egg floatation as a means to estimate the stage of nest incubation for prairie grouse, and extends float curves developed for other species of upland gamebirds (Westerskov 1950). Use of float curves developed for pheasants and partridge consistently overestimated the age of clutches of greater prairie-chickens by an average of ~2 days and the magnitude of the error increased with stage of incubation. We expect that our float curves should provide improved estimates of incubation stage for the nests of other grouse. However, grouse biologists would be prudent to calibrate these float curves by collecting egg flotation data from their own known-age nests to account for potential interspecific variation the effects of egg size on buoyancy and rates of embryonic development.

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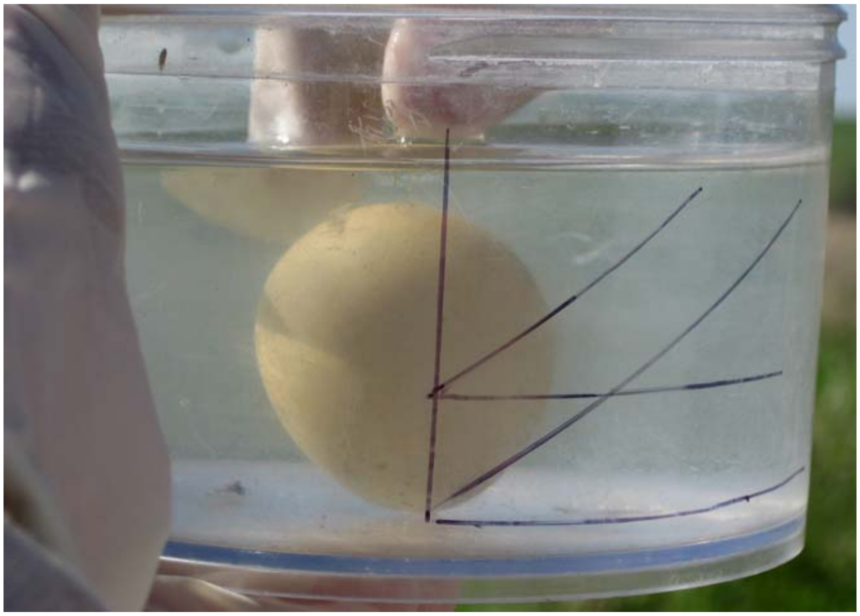

Figure A.1. Estimating the float angle or height of a prairie-chicken egg. The egg is floating at ~90 degrees and is not yet buoyant.

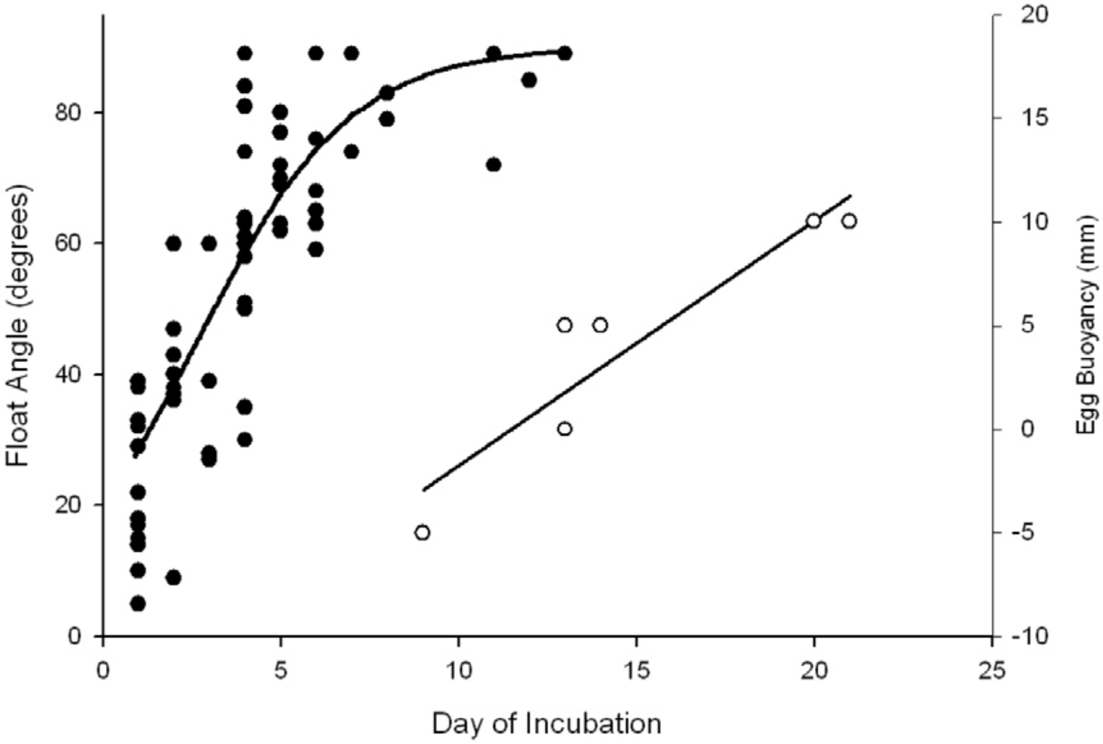

Figure A.2. Egg angle (filled circles) and egg buoyancy (open circles) for prairie-chicken nests of known age that were floated during incubation. Egg buoyancy refers to distance for the top of the egg to the surface of the water (in mm).