LEKKING AND NESTING RESPONSE OF THE GREATER PRAIRIE-CHICKEN TO BURNING OF TALLGRASS PRAIRIE

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ABSTRACT

In the southern Great Plains, the greater prairie-chicken (*Tympanuchus cupido*) is confined to tallgrass prairie, a habitat now largely converted to agriculture. Remaining prairie is highly fragmented and subjected to land management practices that greatly alter the ecosystem of this species. Chief among these practices are deliberate, large-scale spring burns associated with early intensive stocking of cattle. We used extensive data to infer how such fires affect the prairie-chicken's lekking and nesting behavior. From 1998 to 2000, 60–79.4% of our study area—a 45,000-ha expanse of tallgrass prairie in north-central Oklahoma—was burned in spring. Prairie-chickens tended to lek on unburned areas but not in a pattern that differed from random habitat choice. Leks on burns tended to be <200 m from unburned prairie. Females strongly avoided nesting in areas burned in spring 1998 and 1999 ($n > 25$ nests/y). Nesting effort was poor in 2000, prohibiting statistical analysis, but 5 of 8 nests were on unburned prairie. Incorporating data from 1997 ($n = 12$ nests), only 14 of 74 nests were placed on burned prairie, and only 5 of the 64 nests from 1998 to 2000 were located on prairie burned all three of those years. Avoidance of burns was particularly strong before June. Despite strong avoidance, nest success did not differ between burned or unburned prairie. Our findings raise two concerns: 1) if leks are established only <200 m from unburned prairie, then an increase in the proportion of burns may inhibit lek formation, and, more important, 2) if females avoid nesting on recent burns, then an increase in the proportion of burns may cause a female to concentrate nesting effort on small patches (or forego nesting). We recommend moderation of spring burning (e.g., patch burning) of tallgrass prairie, lest the greater prairie-chicken be driven further from its already piecemeal habitat.

keywords: greater prairie-chicken, leks, nest placement, Oklahoma, spring burns, tallgrass prairie, *Tympanuchus cupido.*

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INTRODUCTION

Only about 4% of the original extent of tallgrass prairie remains (Samson and Knopf 1996). Birds and other organisms dependent on this habitat have declined concomitantly, and many species have become of high conservation concern. Emblematic of this habitat is the greater prairie-chicken (*Tympanuchus cupido*), a species whose fate has followed the prairie's fate. Even where tallgrass prairie remains—where it has not succumbed to the plow—it is impacted by land management, particularly those practices associated with cattle ranching (Robbins et al. 2002). Chief among these management tools is prescribed fire.

Fire is an integral component of the prairie ecosystem (Collins and Wallace 1990), with natural fires occurring in tallgrass prairie once or twice per decade (Reichman 1987). Currently, most natural fires are suppressed, yet prescribed fires are used to produce more forage for cattle, particularly as a means of implementing early intensive stocking (Smith and Owensby 1978). Spring burning generates greater plant growth (Hadley and Kieckhefer 1963, Hulbert 1988), in part by removing rank vegetation that limits productivity (Knapp and Seastedt 1986), but may offer cover for organisms inhabiting the grassland. Relative to unburned areas, recently burned areas often harbor significantly greater abundance or biomass of herbivorous arthropods, particularly grasshoppers (Orthoptera: Acrididae) (Warren et al. 1987, Evans 1988, Swengel 2001, Shochat et al. 2005).

Wright (1974:8) asserted that the ''prairie chicken . . . [is] favored by fires which create variety in habitat,'' but whether this variety is beneficial to the species is an open question. Moreover, there may be tradeoffs associated with burning; for example, increases in arthropod biomass may benefit the greater prairie-chicken, but a loss of cover may hurt it, a similar tandem of benefit and cost described for the closely related lesser prairie-chicken (*T. pallidicinctus*; Boyd and Bidwell 2001). In addition to tradeoffs, different sexes or life stages may respond differently to burned habitat.

Using extensive lek and nest data from a 4-y study of habitat use and reproductive ecology of the greater prairie-chicken, we determined whether this species responds positively, negatively, or not at all to burning of the tallgrass prairie in spring. Although availability

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of lek habitat is rarely limiting, it is possible that males avoid establishing leks on recent burns; thus, we determined if lek placement (and lek size) was associated with burning. Likewise, nesting females may avoid burns, so we examined whether nest placement was associated with burning. We further examined how nest success, clutch size, brood size, and brood placement associated with burns.

STUDY AREA

The study area encompassed approximately 45,000 ha of tallgrass prairie in north-central Osage County, Oklahoma, its northern edge abutting Kansas (lat 36°46′–37°00′N, long 96°22′–96°40′W). The area was in a southern extremity of the Flint Hills geological system, which extends through central Kansas southward from near the Nebraska border. The Flint Hills comprise largely unplowed (soils are underlaid with rock) tallgrass prairie, though much of this region is grazed heavily and burned annually (Zimmerman 1997, Robbins et al. 2002). Habitat in our study area was relatively homogenous prairie, with no cultivation, no significant development, and few fences. The few roads were primarily graded dirt or gravel without shoulders. Deciduous woodland (<5% of the area) occurred only in a small portion of the southeastern corner of the area and in narrow corridors along two creeks.

Habitat on the study area was tallgrass prairie. Prescribed fire created some spatial and temporal heterogeneity in the study area. Cattle grazing usually followed burning (see below), the typical grazing system being early intensive stocking: steers are brought to the ranches for approximately 100 d from April to July, allowing the range to recover in autumn and winter (Smith and Owensby 1978). Cow–calf operations occupied approximately 10% of the study area; such operations avoid annual burns and graze at a lower stocking rate but continue throughout the year. A low density of American bison (*Bison bison*) grazed approximately 5% of the study area year-round, all of it on The Nature Conservancy's Tallgrass Prairie Preserve (the southeastern quarter of the study area). Patches (<100 ha) of this preserve were burned sporadically. A small fraction (<1%) of the study area was hayed each year. Rainfall during our study was higher (112.7–134.7%) than the long-term (1949–2003) average ($\bar{x} \pm$ SD = 97.0 ± 23.6 cm/y), but annual temperature was average (97.1–104.0%).

Between 60% and 80% of the study area was burned annually, typically in early spring (March–April). We mapped the extent of these burns in 1998, 1999, and 2000, each year between 1 January and 31 May. We classified an area as ''burned'' only if it had burned since the previous growing season (i.e., burns >1 y old were excluded). Ground maps were transferred into ArcView 3.3 (ESRI Software, Redlands, CA) using base maps from Rea and Becker (1997).

METHODS

Radio Tracking

We tracked radio-tagged greater prairie-chickens year-round from April 1997 to July 2000. Birds were trapped on leks using walk-in funnel traps connected by 8 m of plastic drift fence arrayed in a zigzag pattern. Each bird was fitted with a bib-mounted radio-transmitter and a loop antenna (AVM and Telemetry Solutions [ATS], Concord, CA) weighing 18 g, approximately 2% of a prairie-chicken's body mass (800–1,000 g). Tracking equipment consisted of 5-element, handheld Yagi antennas and ATS model R2000 or R4000 receivers. On average we tracked a bird once every 3 d at varying times of day. For all-day tracking, conducted sporadically throughout the study, we recorded a bird's location at least once every 30 min, more frequently if a bird moved >1 km. The vast majority of bird locations were from direct homing; <1% of locations were from triangulation. Two person-days per week were devoted to finding ''lost'' birds—i.e., individuals not detected for 2 weeks. We also conducted wide aerial transects for lost birds 5–6 times/y, extending 2–3 km past known bird locations.

We surveyed the study area for active leks from 27 March to 7 May each spring, always between 30 min before dawn and 2.5 h after dawn and only on mornings with good weather. We spent an hour on each section surveyed and recorded the number of birds at each lek.

If a female tracked in spring occupied the same location for 2 consecutive days or was otherwise thought to be nesting, we approached her cautiously to determine if she was on a nest. If so, we placed a marker radio at the nest's location so the nest could be monitored from afar, thus minimizing disturbance to the female. We monitored all nests every 2–3 d. We did not routinely flush a female to determine nest contents, but if a female flushed of her own accord or if she had been incubating for several weeks, we gathered data on clutch size (66 of 74 nests).

Statistical Analyses

We examined lek and nest placement under a null model assumption that if either was random then each would occur in the same proportions as those of burned versus unburned prairie. This model assumes that all of the study area was available for use, an assumption we think is valid given that the majority of the study area is tallgrass prairie with little soil disturbance or woody vegetation (see Study Area). Under this null model, lek or nest placement could be tested with a χ^2 goodness-of-fit test. All statistical tests can be found in Sokal and Rohlf (1995).

We assessed site fidelity—here defined as the tendency for leks to have the same geographic center across years—using Cochran's *Q*, a nonparametric test for repeated-measures data that are dichotomous (i.e., a lek was present or absent from a particular location in a given year). We used the nonparametric Wilcoxon rank-sum test to determine if lek size tended to differ on burned versus unburned prairie.

For the timing of nest placement, we assessed nesting before and after 1 June using a Mantel–Haenszel χ^2, a test of frequencies divided into discrete groups (in this case time of year). We assessed differences in nest date with a one-way analysis of variance (ANOVA) with date as the response and burned versus unburned as the categorical variable. For ANOVAs, we report effect size as $\boldsymbol{d}$ (Cohen 1988).

Our assessment of reproductive effort was severalfold. We constructed survival curves for nests using a Kaplan–Meier product-limit estimator and compared curves on burned versus unburned prairie with a log-rank χ^2 test. We compared productivity by burn treatment for clutch size and fledgling production. In both cases we treated nest date as a covariate and compared the response variables with an analysis of covariance (ANCOVA).

RESULTS

Lekking Behavior

The geographic center of leks tended to shift from year to year, such that birds did not return to fixed locations but moved according to changing conditions. As a result, site fidelity was not a strong factor in lek location, in that interannual locations were only marginally correlated (Cochran's *Q*-test: $Q = 4.33$, df = 2, $P = 0.11$), a finding consistent with past studies (e.g., Merrill et al. 1999). Male prairie-chickens tended to lek on unburned prairie (Figure 1), but they did not choose unburned habitat differently from a random choice of available unburned habitat (goodness-of-fit test: $0.22 < \chi^2 < 4.46$, df = 1, $P > 0.10$, $20 < n < 27$ leks). Even so, leks on burned prairie tended to be <200 m from unburned prairie: 54 of 79 leks (68.4%) surveyed during 1998–2000 had unburned prairie somewhere within this radius, including on the lek itself. Only 21 of 55 (38.2%) leks were on such land burned in each of the three springs from 1998 to 2000. Regardless, lek size tended to be larger on burned ($\bar{x} \pm$ SD = 7.4 ± 5.6 birds) than on unburned ($\bar{x} \pm$ SD = 5.1 ± 3.7 birds) prairie (Wilcoxon rank-sum test: $W_s = 1{,}216$, df = 1, $P < 0.06$).

Nesting Behavior

Females strongly avoided nesting in areas burned in spring 1998 (Figure 2A; $\chi^2 = 64.84$, df = 1, $P < 0.0001$, $n = 28$ nests) and in spring 1999 (Figure 2B; $\chi^2 = 29.64$, df = 1, $P < 0.0001$, $n = 26$ nests). Nesting effort was poor in 2000, prohibiting statistical analysis, although 5 of 8 nests were on unburned prairie even though 63.6% of the area had been burned that spring. Incorporating data from 1997 ($n = 12$ nests), only 18.9% (14 of 74) of the nests were placed on burned prairie, and only 5 of the 64 (7.8%) nests from 1998 to 2000 were located on prairie burned in each of the three years.

Females particularly favored nesting on unburned prairie before June (Figure 3; Mantel–Haenszel $\chi^2 = 17.81$, df = 1, $P < 0.0001$, $n = 74$), just after the approximate midpoint (29–30 May for our data) of the prairie-chicken's nesting season. Indeed, on average, nests were found on burned prairie ($\bar{x} \approx$ 07 June, SD = 17 d) >3 weeks later than they were found on unburned prairie ($\bar{x} \approx$ 12 May, SD = 10 d), a significant difference in nest timing (ANOVA: $F_{1,70} = 55.94$, $P < 0.0001$, $n = 74$, $\boldsymbol{d} = 2.23$).

Despite avoidance of burned prairie and even though nests on unburned prairie survived, on average, slightly longer than nests on burned prairie ($\bar{x} \pm$ SE = 15.4 ± 1.2 d vs. 13.9 ± 2.3 d), nest survival as a whole did not vary relative to burning (Figure 4). However, nests on unburned prairie were more productive, with clutch size averaging nearly 2 eggs greater and fledglings averaging nearly 5 greater (Table 1).

Determining whether smaller clutch sizes were an effect of burning per se is confounded by the diminution of clutch size with later laying date (linear regression: $F_{1,62} = 31.47$, $P < 0.0001$, $n = 64$, $r^2 = 0.34$) and renesting attempts (ANOVA: $F_{1,64} = 7.16$, $P < 0.01$, $n = 65$, $\boldsymbol{d} = 0.96$), itself a function of laying date. Accounting for the effects of nest date—i.e., incorporating nest date as a covariate in a linear model—implies that neither burns (ANCOVA: $F_{1,62} = 0.26$, $P > 0.50$, $n = 64$) nor nest attempts (ANCOVA: $F_{1,62} = 0.02$, $P > 0.80$, $n = 64$) had an effect on clutch size. Likewise, once accounting for nest date, brood size was apparently not related to burning per se (ANCOVA: $F_{1,22} = 1.86$, $P > 0.10$, $n = 24$).

In contrast to nest survival, brood survival may be affected positively by proximity to a burn edge: 3 of 7 (43%) broods from nests >500 m from a burn were depredated completely within 1 week of hatching, yet none of 13 nests <500 m from a burn were lost completely.

DISCUSSION

Lekking Males

Our data suggest that lekking male greater prairie-chickens are not affected adversely by spring burns. Prairie-chickens lek in open, short habitat (Hamerstrom et al. 1957), so it is conceivable that regular burning (or grazing) is needed to create open patches with short grass or forbs that are favored for lek sites. This hypothesis is supported by our observation that larger leks tended to be on burned prairie. Even so, the tendency for leks on burned prairie to be near unburned prairie suggests that birds sought lekking locations within a short burst of flight from denser cover, presumably as a means of individuals reducing their risk of predation.

Regular burning may have an ancillary benefit. Greater prairie-chickens avoid lekking near forested habitat (Merrill et al. 1999), perhaps including intrusive woody plants such as the invasive eastern red cedar (*Juniperus virginiana*), a "weedy" species currently claiming large tracts of tallgrass and mixed-grass prairie (Briggs et al. 2002). Regular fires inhibit

Fig. 1. Greater prairie-chicken leks (dots) in (A) 1998, (B) 1999, and (C) 2000 in relation to spring burns, Osage County, Oklahoma. Dot size varies according to lek size (small dot = 1–5 males; medium dot = 6–10 males; large dot = 11–25 males). The heavy black outline delineates the study area. Unburned patches are shaded gray.

the spread of woody vegetation and promote the spread of grass and forb species, thus contributing to a healthy prairie ecosystem and its component avifauna (Reinking 2005).

Nesting Females

Nesting females strongly avoided prairie burned that spring (Figure 2), at least for their first nest attempts (Figure 3), but they preferred burned prairie for subsequent nest attempts; specifically, after May grassland vegetation had recovered from a burn to a sufficient extent (see Robel et al. 1998) that females were less apt to avoid burned areas. Although prairie-chicken nests may be lost to fire directly (Zimmerman 1997), we suggest that the major result of spring burns is an initial reduction in what females view as suitable nesting habitat. Many birds have facultative responses to conditions (Newton 1998), meaning they may nest ‘‘out of season’’ if conditions are favorable or may forego nesting ‘‘in season’’ if conditions are unfavorable (e.g., Bolger et al. 2005). We hypothesize that if

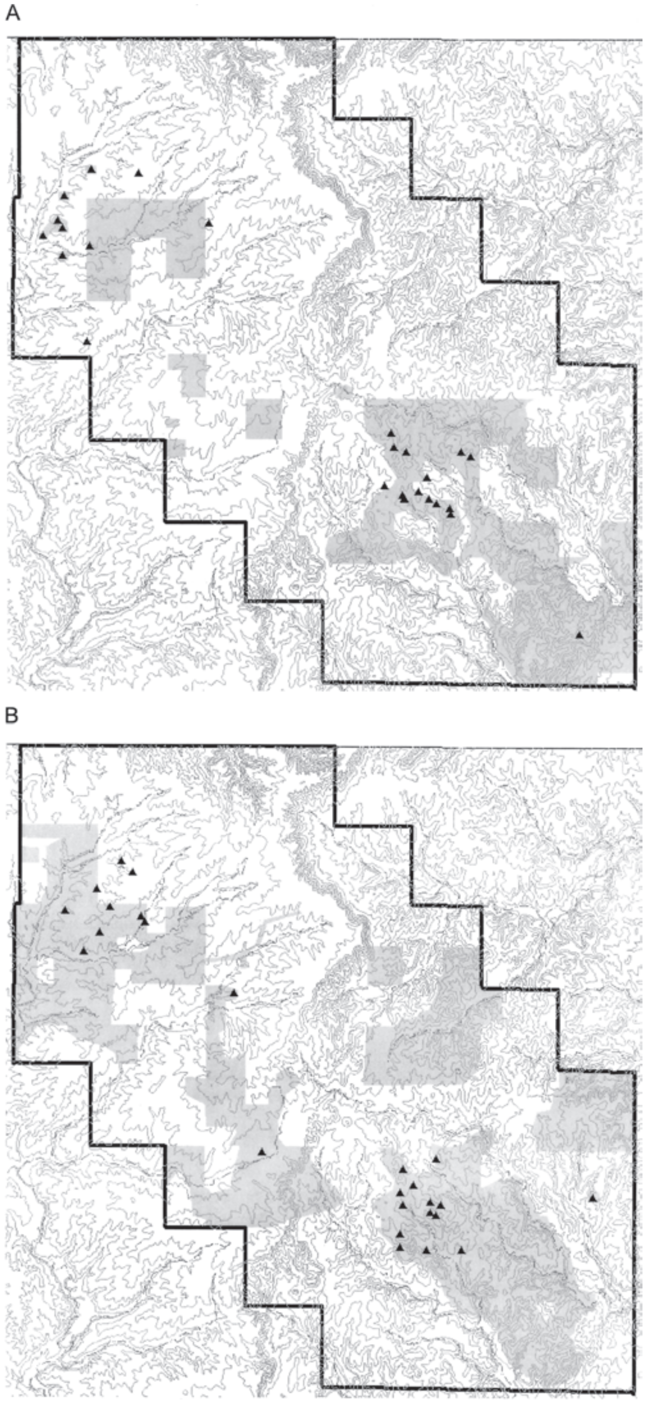

Fig. 2. Greater prairie-chicken nests (triangles) in (A) 1998 and (B) 1999 in relation to spring burns, Osage County, Oklahoma. The heavy black outline delineates the study area. Unburned patches are shaded gray.

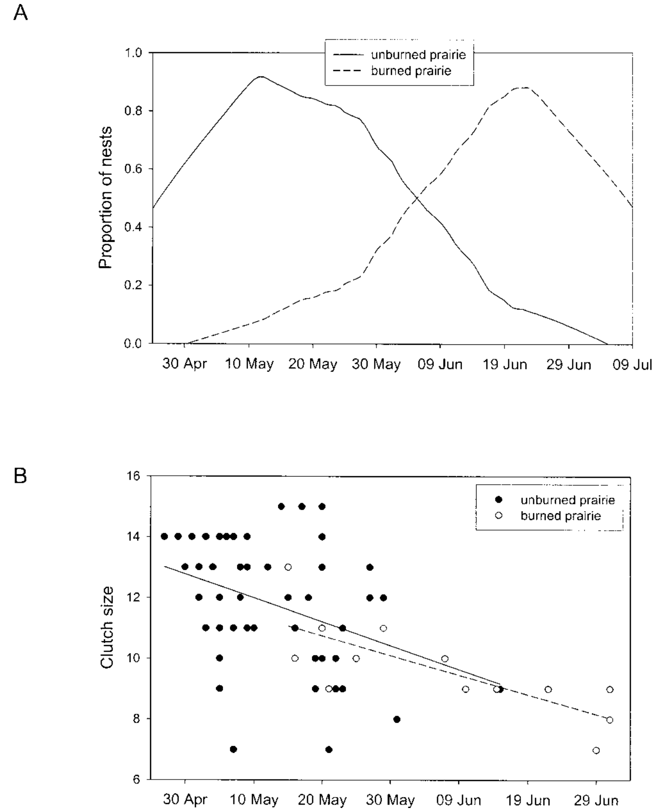

Fig. 3. Greater prairie-chicken nests, Osage County, Oklahoma, 1998–2000. (A) Proportion of nests in burned and unburned tallgrass prairie across the nesting season. Curves were derived from LOESS smooths (f = 0.5) of frequency data (accumulated nests per 5-d period). Vegetation recovers as the season progresses, so females are less likely to avoid burned areas later, with early June being a transition point. (B) Clutch sizes from individual nests plotted against nest date. Regardless of burning, regressions of clutch size against date have the same slope (solid = unburned, dashed = burned).

prairie is burned extensively, females may wait to nest until they view conditions as being more favorable—in this case, until the prairie has recovered to an extent that a nest can be concealed adequately. Before fire suppression and wide cultivation of the prairie, large fires may have had a similar effect, but females then may have been able to disperse to suitable habitat contiguous with their home range. Extant prairie is currently highly fragmented, and females may not be able to move readily to favorable unburned patches.

It is nearly universal that, within a species, avian clutch size decreases as the breeding season progresses (Klomp 1970, Winkler and Walters 1983). Our data show the same pattern for the greater prairie-chicken. Causes for this pattern are unclear, but if it is independent of effort—if clutch size is smaller later in the season regardless of whether the female is on her first, second, or third nesting attempt—then output will be lower by the time females begin to occupy areas burned that spring. Thus, there is reason to expect our observed pattern of lower reproductive output on burns.

We can only speculate why broods suffered apparently higher losses farther from burns. A plausible hypothesis is that accumulation of litter and tangled vegetation from the previous year's growth hampers brood movement, making them less able to escape a predator, an idea supported by our observation that most females that nested in unburned prairie typically moved their broods to recently burned prairie shortly after hatching. But movement to recent burns could be because female prairie-chickens preferentially select

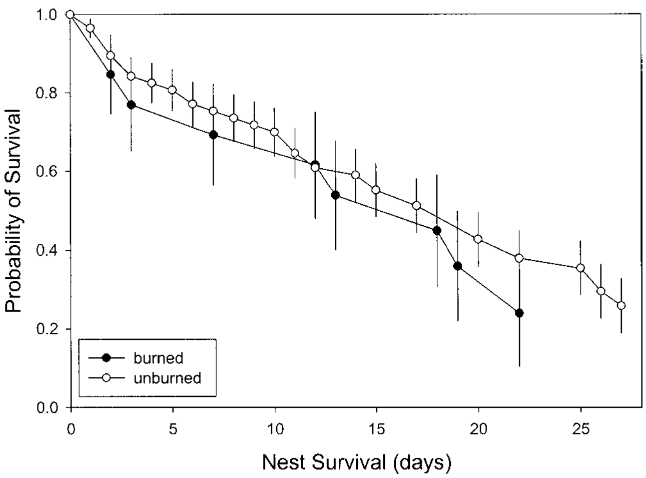

Fig. 4. Greater prairie-chicken nest survival in relation to spring burning of tallgrass prairie, Osage County, Oklahoma, 1998–2000. The Kaplan–Meier survival curve for nests on burned prairie appears to be lower, but standard errors overlap sufficiently to make the apparent difference insignificant (log-rank test: $\chi^2 = 0.29$, df = 1, $P > 0.50$, $n = 70$ nests).

Table 1. Productivity of greater prairie-chicken nests on burned and unburned tallgrass prairie, Osage County, Oklahoma, 1998–2000. Statistical tests for differences between means include estimates of the effect size (***d***). Although the difference appears to be associated with burning of prairie, the effect is more likely related to when the nest was initiated (see text). Even so, because a much higher proportion of later nests are in burned prairie (Figure 3), they are necessarily less productive.

Variable	Burned	Unburned
Clutch size		
Sample size	13	53
Mean	9.62	11.56
Standard deviation	1.50	2.35
Standard error	0.42	0.32
ANOVA results	$F_{1,62} = 8.09$, $P < 0.01$, $\boldsymbol{d} = 0.88$	
Number of fledglings		
Sample size	4	20
Mean	6.50	11.20
Standard deviation	2.08	2.48
Standard error	1.04	0.55
ANOVA results	$F_{1,22} = 12.44$, $P < 0.002$, $\boldsymbol{d} = 1.93$	

prairie with higher levels of invertebrate biomass (Hagen et al. 2005), a feature of recent burns (Warren et al. 1987, Evans 1988, Swengel 2001).

If these hypotheses hold true and the observations remain consistent, together they present a conundrum for nesting greater prairie-chickens. Increased or continued extensive burning may cause females to forego nesting until a later date, by which time their reproductive potential will be diminished. Moreover, if broods require more open prairie to increase their odds of escaping predators, then females have another reason to wait for burns to recover or, at the least, to find suitably concealed nest sites (i.e., those in unburned prairie) near areas burned that spring. In either case, if burning is too extensive, then the predicted reduction in reproductive output on burned plots, a result of later nesting there, could reduce population size to a critically low level as a cumulative effect over time. Lastly, because our study was conducted during four years that, by chance, had higher than average rainfall, it is possible that burned prairie recovered more quickly than usual. We speculate that burns would recover later, and perhaps not to a sufficient extent, during dry years.

MANAGEMENT IMPLICATIONS

Our data suggest that both male and female greater prairie-chickens favor a patchwork of burned and undisturbed tallgrass prairie. Lekking males may prefer burned sites, but they often lek near patches of residual tallgrass, presumably because these patches provide escape cover. Likewise, breeding females avoid placing nests in burned areas until the areas have recovered sufficiently to provide concealment, but those females whose clutches hatch typically move broods into a recently burned area, perhaps because small chicks can better maneuver through its more open understory, but more likely because recent burns have elevated invertebrate biomass on which chicks depend (Boyd and Bidwell 2001, Hagen et al. 2005).

Fuhlendorf and Engle (2004) noted that rangelands, including the prairie, have long been managed with the objective of reducing inherent landscape heterogeneity. In the tallgrass prairie, such management includes suppressing natural fires, spreading cattle grazing evenly, and setting numerous spring fires, enough that much of the habitat is burned annually. In concert, then, this effort has greatly minimized the extent of unburned tallgrass prairie. But the greater prairie-chicken prefers tallgrass prairie, of at least 1 y residual growth for nesting. As a result, management practices will need to change if we hope to conserve viable populations of this species.

A key change involves the timing and extent of fires and the associated extent of cattle grazing. Cattle gain weight more quickly when foraging on recently burned prairie (Zimmerman 1997), a result of increased forage quality and primary productivity; therefore, ranchers have an economic incentive to continue with spring burns. Yet such burns need not cover vast areas nor affect the same areas year after year. A rotation of smaller burns (and their associated grazing pressure)—the basic idea of patch burning (Johnson 1997, Fuhlendorf and Engle 2004)—would create the patchwork of burned and unburned prairie necessary for the greater prairie-chicken.

Regarding the prairie-chicken specifically, we encourage future researchers to focus on landscape-level patterns of nest and brood success on burned versus unburned prairie. For example, what ratio of burned to unburned prairie is ideal for the greater prairie-chicken? Does this ratio change with the level of habitat fragmentation? Is there a temporal pattern to burning that best suits the species? These questions could be answered with field experiments established with the cooperation of landowners, experiments in which the extent and timing of burned plots are controlled.

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