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DECLINE OF A KANSAS FLINT HILLS GREATER PRAIRIE-CHICKEN POPULATION OVER 25 YEARS

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ABSTRACT

The Greater Prairie-Chicken (*Tympanuchus cupido*) is an iconic grassland species found predominantly in tallgrass and mixed-grass prairie. The species has declined dramatically across its range over the past century, and is now largely limited to the central and northern Great Plains of the United States. To assess its conservation status in an area once supporting a robust population, we resurveyed a 500 km^2 area of mostly tallgrass prairie in the Kansas Flint Hills in the springs of 2022 and 2023 after an interval of 25 years. In 1997, the area supported 31 leks, with up to 30 individuals present at a lek. During the 2022 surveys, we found lekking activity at 9 sites, whereas in 2023 activity was noted at only 5 sites; the maximum number of birds present at a lek in 2022/2023 was 12. Our quarter-century change assessment thus revealed at least a 70% reduction in lek numbers across the study area, as well as a considerable reduction in maximum lek size. We analyze and discuss landscape features that are associated nonrandomly with lek losses, including woody plant encroachment and frequent spring pasture burning, and reflect on prospects for the future of this species.

INTRODUCTION

Like most North American grassland birds (Rosenberg et al. 2019), the Greater Prairie-Chicken (*Tympanuchus cupido*) has suffered major declines over the last century (Johnsgard 1973, Johnson et al. 2020, McNew et al. 2023). In the 1880s, the species was thought to have numbered in the tens of millions, with a geographic distribution extending from the Great Plains to the eastern seaboard (Johnsgard 1973). However,

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even by the final decade of the 1800s, the species had declined across much of its range, including in Kansas; early naturalist Nathaniel Goss noted as early as 1891 that the species was declining rapidly (see summary in Horak 1984). By the 1950s, much of the eastern portion of the species' geographic distribution had been lost, and the stronghold of its populations in Kansas was considered to be the Flint Hills, associated with the last intact major segments of tallgrass prairie (Baker 1953, Svedarsky et al. 2003).

Factors contributing to this decline in the Flint Hills include habitat loss and fragmentation, woody plant encroachment, invasive species, loss of native plant diversity from indiscriminate use of herbicides, and the practice of annual spring burning of the same acres in key habitat (often combined with high-intensity cattle stocking for the first half of the growing season) (Horak 1984, Robbins et al. 2002). These factors continue to suppress Greater Prairie-Chicken populations in the Flint Hills, with a decline estimated to be as high as 75% (Svedarsky et al. 2000, Robbins et al. 2002, Pitman et al. 2012, Johnson et al. 2020, Gehrt et al. 2022).

This paper focuses on Greater Prairie-Chicken population status within a segment of its Flint Hills range in east-central Kansas, in Greenwood County, to test relative population stability over the last 25 years. We take advantage of an unpublished 1997 data set by co-author, Obermeyer, to offer a picture of a quarter-century of change in prairie-chicken populations. We emphasize that this study covers a part of a prairie region that was long considered as the stronghold of the species' distribution and abundance in the state (Baker 1953). As such, trends and changes from our study may have important implications for the overall conservation status of the species, and particularly in Kansas and neighboring states.

METHODS

Field work in 2022 and 2023 aimed to replicate the 1997 survey methodology as closely as possible via direct consultation regarding methodology. The study area, definitions, and methods described below match what Obermeyer did in 1997, and our recent surveys followed them as closely as possible. Approximately 64% of the study area consists of intact, native tallgrass prairie, and another 30% consists of prairie fragments, based on interpretation of Landsat Thematic Mapper (TM) satellite imagery (The Nature Conservancy Osage Plains/Flint Hills Prairie Ecoregional Planning Team 2000). All of this area is in private ownership, with varied land management practices, ranging from annual burning of grasslands to areas where woody plants have been allowed to encroach, owing in part to lower burning frequency.

Of necessity in a study across such a broad geographic area, we focused on distributions of prairie-chicken leks rather than nests or individuals, during spring surveys. We defined Greater Prairie-Chicken leks as assemblages of at least two males for the purpose of display and mating. We assessed the spatial distribution of leks across a study area of ~500 km^2 of native rangeland in eastern Greenwood County, Kansas (Figure 1). Leks are traditional display sites of long duration and relative

stability; they are often located on hilltops (Gregory et al. 2011). Although males are counted much more easily than females (McNew et al. 2011), and leks may shift, appear, disappear, split, or fuse within and between years (Hovick et al. 2015a), their high visibility offers a convenient and reliable index to population size.

To detect, locate, and characterize lek distributions across the study area, in 1997 and in 2022-2023, we drove and listened along every road and dirt track in the study area (see details below; Figure 1). The survey protocol enabled us to be within 1200 m

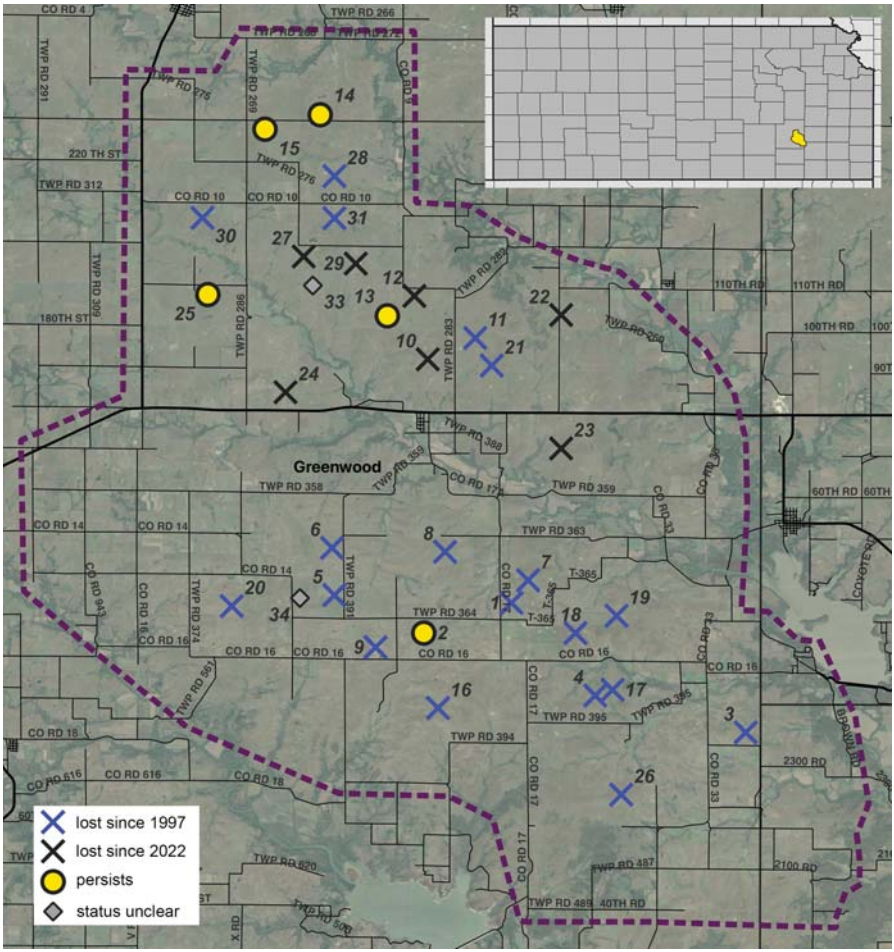

Figure 1. Greater Prairie-Chicken lek status across the study area in eastern Greenwood County, Kansas. Shown are the 31 leks detected in the 1997 surveys, which either have persisted (yellow circles), or have been lost since the original surveys (X's). Blue X's indicate leks lost since the 1990's; the Black X's indicate leks apparently lost between 2022 and 2023. Also shown are two sites where birds were detected in 2022, but were not clearly documented as constituting a lek and were not present in 2023, such that they are considered to be of unclear status. The inset map shows the position of the study area (in yellow) in the state of Kansas. Background imagery: from Google Earth.

of almost all points within the study area. All routes were run at least once in each of 2022 and 2023 under ideal weather conditions; many lek sites were visited multiple times. To detect prairie-chickens booming on leks, morning listening surveys were conducted between 30 minutes before sunrise and 120 minutes after sunrise at ~1 km intervals along all available roads and tracks in the study area. Surveys were conducted only on low-wind mornings (wind speed <15 km/hr) between 20 March and 6 April in 2022 and 2023. Although listening stops were spaced at regular, 1 km intervals, on occasion, we adjusted the position of stops by a few tens of meters to take advantage of ideal points for listening, such as hilltops. Via this protocol of repeated site surveys, we are confident that we detected most, if not all, active leks.

A second field phase in this study was an assessment of each lek site to pinpoint lek locations and count numbers of birds present at each lek, which was accomplished concurrently with the first phase, as leks were detected, though these follow-up visits were always on separate mornings from initial detections. In 1997 and in 2022-2023, we walked to each site where we detected display activity to locate precisely each lek and to flush and count birds. In 2022-2023, we also walked to each of the 1997 lek sites (i.e., including those with no recent activity) to confirm their status. These second visits were done on windless mornings, again from one-half hour before sunrise to two hours after sunrise, and in all cases with landowner permission. Numbers of birds flushed from each lek and GPS locations of leks were recorded. Because the focus of this study was to document the presence and spatial distribution of leks rather than variation in lek size, we visited leks only often and long enough to be certain of their use, to minimize negative impacts of our survey activities. In infrequent cases in which survey results were inconclusive, or enigmatic, such as a lek disappearing or birds heard booming in a place not known to hold a lek, we visited the site on multiple mornings (up to five times) to clarify and corroborate the initial observation.

To compare survey results between the two time periods, we used univariate randomization approaches based on recently published methods (Cobos and Peterson 2022). Multivariate approaches were not used in view of the relatively small overall sample size (N = 31 leks). We characterized each of the 31 leks detected in the 1997 study with regard to six factors: (1) maximum number of birds at the lek in 1997, (2) distance to the nearest woodland, (3) distance to the nearest road (note: no significant changes occurred in roads over the 25-year time span), and (4) distance to the nearest house. At some point in time between the two survey periods, a single residence was built near lek #24. No major development of wind farms, transmission lines, or oil and gas drilling has occurred since the 1997 survey. The 1997 population at each lek was derived from the original data tables (Obermeyer, unpubl. data); the three distance measures were derived from measurements applied to Google Earth imagery accessed in May 2023.

The fifth dimension used to characterize leks was the relative topographic elevation (RE) of each lek, which is known to be important in driving lek location (Gregory et al. 2011). RE was measured using the finest-resolution digital elevation model (DEM) available with acceptable error levels: the GMTED 2010 data product, with a spatial resolution of about 30 m. We related elevation from the DEM at the

center-most pixel of the lek (x_i) to the average elevation of the 7 x 7 pixels surrounding the focal pixel ($\bar{x}$), calculating percent elevation as $RE = 100(x_i - \bar{x})/\bar{x}$. With this index, a high value indicates an elevated hilltop with respect to the surrounding ~105 m (3.5 pixels) of topography. Last, we calculated burn frequency over 2015-2022, based on spring burn maps derived from MODIS satellite data through 1 May of each year using a methodology tested in the Flint Hills region (Scholtz et al. 2020). The burn summaries were kindly provided by Jayson Prentice (Kansas Department Health and Environment; Figure 2).

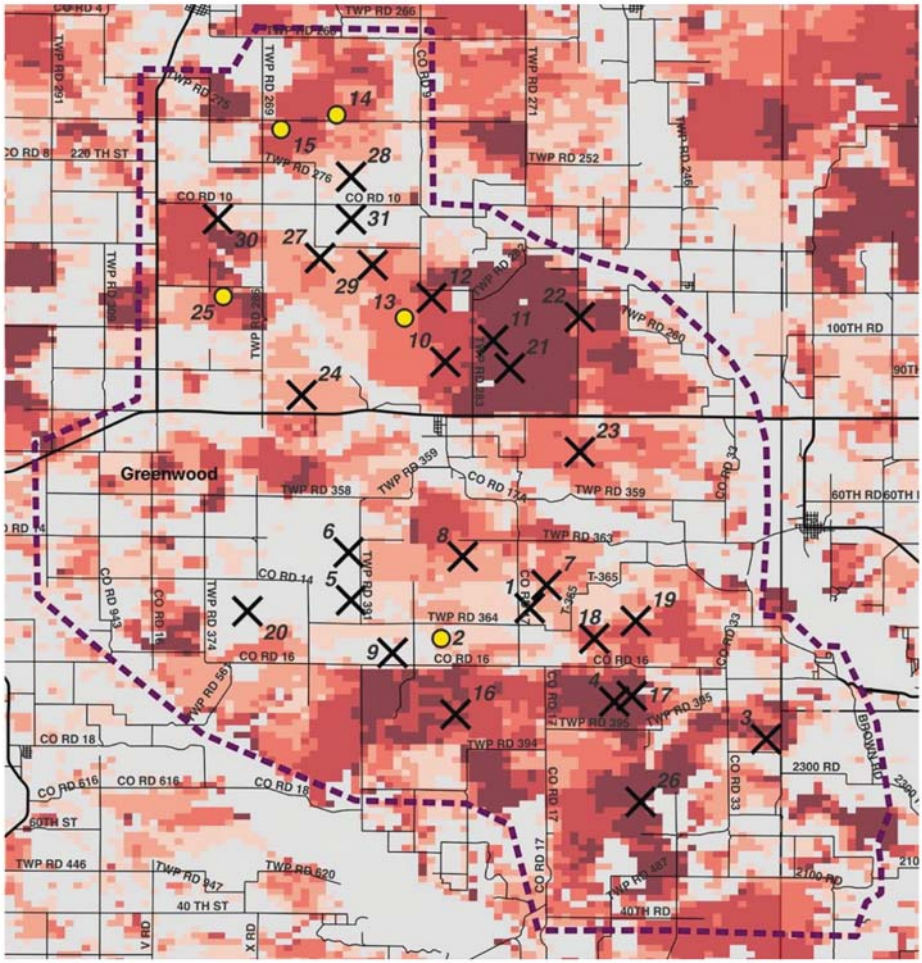

Figure 2. Spatial distribution of leks meeting different fates (X = lost, yellow circle = persists) between 1997 and the present, in relation to frequency of spring burning. Burn frequency is shown as 0 = no burning, and 4 successive shades of red representing 1, 2, … 5 out of 5 years burned in 2018-2022.

As fewer than one-third of the 31 leks persisted over this time interval (see Results), we assessed statistical significance of the driver variables described above by resampling 100 sets of 5 or 9 leks at random from among the 31, and characterized

each of those replicate samples as the average value of each of the six characteristics listed above. We then compared the observed average value of each of the characteristics to the null distribution, and counted as statistically significant those cases in which the observed value fell in the extreme 5% of the null distribution (Cobos and Peterson 2022). We used one-tailed tests based on the hypotheses that leks would persist if they were (1) larger in 1997 in terms of maximum number of individuals; (2) relatively far from woodlands, roads, or houses; (3) with higher RE values, and (4) higher burn frequency (i.e., less subject to woody plant encroachment). We also tested (5) for a possible tendency for leks to persist at intermediate burn frequencies, by comparing observed variance in burn frequency with null expectations for variance in burn frequency. All probability values were calculated as direct counts out of 100 resampled values.

To assess the presence of Henslow's Sparrow (*Centronyx henslowii*) in the study area—an indicator of quality grassland bird nesting habitat (Herse et al. 2017, Stumpf and Muise 2023)—Robbins conducted early summer road transect surveys in grassland habitat across 21 km in the southern half of the study area on 18 June 2023, and 24 km in the northern half of the study area on 19 June 2023.

RESULTS

In 1997, 31 leks were located across the study area, with a maximum of 30 individuals present at one lek. In 2022, only 9 of the original 31 lek sites remained active; no activity was observed at any other site in the study area, except as noted below. In 2023, only 5 of the 9 leks active in 2022 remained active, and no additional leks were found (Figure 1). The maximum number of individuals at any individual lek in the 2022-2023 surveys was 12. All of the 2022-2023 leks were close to or identical to sites that had been identified in 1997 surveys, and no new leks were detected in 2022-2023 (Figure 1). In 2022, single birds were reported at two sites by observers not associated with our survey teams; both sites were checked on multiple occasions in 2023, but with no further detections (these sites are shown as "status unclear" in Figure 1). Repeated visits to the leks that were active in 2022 but not in 2023 on multiple occasions in 2023 confirmed that they were not active in 2023; future surveys are planned for these sites, to evaluate whether these year-to-year reductions represent long-term losses (see note in Discussion).

Our analyses included six potential landscape drivers of lek losses: 1997 lek size, distance to woodland, distance to road, distance to house, topographic position, and burn frequency (Figure 2). Of these drivers, considering the reduction of number of leks from 31 to 9 between 1997 and 2022, our randomization tests detected significant relationships for only two (Figure 3): leks with smaller initial (1997) population sizes were more likely to be lost ($P < 0.01$), as were leks closer to forest or woodland ($P = 0.02$). The same results were obtained when we considered the reduction in number of leks from 31 to 5 between 1997 and 2023, with only initial lek size and distance to forest being significant ($P < 0.05$). The other potential drivers were not statistically significant ($P > 0.05$): i.e., persistence versus loss of leks was not distributed nonrandomly with respect to proximity to roads, proximity to houses, relative

elevation, or average burn frequency. Further exploration of burn frequency, via a variance measure instead of an average, was complicated; that is, there were no apparent patterns for leks found in 2022 ($P > 0.13$), but leks found in 2023 appeared to be concentrated in areas of intermediate burn frequencies, though the randomization tests were not statistically significant ($P > 0.09$; Figures 2 and 3).

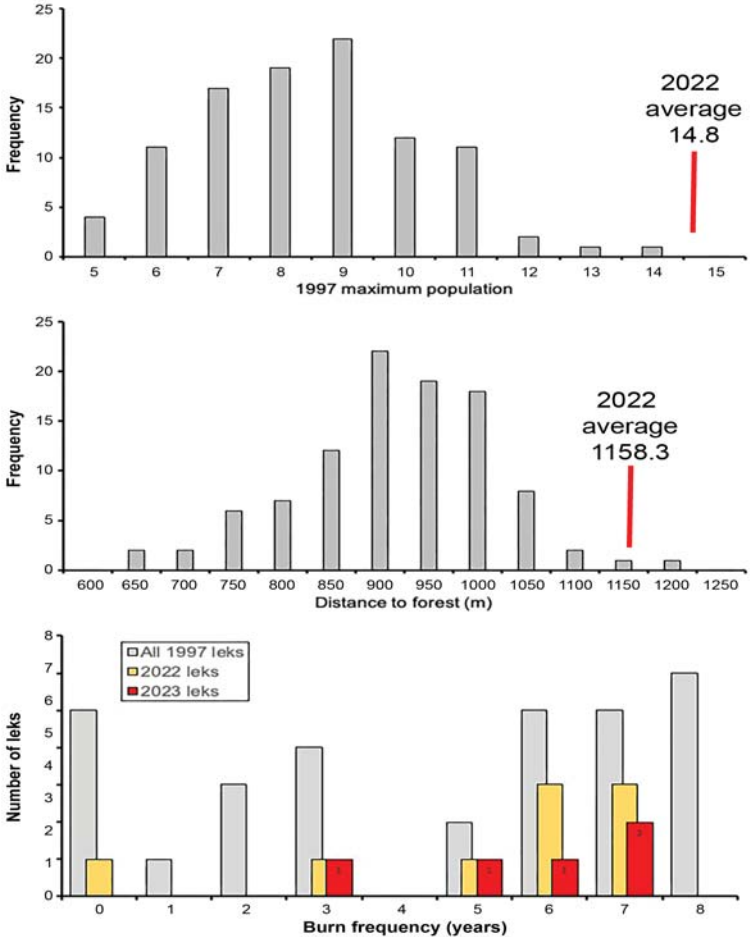

Figure 3. Randomization tests used to assess the nonrandom nature of associations between lek persistence from 1997 to 2022 and (top panel) 1997 maximum number of birds present, and (middle panel) distance to the nearest forest or woodland in 2022. The red lines show the observed values of the averages of each characteristic across the nine leks that persisted until 2022, whereas the frequency histograms (gray bars) show distance values resulting from 100 random resamplings of nine leks (i.e., the number of leks that persisted) from among the 31 leks present in 1997. Statistical significance is established if the observed value falls in the extreme 5% of the null distribution. The bottom panel shows the distribution of leks with respect to burn frequency during 2015-2022: the full original set of 31 leks is as gray bars, the subset of leks that survived until 2022 is in yellow bars, and the subset of leks active in 2023 is in red bars.

DISCUSSION

Eastern Greenwood County Population Decline

The tallgrass prairie in Greenwood County, Kansas, covers >2500 km^2, and represents ~85% of the county's landcover (Mohler and Goodin 2012). The 1997 surveys focused on a ~500 km^2 area mostly covered by tallgrass prairie pastureland in the eastern part of the county, which supported a significant population of Greater Prairie-Chickens at that time. Although numbers of active leks do not translate directly into population estimates (Horak 1984), the scale and pervasive nature of the decline of prairie-chicken populations in the region are clear from our repeat surveys. Of the 31 leks present in 1997, 22 had disappeared by 2022, and 26 may have disappeared by 2023; that is, the great majority of the leks in the study area disappeared over the 25-year time span between the two studies, while no new leks were detected.

We emphasize that our initial broad, road-based surveys were designed to detect leks across almost all of the study area, yet we only found leks at or very near to sites that held leks in 1997; simply put, we found no evidence of establishment of any new leks over the period between our historical and recent surveys. Among our recent surveys, we visited 5 leks on multiple days in 2022; in 2023, we visited another 5 leks on multiple days. In only one of these cases were birds present on one visit and not on another. Thus, the repeatability of our detections of prairie-chickens within years was quite high, such that we have no evidence that non-detection could be playing a role in creating false patterns of lek persistence or loss between the different survey efforts. Of special interest and relevance were the four leks that had birds in 2022 but not in 2023, with 2023 absence confirmed via multiple visits to three of them (leks visited 4, 4, 2, and 1 times); on no occasion in 2023 did we detect birds at those leks. In one case, a 2022 lek had possibly merged with a nearby lek; in the remaining cases, however, the birds present in 2022 were simply not there in 2023. Whether these changes over one year represent real population losses, merging of adjacent leks, or simply lack of activity during a drought year remains unclear. [Note added in proof: a visit on 11 April 2025 confirmed presence at the four leks visited that were active in both 2022 and 2023, and confirmed absence at all four of the leks with activity in 2022 but not in 2023; interestingly, however, one lek documented in 1997, but not in either of 2022 or 2023, appeared to be active again.] A clearer understanding of these dynamics and trends will have to await future assessments by us.

Drivers of Greater Prairie-Chicken Loss

This study was preceded by a more detailed and controlled analysis of Greater Prairie-Chicken lek occupancy during 1981-2008 across a relatively small area of Konza Prairie Biological Station, also located in the Kansas Flint Hills tallgrass prairie (McNew et al. 2012). That study used the power of long-term datasets and purposeful habitat manipulations of the biological station to arrive at detailed interpretations: probability of colonization for an unoccupied site was associated negatively with proportional woodland cover of the site and grazing, but probability of local extirpation was affected by a statistically non-significant set of interactions between

grazing and average burn frequency. Although our study was unable to control and document grazing landscape variables like McNew et al. (2012), we examined a similar time span on a Kansas landscape located farther south. Another analysis, by Whetten et al. (2024), is intriguing in that it apparently used data from a broad region (i.e., across the state of Kansas), but details of methods are incomplete (e.g., no description of statistical methods), so we will have to await a more comprehensive presentation of this set of analyses.

Our results indicate that initial population size and proximity to wooded areas are important factors associated with loss of Greater Prairie-Chicken leks across our study site over the past quarter-century. The effect of initial population size is self-evident, as loss of even a few individuals from a lek may cross a critical threshold of including sufficient numbers of displaying males needed to attract females; this initial population size effect on Greater Prairie-Chicken lek persistence has been documented in previous studies (Winder et al. 2015). Whetten et al. (2024) analyzed Greater Prairie-Chicken lek survey data across Kansas for 1993-2023, and concluded that larger leks (i.e., relatively high interannual average attendance) had a higher probability of persisting. We suspect that the Allee Effect (Courchamp et al. 2008), in which smaller leks would experience elevated probabilities of loss, may be at play.

Woody plant encroachment is a near-ubiquitous process in tallgrass prairie (Engle et al. 2008, Peterson et al. 2024), including the Flint Hills landscape (Van Auken 2000, McKinley and Blair 2008, Van Auken 2009, Veach et al. 2014). Although large areas of open prairie remain in our study area, much of the Flint Hills region has experienced woody encroachment over the past century owing to fire suppression, tree plantings, and more recently, perhaps, the rise in atmospheric carbon dioxide that may accelerate woody plant adaptability in warm season grasslands (Ratajczak et al. 2016). Greater Prairie-Chickens appear to respond negatively to woody vegetation coverage (McNew et al. 2012), which is reflected in the results of this study: distance to forest was a significant factor associated with lek loss, matching patterns visible in the analyses of McNew et al. (2012) and Whetten et al. (2024; their Figure 2).

Extensive spring pasture burning homogenizes habitat structure and removes residual cover (thatch) at a crucial point in the life history of many grassland-obligate species, including prairie-chickens. Repeated annual spring burning has been identified previously as a factor likely driving Greater Prairie-Chicken population declines (Robbins et al. 2002, Hovick et al. 2015b, McNew et al. 2015, Winder et al. 2017, Winder et al. 2018). In this study, mapping spring-burned areas over an 8-year time period suggested that leks in areas with intermediate burn frequencies may be more likely to persist, although statistical tests were inconclusive. Mohler and Goodin (2012) documented, via analyses of remotely sensed (MODIS) data, extensive spring (1 March-10 May) burning in Greenwood County, including our study area, over an 11-year period (2000-2011). On average, 40% of the grassland in Greenwood County was burned each year during that period (Mohler and Goodin 2012). The Scholtz et al. (2020) burn summaries indicated a comparable average annual burn percentage of 39.2% in our study area (28.7% in 2018, 44.4% in 2019, 46.0% in 2020, 29.7% in 2021, 47.3% in 2022).

Burning across our study site and across much of the Flint Hills typically occurs when prairie-chickens are courting and laying eggs. The lack of an older herbaceous layer reduces ideal nesting habitat for females and brood habitat for chicks (Johnson et al. 2020). It also negatively affects other grassland obligate bird species, particularly Henslow's Sparrows (Busby and Zimmerman 2001). Henslow's Sparrows breed only in tallgrass prairie that has not been burned for at least one year, and typically two to three years prior to the April-August breeding season (Powell 2008). Because nesting Henslow's Sparrows are so closely associated with accumulated residual vegetation (thatch), this species can serve as a biomonitor for suitable Greater Prairie-Chicken nesting habitat (Herse et al. 2017, Stumpf and Muise 2023). As an indication of the limited nature of nesting habitat availability in the study area, and underscoring the extent of burning in the study area, only two singing male Henslow's Sparrows were detected in our 2022-2023 surveys.

A further factor that may play an important role in driving Greater Prairie-Chicken population declines is broadcast spraying of herbicides. Chemical treatments have been used in the study area to control woody vegetation and sericea lespedeza (*Lespedeza cuneata*), a problematic invasive plant species in tallgrass prairie. Indiscriminate broadcast spraying of broadleaf herbicides can simplify native plant communities dramatically (Sherrill et al. 2022). We noted that prairie plant communities across our study area appeared mostly devoid of broad-leaved plants, likely reflecting a combination of such spraying activities and annual spring burning. However, we were unable to obtain any data on the frequency or spatial distribution of such spraying across the study area, so we are able only to speculate on its effects on prairie-chickens.

Perspectives on Rangewide Decline

The continued range contraction of Greater Prairie-Chicken populations (Svedarsky et al. 2000) has resulted in the species being listed as Near Threatened on the IUCN Red List of Threatened Species (IUCN 2020). Indeed, the past three decades have witnessed the disappearance of the species from multiple localities in west-central Missouri (Robbins 2020) and eastern Kansas (persp. observ.). This study focused on a significant block of tallgrass prairie habitat within the largest remaining area of tallgrass prairie in North America, the Flint Hills (The Nature Conservancy Osage Plains/Flint Hills Prairie Ecoregional Planning Team 2000). We documented a large-scale decline of the population across that region over the last 25 years.

The idea that range-edge populations may be lost quickly, causing rapid and dramatic retractions in the extent of occupancy by a species, is well known, and is expected in the face of environmental changes that negatively affect populations of the species (Channell and Lomolino 2000). The first Greater Prairie-Chicken populations to be lost were located on the eastern fringe of the species' range (Johnsgard 1973), including the now-extinct Heath Hen (*T. c. cupido*), and populations continue to be lost or to decline along all margins of the species' geographic range (Minish 1990, Westemeier et al. 1998, Bellinger et al. 2003). This study is unique in that it covers a 25-year time span with repeated methodology in a location that—at

least historically—was considered a robust population center for prairie-chickens. As documented above, our results indicate a precipitous species decline across the study area.

Woody plant encroachment, combined with unfavorable nesting habitat as a result of high burn frequency and intensive grazing over core areas of the Flint Hills, has likely had negative impacts on Greater Prairie-Chickens (Robbins et al. 2002, McNew et al. 2012), as well as other grassland biota (Coppedge et al. 2001, Grant et al. 2004, Powell 2008, Fuhlendorf et al. 2017). This study adds further documentation of these negative effects on Greater Prairie-Chicken populations over a relatively broad spatial scale; we are in the process of replicating this analysis in other repeat-survey opportunities on Kansas prairies. The combined effects of a scarcity of nesting habitat in core areas of the species' range along with encroachment of woody plants portends a worrisome future for Greater Prairie-Chickens.

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