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Rangeland Ecology & Management 68 (2015) 298–304

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Alternative Rangeland Management Strategies and the Nesting Ecology of Greater Prairie-Chickens☆,☆☆

Lance B. McNew [a,*], Virginia L. Winder [b], James C. Pitman [c], Brett K. Sandercock [d]

[a] Assistant Professor, Department of Animal & Range Sciences, Montana State University, Bozeman, MT 59717, USA
[b] Assistant Professor, Department of Biology, Benedictine College, Atchison, KS 66002, USA
[c] Small Game Coordinator, Kansas Department of Wildlife, Parks, & Tourism, Emporia, KS 66801, USA
[d] Professor, Division of Biology, Kansas State University, Manhattan, KS 66506, USA

ARTICLE INFO

Keywords:
game bird
habitat use
intensive early stocking
nest survival
patch-burn grazing
prescribed fire
resource selection
Tympanuchus cupido

ABSTRACT

Population declines of grassland birds over the past 30 yr have followed the widespread implementation of intensive rangeland management practices that create homogenous grassland habitats. Patch-burn grazing (PBG) was tested as an alternative management technique that is ecologically similar to historically heterogeneous fire and grazing regimes and holds promise as a rangeland management tool that may benefit grassland wildlife. We conducted a 3-year study to compare nest-site selection and nest survival of greater prairie-chickens, an umbrella species for tallgrass prairie conservation, on private lands managed with PBG or intensive fire and grazing in the Flint Hills of Kansas. The goal of our field study was to evaluate the relationships among rangeland management practices, habitat conditions, and nesting ecology of greater prairie-chickens. Nest-site selection and nest survival of prairie-chickens were both directly related to vertical nesting cover, which was determined by the fire return interval of a pasture. Nesting habitat was affected little by stocking rate in PBG management regimes because preferred nest sites were unburned patches that were not grazed by cattle. Overall, the quantity and quality of nesting sites was improved under PBG management when compared with more intensive rangeland management regimes. Our results join a growing body of evidence that rangeland management strategies that mimic historical heterogeneous fire and grazing regimes benefit native species of prairie wildlife.

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Introduction

Tallgrass prairie is the most intensively altered biome in North America with more than 95% lost to rowcrop agriculture or other development during the last century (Samson et al., 2004; Hoekstra et al., 2005). The Flint Hills ecoregion of eastern Kansas and Oklahoma contains the largest remaining tracts of tallgrass prairie and supports populations of many sensitive species of wildlife (Powell, 2006; With et al., 2008). The Flint Hills ecoregion is vital to the long-term persistence of many obligate grassland birds (Svedarsky et al., 2000; With et al., 2008). The Flint Hills is generally unsuitable for cultivation but supports an economically important cattle industry, with cattle grazing occurring on > 90% of its native prairies (With et al., 2008). During the past 30 yr, rangeland management has intensified with a shift from periodic prescribed burning and season-long grazing of cows and calves, to intensive early stocking of steers during April–July combined with annual spring burning (IESB) (Smith and Owensby, 1978). IESB benefits cattle production in the short-term by promoting the growth of high quality forage and allows ranchers to stock ranges with cattle early. However, IESB may negatively affect native wildlife by reducing structural heterogeneity of grassland habitats, and implementation of IESB has coincided with population declines among grassland birds (Reinking, 2005; Fuhlendorf et al., 2006; Rahmig et al., 2008).

Patch-burn grazing (PBG) has been proposed as an alternative management technique that increases plant diversity and structural heterogeneity of grazed grasslands while providing viable revenue for cattle producers and landowners (Fuhlendorf and Engle, 2001, 2004). PBG is a rotational burning management scheme that is ecologically similar to presettlement grazing—fire interactions and could improve habitat conditions for many declining prairie species (Churchwell et al., 2008; Coppedge et al., 2008; Powell, 2008). Recent studies have shown that PBG holds promise as a conservation tool and is also economically viable as an alternative to more intensive rangeland management practices (Rensink, 2009; Limb et al.,

☆ Research was funded in part by the Kansas Department of Wildlife, Parks, and Tourism, Kansas State University, and the U.S. Fish and Wildlife Service.
☆☆ At the time of research, McNew and Winder were Postdoctoral Research Associates, Division of Biology, Kansas State University, Manhattan, KS 66506, USA.
* Correspondence: Lance B. McNew, Department of Animal and Range Sciences, Montana State University, PO Box 172900, Bozeman, MT, USA.
E-mail address: lance.mcnew@montana.edu (L.B. McNew).

http://dx.doi.org/10.1016/j.rama.2015.03.009
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2011). Wildlife biologists have speculated that widespread implementation of PBG could result in significant improvements in the quality of habitats for grassland birds in tallgrass prairie ecosystems (Fuhlendorf et al., 2006). However, studies evaluating the effectiveness of PBG as a conservation strategy to improve population viability of grassland birds in unfragmented tallgrass ecosystems have been limited.

The greater prairie-chicken (*Tympanuchus cupido*; hereafter "prairie-chicken") is an obligate grassland bird and umbrella species for tallgrass prairie conservation (Poiani et al., 2001; Johnson et al., 2011). Population declines of prairie-chickens have paralleled continental losses of native tallgrass prairie, and much of the species' remaining distribution occurs in the relatively unfragmented Flint Hills ecoregion. Consistent with declines in other grassland birds, prairie-chicken numbers in the Flint Hills have decreased by as much as 50% over the last 30 yr (Pitman, 2012). Prairie-chickens require a diverse mosaic of floristic and structural grassland habitats for successful reproduction and survival: open sites at relatively high elevations for display arenas or leks, dense vegetative cover for concealment during nesting, and intermediate vegetative structure rich in forbs for brood-rearing (Svedarsky et al., 2000; Johnson et al., 2011). Our recent research indicates that high predation on nests and young is the primary cause of population declines, and that predation risk is linked to a lack of adequate vegetative cover at prairie-chicken nest sites in the Flint Hills (McNew et al., 2012a, 2014). However, the relationships between rangeland management practices, nesting cover, and prairie-chicken fecundity have not been evaluated.

More than 95% of the remaining native tallgrass prairie in the Flint Hills ecoregion is privately owned with the vast majority (~91%) managed for cattle production (With et al., 2008). Information on how standard and alternative (e.g., PBG) rangeland management practices affect space use and demography are needed to build effective conservation strategies for prairie-chickens in the ecoregion. The goal of our field study was to evaluate the relationships between rangeland management practices, habitat conditions, and nesting ecology of prairie-chickens in the central Flint Hills. Our objectives were to evaluate 1) the degree to which rangeland management factors such as fire return interval and stocking rate influenced vegetative structure and composition of prairie-chicken habitat, 2) how vegetative conditions influenced selection of nest sites and nest survival of prairie-chickens in areas managed with PBG versus areas managed with standard management regimes like IESB, and 3) the effectiveness of PBG as a rangeland management technique to improve habitat conditions for prairie-chickens.

Methods

Study Area

Our field study was conducted in a 5-county area (Butler, Chase, Greenwood, Lyon, and Morris Counties) in the central Flint Hills ecoregion of Kansas during 2011–2013. The Flint Hills ecoregion is a landscape of relatively unfragmented tallgrass prairie, and native grassland managed for cattle production was the dominant land cover type on our study area (>90%). Our study included 72.2 km^2 of grassland on 2 properties managed with PBG and ca. 479 km^2 ha of grassland on 78 properties managed with standard rangeland management practices in the Flint Hills, predominantly IESB (hereafter 'intensive').

We conducted research at two large ranching properties managed with PBG: Tallgrass Prairie National Preserve in Chase County and the privately owned Browning Ranch in Chase and Greenwood Counties (Fig. 1). The 4,407-ha Tallgrass Prairie National Preserve is owned by The Nature Conservancy and managed by the National Park Service. Most pastures are grazed with steers during all or part of the growing season during April–October (1.59 ± 0.73 animal unit months per hectare [AUM·ha-1]); one 445-ha pasture is grazed year-long by bison (0.45 AUM·ha-1). We pooled bison and cattle PBG pastures into a general PBG treatment because the effects of grazing by bison and cattle on tallgrass prairie vegetation are comparable (Towne et al., 2005), and have similar effects on the long-term habitat use by prairie-chickens (McNew et al., 2012b). The privately-owned 2,812-ha Browning Ranch had a mean stocking rate of 2.0 ± 0.84 AUM·ha-1 during April–August in 2011–13. A total of 11 pastures (488 ± 125SE ha pasture-1) at both PBG properties were divided into 2 or 3 patches (i.e., half or third of pasture) with fire breaks not cross-fences, and each patch was burned rotationally every second or third year. Under a PBG management regime, cattle have freedom to move among patch treatments within a pasture but spend the majority of their time grazing on the most recently burned patches that were typically burned in the preceding spring (Fuhlendorf and Engle, 2004).

Management strategies on the PBG properties were consistent over our 3-yr field study, but fire and grazing applications on the intensive properties varied from year to year and were dependent upon weather conditions and individual ranch managers. In the past, intensive properties were managed with IESB with a stocking rate of ca. 3–4 AUM·ha-1 during April–July. However, drought conditions in 2012 and 2013 resulted in many property managers foregoing burning pastures and switching to lower stocking rates during these growing seasons. Thus, stocking rates during the study on reference properties ranged from 1 to 6 AUM·ha-1, though stocking rates ≥ 3 AUM·ha-1 were rare.

Field Methods

We captured prairie-chickens during March–May at 34 leks (25 leks on 9 intensive ranches, 9 leks on 2 PBG ranches with walk-in traps or drop-nets). We equipped females with VHF radio-transmitters (model A3950, Advanced Telemetry Systems, Isanti, MN), and located nests via daily telemetry of radio-marked females during egg-laying and incubation (McNew et al., 2013). If telemetry indicated a female had departed a completed nesting attempt, we visited the nest site to identify nest fate. We classified nest fate as successful (produced ≥ 1 one chick) or failed based on pipped vs. broken eggshells, signs of predator activity at the nest site, and female behavior (McNew et al., 2014).

We surveyed habitat conditions within 3 d of hatching or failure at nests. We conducted parallel habitat surveys at random points located within 5-km of nest locations (McNew et al., 2013, 2014). We evaluated an index of vertical nesting cover by averaging 4 visual obstruction readings (VOR) at a distance of 2 m and a height of 0.5 m (Robel et al., 1970) and estimated the proportion of grass, forb, shrub, and bare ground cover in a 20 × 50 cm quadrat frame at 12 subsampling locations within 6 m of each nest or random point (Daubenmire, 1959). We recorded the distance (m) and height (cm) to nearest shrub in the field and estimated the distance (m) from each nest to nearest state highway, county road, nongrassland habitat edge and water edge using ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA). For landcover analyses, we used the 30-m resolution land cover map depicting 11 biologically relevant landcover classes in Kansas in 2005, which has an average overall accuracy of 86% (Whistler et al., 2006). We included road system datasets for Kansas in 2006 (Kansas Department of Transportation: Bureau of Transportation Planning). We gathered information on rangeland management for every patch or pasture in the study area for each year of study by interviewing property managers to determine years since last prescribed fire and stocking rate (AUM·ha-1) for each nest or random point. We considered the potential lag effects of previous fire history by determining the number of years between 2000 and 2011 a nest site or random point burned using a fire classification map for our entire study area based on remote sensing (Mohler and Goodin, 2012a,b).

Statistical Analyses

Habitat conditions

We tested the effects of rangeland management practices on habitat conditions using generalized linear models. Elsewhere, we have shown

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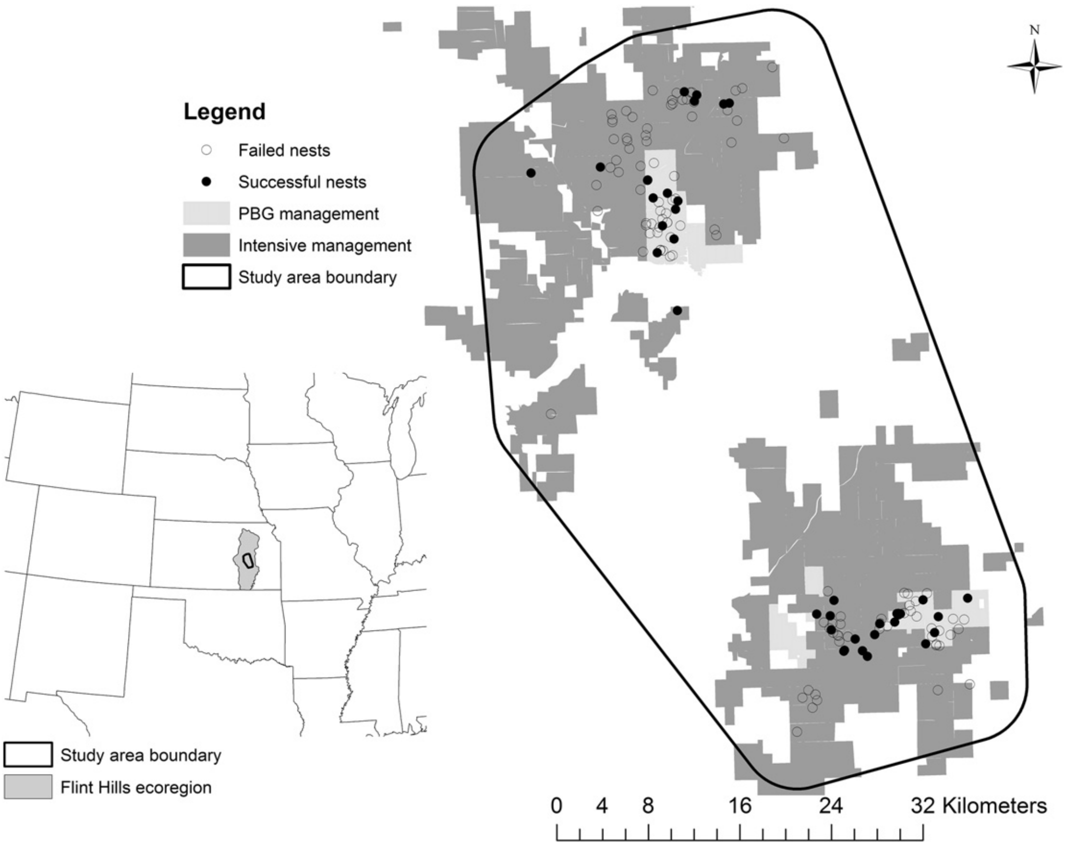

Fig. 1. Location of field sites for study of greater prairie-chicken nesting ecology in the Flint Hills of Kansas, USA 2011–2013. Properties represented with light gray were managed with patch-burn grazing; properties in dark gray were managed with more intensive burning and grazing treatments. The Flint Hills ecoregion is depicted in grey on the inset map.

that nest-site selection and nest survival of prairie-chickens breeding in intensively managed grasslands were determined primarily by visual obstruction (McNew et al., 2013, 2014). Therefore, we explicitly tested the relationships between VOR and three predictor variables: stocking rate (AUM·ha-1), years since last fire, and the frequency of fire over the preceding 10 yr. We used linear models with Gaussian (normal) error structure to build models, and Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to evaluate and compare candidate models with a null model (Burnham and Anderson, 2002).

Nest site selection

We randomly selected a single nesting attempt per female per year to reduce potential autocorrelation among nests in the sample (McNew et al., 2013). To examine relationships between nest-site selection and habitat conditions, we explored nonlinear responses to each covariate before fitting models with resource selection functions. We evaluated generalized additive models (GAMs) with nests and random points as binary responses and fitted smoothing splines to univariate habitat predictors to model potential nonlinear relationships (Fig. S.1) (Wood, 2006). We inspected plots of predicted relationships and partial residuals to transform smoothed variables into polynomials that approximated nonlinear relationships (Crawley, 2005). We hypothesized that behavioral responses to some habitat variables, such as distance to edge, may exhibit a threshold pattern so we tested pseudothreshold models by evaluating the natural log of the explanatory variable (ln[x+0.001]) (Dugger et al., 2005).

We evaluated nest site selection using a resource selection function where nest sites (use) and random points (available) were treated as independent samples (Manly et al., 2002). We used generalized linear models with the logistic link function, a binomial error structure, and linear or nonlinear responses to fixed effects following patterns from our GAM analyses to evaluate logistic models. We developed a candidate set of nest-site selection models based on *a priori* hypotheses and evaluated relative model support using AIC_c (Burnham and Anderson, 2002). We evaluated main effects of management treatment (intensive, PBG) and stocking rate (AUM·ha-1), and three covariates including habitat measurements, years since fire, and historical fire frequency. We excluded models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter if confidence intervals indicated the parameter was noninformative (or $\Delta AIC_c \leq 4$ if $\Delta K = 2$, Burnham and Anderson, 2002; Arnold, 2010). All statistical analyses were performed in R (ver. 2.4; R Development Core Team, 2011, Vienna, Austria), where GAM models were fit with the mgcv package (Wood, 2006; Bates et al., 2012).

Nest survival

We used the nest survival procedure of program Mark (ver. 7.1) to test competing models and estimate daily survival rates of nests during a 106-d nesting period between 18 April and 1 August (White and Burnham, 1999; Dinsmore et al., 2002). We previously found that variation in nest survival was explained primarily by habitat conditions assessed at the scale of the nest site (McNew et al., 2014). Thus, we modeled nest survival as a function of habitat covariates at the nest site that may be influenced by fire and grazing, including VOR, proportion grass, and proportion forbs. We also modeled the effects of rangeland management treatment, stocking rate, years since fire, and historical fire frequency. All models were constructed using the logit-link function, and model selection was based on differences in AIC_c (ΔAIC_c) and evidence ratios from Akaike weights (Burnham and Anderson, 2002). To reduce the candidate set, we first evaluated models with the temporal effects of day of the nesting season and age of the nest. Next, we built and evaluated models with treatment effects and linear or nonlinear covariates identified with GAM analysis. We evaluated models with 9 main effects and potential interactions hypothesized

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to affect nest survival (Table S.1) (McNew et al., 2014). We excluded models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter if confidence intervals indicated the parameter was noninformative (Burnham and Anderson, 2002). We used R (R Development Core Team, 2011) and the package RMark (Laake and Rexstad, 2008) to construct nest survival models for program MARK. We extrapolated the overall nest survival probability as the product of daily survival probabilities for the mean nest exposure period (38 d) and calculated variances of extrapolated nest survival using the delta method (Powell, 2007).

Results

Habitat Conditions

We evaluated the relationships between VOR and factors associated with rangeland management for 143 random points within the study areas. Four models were supported by the data and a lack of a single parsimonious model was caused by interactions among the three rangeland management effects (Table 1). Models with rangeland management treatment (intensive or PBG), AUM·ha-1, and years since fire (YSF) outperformed a constant model as well as models with single main effects (Table 1). Models with a legacy effect of fire frequency over the preceding decade received no support. Visual obstruction increased with years since fire for both PBG and intensive rangeland management, but decreased with stocking rate on properties managed with intensive management (Fig. 2).

Nest Site Selection

About 6,817 ha (12%) of the area available to nesting prairie-chickens (i.e., areas within 5-km of a lek of capture) was managed with PBG; the remainder was managed with intensive rangeland management regimes. We located 60 (42%) nests on properties managed with PBG and 83 (58%) nests on adjacent properties managed with intensive management. Within the PBG properties, prairie-chickens preferred patches that were burned 1–2 years prior to nesting (Fig. 3). Compared with random points, nest sites were closer to leks, had greater forb coverage and VOR, and less bare ground (Table 2).

We located 143 prairie-chicken nests (109 first nests, 34 renesting attempts) laid by 93 individual females during 2011–2013. We randomly selected one nesting attempt for each female per year to evaluate resource selection functions, resulting in a reduced sample of 109 nests. A single model that included a quadratic effect of VOR and negative linear effect of distance to lek received the most support ($w_i = 0.7$; Table 3). Models that included the quadratic effect of VOR had virtually all support ($w_i > 0.99$) and indicated that the relative probability of an area

Table 1
Model selection for models evaluating the effects of rangeland management factors on visual obstruction reading (VOR) in Kansas, 2011–2013.

Model factors[1]	K[2]	Dev	AIC_c	ΔAIC_c	w_i
Treatment + AUM + YSF[3]	4	357.8	368.2	0.0	0.26
AUM + YSF	3	360.8	369.0	0.8	0.18
Treatment*AUM + YSF	5	357.0	369.7	1.5	0.13
Treatment*YSF + AUM	5	357.5	370.1	1.9	0.10
Treatment + YSF*AUM	5	357.7	370.3	2.1	0.09
YSF + AUM^2	4	360.0	370.4	2.2	0.09
YSF*AUM	4	360.3	370.7	2.5	0.08
YSF + ln(AUM)	3	363.5	371.7	3.5	0.04
AUM + ln(YSF)	3	365.5	373.8	5.6	0.02
Treatment*YSF*AUM	8	356.2	375.6	7.4	0.01
Constant (null)	1	370.7	385.5	17.3	0.00

[1] Only models with Akaike weights (w_i) ≥ 0.01 are presented except for the null model.
[2] K = number of parameters.
[3] AUM indicates animal unit month per hectare; Treatment, intensive vs. patch-burn grazing; YSF, years since fire; +, additive main effects model; *, factorial model with interaction terms; ln( ), pseudothreshold model.

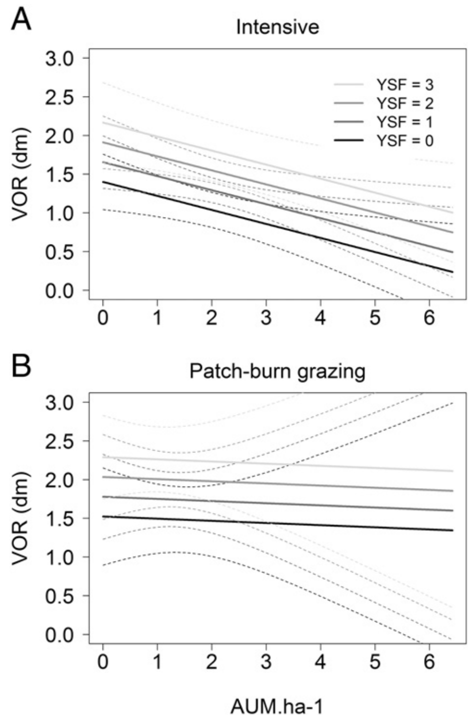

Fig. 2. Relationships between VOR, years since fire (YSF), and stocking rate (AUM·ha-1) for properties managed with **A,** intensive management strategies, and **B,** patch-burn grazing in the Flint Hills of Kansas, 2011–2013. Dotted lines represent 95% confidence intervals. Parameter estimates taken from a parsimonious model with an interactive effect of treatment and stocking rate.

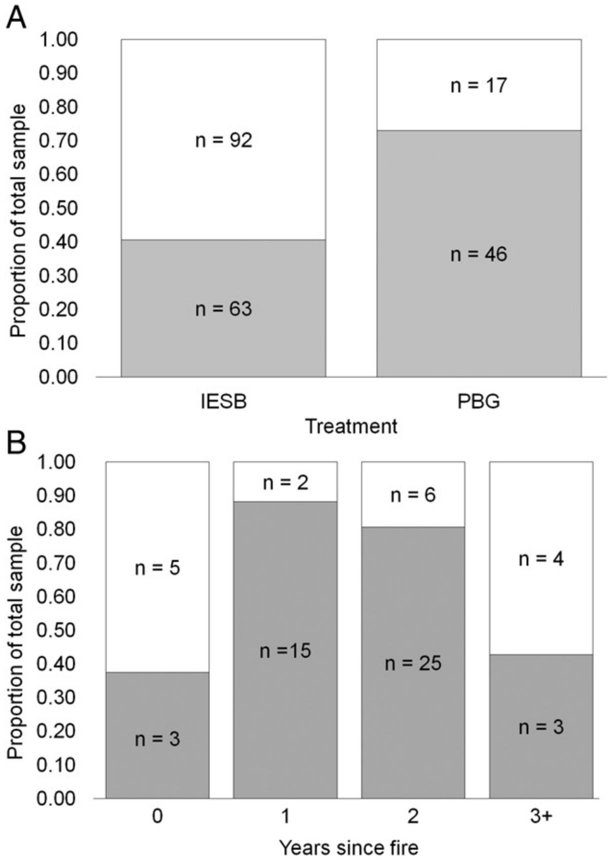

Fig. 3. Proportion of nests (gray) and random points (white) located in (A) intensive (IESB) and patch-burn grazing treatments (PBG), and (B) within burn treatments on patch-burn grazing properties in the Flint Hills of Kansas, 2011–2013.

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Table 2
Mean ± SE habitat measurements assessed at greater prairie-chicken nest locations and random points in the central Flint Hills, Kansas, 2011–2013.

Variable	Nests (n = 143)	Random Points (n = 143)
Distance to nearest lek (km)	1.37 ± 0.16	2.86 ± 0.22
Distance to local road (km)	2.11 ± 0.14	1.79 ± 0.13
Distance to state highway (km)	6.48 ± 0.36	5.98 ± 0.34
Distance to nearest edge (km)[1]	1.07 ± 0.05	0.93 ± 0.05
Distance to water (km)[2]	0.58 ± 0.03	0.50 ± 0.03
Years since last burn	1.55 ± 0.12	1.28 ± 0.11
AUM·ha-1[3]	2.12 ± 0.07	2.07 ± 0.10
Proportion unburned[4]	0.82	0.70
Grass (%)	45.9 ± 2.03	51.1 ± 2.01
Forb (%)	23.3 ± 1.4	17.9 ± 1.4
Shrub (%)	3.4 ± 0.6	2.53 ± 0.4
Bare ground (%)	4.0 ± 0.6	16.4 ± 1.6
Detritus (%)	21.7 ± 2.3	10.9 ± 1.5
VOR (dm)[5]	2.5 ± 0.09	1.39 ± 0.09
Nearest shrub height (cm)	39.2 ± 2.3	48.4 ± 5.4
Nearest shrub distance (m)	12.5 ± 2.4	31.8 ± 4.6
Elevation	437 ± 3.9	416 ± 7.0
Fire frequency (yr)[6]	8.24 ± 0.2	8.21 ± 0.2

[1] Distance to nearest non-grassland land cover type.
[2] Distance to the nearest permanent body of water as depicted by the 2005 Kansas landcover map (Whistler et al., 2006).
[3] AUM indicates animal unit month per hectare.
[4] Proportions of nest and random point locations that were unburned in the current year.
[5] Visual obstruction reading, an index of biomass and nest concealment.
[6] Number of years patch burned during 2001–2011.

being used as a nest site was maximized when VOR was 3–6 dm (Fig. 4). We found relatively little support for effects of years since fire, stocking rate, or fire frequency during the preceding decade (Table 3). Years since fire and stocking rate had significant effects on VOR (Fig. 2), suggesting an indirect influence of rangeland management on nest site selection.

Nest Survival

We included 143 nests in the nest survival analysis. Eighteen of 83 (22%) nests located on intensively managed properties successfully produced ≥ 1 chick, versus 20 of 60 (33%) nests on PBG properties. Mean nest survival was higher in patch-burn than intensive treatments in all years, especially 2013 (2011: 0.22 ± 0.07 vs. 0.12 ± 0.06; 2012: 0.24 ± 0.08 vs. 0.13 ± 0.05; 2013: 0.11 ± 0.05 vs. 0.04 ± 0.02).

Nest survival models with a quadratic effect of VOR received virtually all the support among candidate models ($\Sigma w_i > 0.99$; Table 3). Models with temporal effects (e.g., nest age, day of season) had little support (Table S.1). Daily nest survival increased from a low of < 0.75 when VOR was ≤ 1 dm, to 0.95 when VOR exceeded 5 dm (Fig. 4). Models with the effect of grass cover at the nest site were also supported (Σw_i > 0.99) and indicated a modest but positive relationship ($\beta = 0.02 \pm 0.005$; Table 3). Rangeland management treatment received some support ($\Sigma w_i \approx 0.54$). However, the 95% confidence interval of the effect size (−0.08, 0.74) overlapped 0 and treatment did not significantly improve model fit, suggesting that the effect was noninformative (Table 3). The effects of years since fire and stocking rate on nest survival were not supported ($\Sigma w_i < 0.01$; Table 3), though VOR was related to these rangeland management factors.

Table 3
Model selection results of prairie-chicken nest site selection and nest survival in Kansas, 2011-2013.[1]

Model factors	K[2]	Dev	AIC$_c$[3]	ΔAIC$_c$	w_i	Cum w_i
Nest site selection						
VOR^2 + Distance to lek	4	203.2	211.4	0.00	0.73	0.73
VOR^2 + % forb + Distance to lek	5	203.1	213.4	1.95	0.27	0.99
Constant (null)	1	302.2	304.2	92.80	0.00	1.00
Nest survival						
Treatment + VOR^2 + % grass	5	695.6	705.6	0.00	0.47	0.47
VOR^2 + % grass	4	698.1	706.1	0.48	0.38	0.85
Year + VOR^2 + % grass	7	696.4	708.4	2.84	0.11	0.96
Constant (null)	1	725.6	727.6	727.60	0.00	0.96

[1] Only models with Akaike weights (w_i) ≥ 0.01 are presented except for null models.
[2] K = number of parameters.
[3] AIC$_c$ indicates criterion adjusted for small sample sizes; ΔAIC$_c$ = change in criterion adjusted for small sample sizes; VOR = visual obstruction reading.

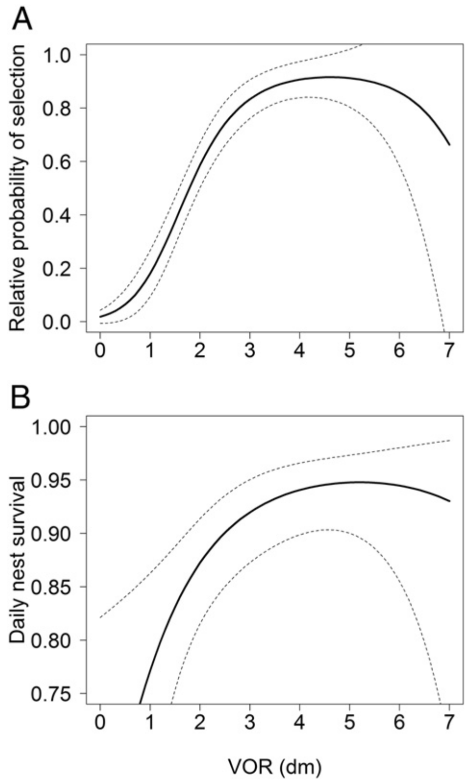

Fig. 4. Relationships for the **A,** relative probability of nest site selection, and **B,** daily nest survival vs. visual obstruction reading (VOR), a measure of nest concealment and index of vegetative biomass in the Flint Hills of Kansas, 2011–2013. Dotted lines represent 95% confidence intervals.

Discussion

Rangeland management actions directly impacted the quality of nesting habitat and indirectly influenced placement and subsequent survival of prairie-chicken nests at our study areas in the Flint Hills. Our results confirm the strong influence of vertical nesting cover on prairie-chicken nesting ecology (McNew et al., 2014), and explain variation in fecundity observed over gradients of rangeland management intensity (McNew et al., 2012a; Robbins et al., 2002).

Nest-site selection and nest survival of prairie-chickens in the unfragmented grasslands of our study areas were largely determined by vertical structure in vegetative cover. Nest-site selection and survival exhibited a quadratic response to VOR, maximized when visual obstruction was 3–6 dm. A quadratic response of nest-site selection and survival to vertical nesting cover is consistent with our previous research in more fragmented landscapes and supports a general recommendation of fire and grazing regimes that provide herbaceous nesting cover for prairie-chickens between 30 and 60 cm in height in tallgrass prairie (McNew et al., 2014). Nesting habitat on private properties managed intensively with annual spring burning and early stocking of cattle were of low quality; less than 2% of available nest locations at our study area had measures of vertical cover of at least 30 cm. Areas with optimal nesting cover between 30 and 60 cm were 8 times more prevalent in PBG treatments but still represented only 16% of available nesting locations.

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We found a direct relationship between VOR and factors determined by rangeland management practices, confirming proposed links between the negative effects of annual burning and intensive early cattle stocking on the quality of prairie-chicken nesting habitat (Robbins et al., 2002; McNew et al., 2012a, 2014). Interestingly, we observed different influences of stocking rate on vertical nesting cover between the two rangeland management treatments. Nesting cover decreased with stocking rate on properties managed with more traditional intensive burning and grazing regimes, but was relatively unaffected by stocking rate on properties managed with PBG. Variable responses among the different rangeland management treatments can be explained by the grazing behavior of cattle. Pastures managed with intensive early stocking and annual burning were burned in their entirety, resulting in uniform grazing by cattle. In PBG treatments, cattle focused their grazing activity on patches burned in the current year, effectively resting unburned patches (Fuhlendorf and Engle, 2001). Thus, up to two-thirds of a pasture in a PBG treatment received little to no grazing, and nesting cover on unburned patches was relatively unaffected by stocking rate within a pasture.

Quality of nesting habitat has direct influence on productivity in grouse (Bergerud, 1988; Pitman et al., 2005), and nest survival is a limiting factor for prairie-chicken populations (Peterson and Silvy, 1996; Wisdom and Mills, 1997; McNew et al., 2012a). Thus, information on the relationships between nest survival and rangeland management practices is critical for the conservation of prairie-chickens because the species occurs mainly on private rangelands managed for cattle production. Mean nest survival ($\pm$ SE) on patch-burn properties (0.21 ± 0.05) was twice as high as that on intensive properties (0.10 ± 0.03), suggesting a benefit of PBG to prairie-chicken populations. However, nest survival at both treatments was well below the threshold of 0.50 recommended to maintain a stable population of prairie-chickens (Westemeier, 1979; McNew et al., 2012a). Depressed nest survival may have been caused by drought conditions during the last 2 yr of our study in 2012–2013 (National Climatic Data Center, 2014). The growth of herbaceous plants that provide concealment for nests was reduced during drought years and nest survival was likely negatively impacted, especially in burned areas without residual plant growth from the preceding year (Leopold, 1933; Hernández et al., 2005). We expect the benefits of PBG to be even more pronounced in years with normal precipitation. Future research should evaluate interactive effects of weather and rangeland management on habitat quality, and identify the long-term effects of PBG on productivity and population dynamics.

In addition to improving nesting habitats for prairie-chickens, PBG regimes produce a shifting mosaic of vegetation that provides a host of ecosystem benefits. PBG results in an accumulation of fuel on unburned patches which increases the probability and intensity of fire during prescribed burning (Steuter, 1986). Increased fuel loads result in higher fire temperatures which aid in control of noxious weeds and woody plants that compete with native grasses and are unpalatable to cattle (Cummings et al., 2007). Temporally shifting patches of high quality forage disrupts the traditional movement patterns of cattle and reduces soil erosion along fences and cattle trails (J. Koger, Homestead Ranch, Kansas, personal communication). Furthermore, increased spatial heterogeneity of vegetation provides floristic and structural variability that increase grassland wildlife diversity (Fuhlendorf et al., 2006; Churchwell et al., 2008; Coppedge et al., 2008) and provides benefits to pollinators and invertebrate species that provide ecosystem services to temperate grasslands (Swinton et al., 2007; Black et al., 2011).

Implications

Over 90% of the extant distribution of prairie-chickens occurs in areas managed for cattle production. Habitat conditions of managed rangelands and ultimately the conservation of greater prairie-chickens are largely determined by the rangeland and grazing management decisions of private landowners and livestock producers. Our study is of global importance to the conservation of greater prairie-chickens because the core of their extant distribution is within the Flint Hills ecoregion, the vast majority of which is managed for cattle production (Johnson et al., 2011). Our results support a growing body of evidence that populations and communities of grassland birds are driven by the interactions of fire and grazing (Fuhlendorf et al., 2006; Coppedge et al., 2008; Hovick et al., 2014; Sandercock et al., 2015). Prairie-chicken nest-site selection and nest survival were directly related to vertical nesting cover and maximized in patches that were 1–2 yr post-burn. Nesting habitat was not affected by stocking rate in PBG management regimes because preferred nesting locations that resulted in the highest nest survival were unburned patches that were relatively unused by cattle. Overall, the quantity and quality of nesting sites was improved under PBG management. The selective preference for burned patches by cattle suggests that PBG management effectively releases prairie-chicken nesting habitat from the negative effects of overstocking. Previous research has found that revenues from cattle grazing under PBG are comparable to those under more intensive rangeland management regimes in tallgrass prairie systems (Rensink, 2009; Limb et al., 2011) and spatial heterogeneity in habitat conditions resulting from PBG may stabilize livestock productivity in a changing climate (Allred et al., 2014). Therefore, PBG holds promise as a conservation tool for mitigating declines of prairie-chickens and other grassland wildlife in tallgrass ecosystems. A potential obstacle to implementation of PBG as a rangeland management system on private lands is the time and equipment required to prepare and maintain fire breaks. Conservation programs that provide cost-shared support and technical assistance for implementing PBG management programs on private ranches may facilitate adoption by land owners.

Fire and grazing are key ecological disturbance processes that are necessary to maintain tallgrass prairie ecosystems (Fuhlendorf and Engle, 2004). Our results indicate that grassland management practices that resemble historically patchy fire and grazing regimes have the potential to improve demographic performance of prairie-chickens while resulting in profitable cattle grazing. Conservation and educational programs that facilitate a transition from homogenous grassland management to regimes that provide a shifting mosaic in herbaceous plant composition and structure are required to maintain the integrity of tallgrass prairie ecosystems (Fuhlendorf and Engle, 2004).

Acknowledgments

Our study was made possible by the generous cooperation of private landowners who allowed access to their lands, the Tallgrass Prairie National Preserve, and many dedicated field technicians who helped to collect field data. We extend special thanks to William Browning and Jane Koger for allowing access to their ranches and for their dedication to prairie-chicken research and conservation. Kristen Hase and Brian Obermeyer provided advice and logistical support. Funding and equipment were provided by the Kansas Department of Wildlife, Parks, and Tourism, Kansas State University, the National Park Service, and U.S. Fish and Wildlife Service Sportfish and Wildlife Restoration Program. We thank F. McNew and 3 anonymous reviewers for comments that improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.rama.2015.03.009.

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