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Research Paper

Effects of patch-burn grazing on breeding density and territory size of Dickcissels

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ABSTRACT. Ongoing habitat loss and intensification of management of remaining grasslands have led to large population declines of grassland songbirds in North America. As an alternative to intensive and homogeneous use of rangelands, patch-burn grazing creates heterogeneity in vegetative structure across the landscape by restoring the historical interaction of fire and grazing by large ungulates. Patch-burn grazing can increase diversity and abundance of grassland songbirds, but effects on local breeding density and territory size remain unknown, despite both being important in regulating population dynamics of species. Understanding patterns of density and territory size across the landscape is especially important for species experiencing steep declines in breeding habitat, such as grassland songbirds. During a two-year field study, we tested how densities and territory sizes of Dickcissels (*Spiza americana*), a common grassland songbird, varied among treatment units that were managed with patch-burn grazing or annual burning with or without grazing at a tallgrass prairie site in northeastern Kansas. We found that local densities of male Dickcissels did not differ among management regimes. However, within the patch-burn grazing treatment, densities were highest in the patch that was burned the previous year and lowest in the most recently burned patch. Furthermore, densities of male Dickcissels were lower in 2013 than in 2014, especially in burned and grazed units that had little vegetative structure and nest cover after the drought conditions of the previous two years. Territory size was not affected by rangeland management, while local densities of Dickcissels only explained ~10% of the variation in territory size. Our results show that patch-burn grazing does not negatively impact densities of breeding Dickcissels compared to annual burning and grazing. Moreover, Dickcissel populations might benefit from patch-burn grazing if males preferentially settle in unburned patches with high forb cover, especially during or directly following drought conditions.

Les effets du pâturage sur brûlis sur la densité des populations et la taille du territoire des Dickcissels

RÉSUMÉ. La diminution constante des habitats et l'intensification de l'exploitation des prairies restantes ont entraîné d'importantes baisses des populations d'oiseaux chanteurs des prairies en Amérique du Nord. Constituant une alternative à l'utilisation intensive et homogène des pâturages, les pâtures sur brûlis favorisent l'hétérogénéité de la structure végétative dans les paysages en rétablissant l'interaction historique entre le feu et le pâturage des grands ongulés. Les pâtures sur brûlis permettent d'augmenter la diversité et l'abondance des oiseaux chanteurs des prairies, mais leurs effets sur la densité et la taille des territoires des populations locales restent inconnus, bien qu'ils soient importants pour réguler la dynamique de population des espèces. Il est essentiel de comprendre les modèles de densité et de taille des territoires dans l'ensemble des paysages pour les espèces dont l'habitat de reproduction connaît une baisse importante, notamment les oiseaux chanteurs des prairies. Au cours d'une étude de deux ans sur le terrain, nous avons analysé l'évolution de la densité et de la taille des territoires du Dickcissel (Spiza americana), un oiseau chanteur commun des prairies, entre des unités de traitement gérées par le pâturage sur brûlis ou par le brûlis annuel avec ou sans pâture dans une vaste région de prairies d'herbes hautes au nord-est du Kansas. Nous avons constaté que la densité locale des dickcissels mâles n'était pas affectée par les différents modes de gestion. Toutefois, dans le cas du traitement par pâture sur brûlis, la densité la plus élevée correspondait au territoire qui avait été brûlé l'année précédente et la densité la plus faible se trouvait sur le territoire brûlé le plus récemment. En outre, la densité de dickcissels mâles était plus faible en 2013 qu'en 2014, en particulier sur les parcelles brûlées et affectées au pâturage qui présentaient une faible structure végétative et un nombre de nids limités par suite des conditions de sécheresse des deux années précédentes. La taille du territoire n'était pas affectée par la gestion des pâturages, tandis que la densité locale de dickcissels ne permettait d'expliquer qu'environ 10 % des variances en termes de taille de territoire. Nos résultats indiquent que le pâturage sur brûlis n'entraîne pas d'impact négatif sur la densité des populations de dickcissels par rapport au brûlis annuel suivi de l'affectation de la zone aux pâturages. En outre, les populations de dickcissels pourraient bénéficier du pâturage sur brûlis si les mâles s'installent de préférence dans les espaces brûlés présentant une forte présence de plantes herbacées non graminoïdes, en particulier pendant ou immédiatement après des périodes de sécheresse.

Key Words: *distance sampling; grassland; songbird; Spiza americana; tallgrass prairie; territoriality*

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INTRODUCTION

Over the past decades, grassland songbirds have shown some of the greatest population declines among bird communities in North America (Sauer and Link 2011, North American Bird Conservation Initiative 2016). Native grasslands are among the most rapidly declining ecosystems worldwide, with extensive habitat conversion and limited habitat protection (Hoekstra et al. 2005). Compared to preindustrialization, < 3% of North American tallgrass prairie habitat remains (Samson and Knopf 1994, Deluca and Zabinski 2011), and the majority of remaining grasslands are now managed with higher densities of grazing livestock (*Bos taurus*) and more frequent burning than was historically common (Knapp et al. 1999, Fuhlendorf et al. 2006, Mohler and Goodin 2012). Intensive and homogeneous use of managed rangelands leads to higher mass gains for domestic cattle, but reduces spatial variation in vegetative structure and cover in prairie habitats (Knapp et al. 1999, Fuhlendorf et al. 2006). Intensification of livestock production is associated with lower species diversity and abundance of arthropods (Joern 2005), mammals (Ricketts and Sandercock 2016), and grassland songbirds (Fuhlendorf et al. 2006, Powell 2006, Coppedge et al. 2008). Moreover, intensive rangeland management has been linked to increased rates of nest predation and brood parasitism of grassland songbirds (Churchwell et al. 2008, Davis et al. 2016), and is thought to be one of the main drivers of population declines of grassland birds in North America (Samson and Knopf 1994, Herkert et al. 2003, Sauer and Link 2011, North American Bird Conservation Initiative 2016).

Patch-burn grazing has been proposed as a relatively new rangeland management strategy that restores heterogeneity in vegetative structure of grasslands by recreating the historical interaction between fire and grazing by large ungulates (Stebbins 1981, Knapp et al. 1999, Fuhlendorf and Engle 2001). Under patch-burn grazing management, one section of a management unit is burned each year in a two- to four-year rotational scheme, while cattle are free to preferentially graze recently burned patches (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, 2009, Churchwell et al. 2008). The interaction of periodic fire and selective grazing by cattle results in a greater variety of vegetative structure and plant species composition among different management units (Ricketts and Sandercock 2016), and could benefit species diversity and abundance of grassland birds by improving habitat quality for specialists that require relatively undisturbed grasslands (Fuhlendorf et al. 2006, Powell 2006). Moreover, patch-burn grazing might provide habitat that improves the reproductive success of grassland songbirds by decreasing rates of nest predation and brood parasitism (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016). However, to date, the effects of patch-burn grazing management on local population density and territory size of grassland songbirds have not been investigated.

Local population density and territory size often regulate population numbers and are therefore key drivers of population dynamics (Brown 1969, Fretwell and Lucas 1969, Holmes et al. 1996). Both factors are often directly related to local habitat quality, which is predominantly driven by food availability (Stenger 1958, Wilson 1975, Smith and Shugart 1987, Marshall and Cooper 2004). However, other factors such as the availability of nest sites, potential mates, or local abundance and community composition of predators could also play a role (Hinde 1956, Brown 1964, 1969). By improving local habitat quality, patch-burn grazing might reduce territory size and increase local population densities of grassland songbirds. However, a minimum territory size is necessary for successful reproduction, which could restrict the number of breeding pairs that a given area can support, even if habitat quality is high (Fretwell and Lucas 1969, Krebs 1971). Understanding the effects of rangeland management on local population density and territory size is therefore especially important for management of species that have faced large-scale habitat loss, including many species of grassland songbirds.

We examined how local densities and territory sizes of male Dickcissels (*Spiza americana*), a grassland-nesting species, are affected by patch-burn grazing management of tallgrass prairie. Dickcissel populations in the eastern tallgrass prairie region have experienced large-scale declines in recent decades (1966–2015: -1% per year; Sauer et al. 2017), but are still relatively common, especially in grasslands with high forb cover and tall dense vegetation that functions as nest cover (Zimmerman 1971, 1993, With et al. 2008, Rahmig et al. 2009, Sauer and Link 2011). Like many species of territorial grassland songbirds, Dickcissel males defend small territories where foraging and most aspects of reproduction take place, including courtship, mating, and the rearing of young until fledging from the nest (Nice 1941, Finck 1984, Temple 2002). Dickcissels have a mating system based on resource-defense polygyny, and the reproductive success of males is strongly dependent on local habitat quality (Zimmerman 1971, Finck 1984, Sousa and Westneat 2013). Past studies of Dickcissels in Illinois and Kansas have reported large variability in territory size among males (0.3–1.1 ha based on 100% minimum convex polygons), with territory sizes decreasing with increasing habitat quality and local densities of males, but territory size has not been linked to rangeland management in this species (Zimmerman 1966, 1971, Harmeson 1974, Finck 1984).

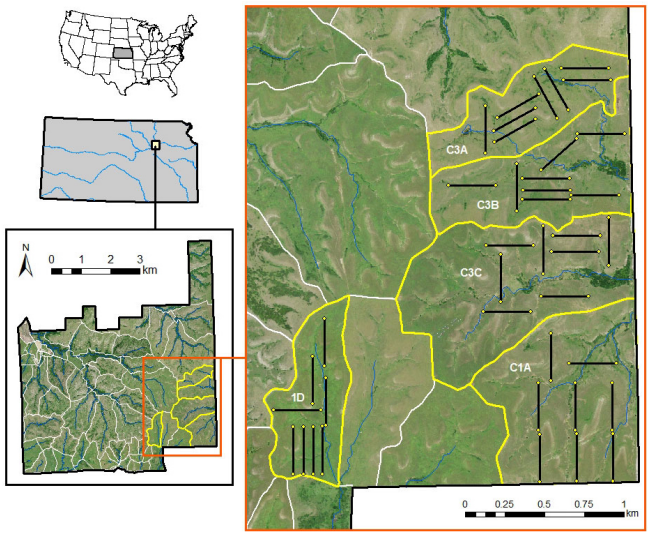
We surveyed male Dickcissels to estimate breeding densities and territory sizes at an experimental tallgrass prairie site in the Flint Hills of Kansas and compared our estimates among a unit that was managed with patch-burn grazing and two units that were annually burned with or without grazing by cattle. Unburned patches in a patch-burn grazing management system could improve the quality of breeding habitat of Dickcissels, as increased forb cover, vegetation height, and litter depth could lead to higher reproductive success (Fuhlendorf et al. 2006, Churchwell et al. 2008, Davis et al. 2016, Ricketts and Sandercock 2016). We therefore predicted that local breeding densities would be greater and territories would be smaller on unburned patches within patch-burn grazing managed units versus recently burned patches or annually burned units with or without grazing. As a second objective, we assessed whether the relationship between rangeland management and territory size of Dickcissels varies throughout the breeding season. Habitat quality of managed prairie can show substantial temporal variation, as the availability of prey items on the landscape increases throughout the breeding season, especially in recently burned pastures (Williams 2016). We therefore predicted that territory size of Dickcissels would decrease throughout the breeding season as habitat quality increases, and we expected to see greater declines in territory size in recently burned patches and management units.

METHODS

Study site and climate

In 2013 and 2014, we conducted our field project at the Konza Prairie Biological Station (hereafter Konza Prairie; 39°05' N, 96° 33' W), which is located in the northern Flint Hills eco-region, one of the largest remaining tracts of native tallgrass prairie (Fig. 1; Samson and Knopf 1994, With et al. 2008). The Konza Prairie is a 3487-hectare tallgrass prairie preserve in northeastern Kansas, and is part of the National Science Foundation-funded Long-term Ecological Research (LTER) Site Program. The Konza Prairie includes a landscape-scale fire and grazing experiment, and consists of > 60 experimental management units that receive different combinations of grazing and prescribed fire. The tallgrass prairie at Konza Prairie is dominated by native warm-season grasses including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), and has a diverse community of broadleaf forbs (Towne 2002).

Fig. 1. A map of our five management units and line transects within each unit (right), at the Konza Prairie Biological Station, northeastearn Kansas (left). Management units are delineated in yellow, while 300-m transects are shown as black lines. Together, C3A, C3B, and C3C were managed with patch-burn grazing (PBG) without cross-fencing, C1A was annually burned and grazed (ABG), and 1D was annually burned and not grazed (ABN).



The climate at Konza Prairie is relatively hot and humid during the growing season, but can exhibit considerable variation among years. Over the past century, the average annual temperature for Konza Prairie has been 13°C, but monthly average temperatures can be as high as 25–26°C in July and August. Annual precipitation averaged 799 mm (SD = 175 mm). About 75% of precipitation falls within the 6-month growing season (March to August), but late summer droughts in July and August are not uncommon (NOAA 2017).

Study species

Dickcissels are small-bodied songbirds (average body mass: males = 28.5 g, females = 25.2 g) that winter in northern South America and primarily breed in the prairie grasslands of the central United States. At Konza Prairie, male Dickcissels begin to arrive and start to establish breeding territories in early May. Females arrive after territories are established, begin nesting in late May, and typically complete their breeding season by early August. Within tallgrass prairie, Dickcissels select breeding habitats with dense cover, moderate to tall (25–150 cm) vegetation, moderate amounts of litter (5–15 cm), and a high number of song perches, where they build an open cup nest slightly raised from the ground (Temple 2002). Female Dickcissels can renest after nest failure, but normally raise a single brood per breeding season (Sandercock et al. 2008, Sousa 2012).

Experimental design

We estimated breeding densities and territory sizes of male Dickcissels in three management units (Fig. 1). Three contiguous management patches (C3A-C; 49.4–102.4 ha) formed a larger unit (219.3 ha) that was managed under a patch-burn grazing management regime with a 3-year fire rotation (PBG). A second management unit (C1A; 93.5 ha) was annually burned and grazed (ABG), and a third unit (1D; 41.6 ha) was annually burned and not grazed (ABN). Grazed units were stocked with cow/calf pairs at a density of 3.24 ha per pair from early May to early October (J. Briggs and K. C. Olsen, *personal communication*). Management units were treated with prescribed fire in early spring between mid-March to mid-April, and had been managed with the specified management regime for three or more years prior to the start of our field study. As a result of different burning and grazing regimes, vegetation composition and structure differed consistently among management units. Grass cover was higher and forb cover was lower in the annually burned and ungrazed unit compared to the patch-burn grazing and annually burned and grazed units. Litter depth was higher in unburned patches within the patch-burn grazing unit compared to recently burned patches and management units. Last, vegetation height, measured by visual obstruction, was highest in the annually burned and ungrazed unit and lowest in the most-recently burned patch in the patch-burn grazing unit (Verheijen 2017).

Densities of male Dickcissels

To estimate local breeding densities of males, we surveyed Dickcissels on eight 300-m line transects within each patch of the patch-burn grazing unit and eight transects in each of the other treatment units. Transects were > 50 m from other transects within the unit and > 100 m from the edge of the unit (Fig. 1). The two transects closest to the center of the management unit were surveyed three times during distinct sampling periods in late May, mid-June, and early July during both years. The other six transects were each surveyed once per year, with two transects surveyed once during each of the three sampling periods. Single transect surveys were generally completed within two hours by a single observer. During each survey, we identified male Dickcissels by plumage or song, and recorded the perpendicular distance of each bird to the transect line with a laser rangefinder (Bushnell, Yardage Pro 700). We also recorded the temperature, wind speed, and cloud cover at the start of each survey. All transect surveys started within a half hour of sunrise and were completed before

11:00 h. We did not conduct surveys during rainy, foggy, or overly windy (> 35 km/h) conditions. For further analysis, we divided our observations into 10-m bins, and truncated the data at a perpendicular distance of 125 m from each transect line because observations beyond that distance were sparse (N = 23).

To obtain unbiased density estimates for male Dickcissels, we used distance sampling techniques available in the "unmarked" package in R (Fiske and Chandler 2011, R Core Team 2017). Distance sampling methods assume that individuals are distributed independently of the line transect, are always detected when directly on the line transect, and do not move before detection, and that distances are recorded accurately (Buckland et al. 2015). The three assumptions were met here because territorial male Dickcissels are loud and conspicuous singers, often perched on top of forbs or shrub patches, and usually allowed observers to approach within ~50 m without being disturbed (B. H. F. Verheijen, *personal observation*). Distance sampling allowed us to estimate bird densities, which is an improvement over using raw counts to estimate abundance per transect (Powell 2006), and corrects for incomplete detection of birds along the line transect by estimating a detection probability curve. The general shape of the detection probability curve can be fit with alternate key-functions. We considered three functions: a half-normal, hazard rate, and a uniform key-function (Buckland et al. 2015).

To correct for any remaining effects of covariates on detection probability, we considered alternative models with effects of temperature, wind speed, cloud cover, year, treatment, patch-within-treatment, and observer, as well as an intercept-only model. The detection probability of grassland birds was expected to decrease with temperature, wind speed, and cloud cover, decrease with increasing vegetation height and structure, and might differ among observers, especially at long distances.

We tested the effects of patch-burn grazing management on Dickcissel density at two different scales. A treatment model included the annually burned and grazed unit, annually burned and ungrazed unit, and patch-burn grazing managed unit as a whole (K = 3), while a patch-within-treatment model included both annually burned management units and all three patches of the patch-burn grazing unit separately (K = 5). We further considered models with fixed effects of year or sampling period, as well as an intercept-only model. We then ran a model-set containing models with all possible combinations of explanatory variables for both the detection probability and density, as well as an intercept-only model, and ran all models with a half-normal, hazard-rate, or uniform key-function. To determine which combination of variables and key-function best explained the detection probability and density of Dickcissels, we ranked models by AICc-values, and tested goodness-of-fit of the top-ranked model with a χ^2 test based on the binned distance data (Burnham and Anderson 2002, Fiske and Chandler 2011). If multiple models were equally parsimonious (ΔAICc ≤2), we used model averaging based on AICc-weights to calculate final parameter estimates and standard errors that accounted for model-selection uncertainty. In preliminary analyses, models with a hazard rate key-function had consistently lower AICc-values than models with a half-normal or a uniform key-function as the detection function (ΔAICc > 7). We therefore report model selection results of models with a hazard rate key-function only.

Territory size

During June of 2013 and 2014, we mapped territory sizes of a subset of breeding male Dickcissels in each management unit. In addition, we mapped the territories of some individuals in both June and July 2014 to assess within-season variation in territory size in a matched-pairs design. Individual male Dickcissels defended separate territories that were much smaller than our management units, and were therefore considered independent samples in our analysis. To be able to identify individuals, we live-trapped Dickcissels with mist nets and recordings of territorial songs, and marked each male with a unique combination of colored leg bands. To increase our sample size, we also sampled a few unmarked males (N = 4) that could be individually identified by distinctive plumage or song variants (Schook et al. 2008). We determined territory size by using a mixture of flush- and spot-mapping (Wiens 1969, Fletcher and Koford 2003, Jones 2011). We flushed a target-bird and recorded locations for the flush and landing sites, and obtained additional locations by observing target-birds from > 50 m to avoid disturbing the behavior of the bird. If we did not obtain enough locations from a target-bird during our initial visit, we returned within the following two days to record additional locations. We recorded locations of all singing perches and boundaries of territorial disputes with other male Dickcissels in UTM coordinates to the nearest meter with a handheld GPS unit (Garmin, GPS 72). Territory mapping started at sunrise and was concluded before 14:00 h to avoid inactivity by males during the hottest part of the day.

For each male Dickcissel where we obtained at least 20 unique territorial locations, we calculated 95% kernel density estimates (KDEs) with the "adehabitatHR" package in R (Calenge 2006, R Core Team 2017). Previous studies have shown that 20 unique locations and 95% surface areas can provide an unbiased estimate of territory size, while excluding outlying locations that are rarely used (Worton 1989, Seaman and Powell 1996, Seaman et al. 1999, Fletcher and Koford 2003). We also calculated minimum convex polygons, but did not include those results because patterns were qualitatively similar to KDEs (Verheijen 2017). When using kernel density estimation, the selection of an appropriate smoothing parameter, *h*, is especially important, because smoothing restricts the distance at which individual locations influence the surface grid (Silverman 1986, Fieberg 2007, Hemson et al. 2005, Leonard et al. 2008). During preliminary analyses, we determined least squares cross-validation (LSCV) techniques were too conservative because interior areas between observations of an individual were often excluded. Conversely, a fixed smoothing parameter was inappropriate because of the large variation among males in territory size and configuration. An individual-specific smoothing parameter that accounted for variation in point density among individuals provided a better fit for each Dickcissel territory, with a mean *h* of 10.2 (range = 4.9-16.8, N = 72 males; Fig. A1.1).

We used general linear models to assess whether territory size of male Dickcissels was affected by year, treatment, patch-within-treatment, time since fire, or the number of observations, and tested for all possible interactions among our explanatory variables. To determine which combination of variables best explained territory size of Dickcissels, we compared AICc-values of all models (Burnham and Anderson 2002), and used model averaging based on AICc-weights if multiple models were considered equally parsimonious (ΔAICc ≤ 2). We further assessed

Table 1. Distance sampling model selection results for male Dickcissels (*Spiza americana*) at Konza Prairie, northeastern Kansas, for 2013 and 2014. Model selection was based on the number of parameters (*K*), Deviance, AIC and ΔAICc values, and Akaike weights (w_i). Possible model structures for the detection probability included an intercept-only model, and models with an observer effect. When modeling Dickcissel density, we considered an intercept-only model, or models with year, survey period, treatment, or patch-within-treatment effects. We only show models where $w_i > 0.01$.

Model Structure		Model Statistics				
Detection	Density	*K*	Deviance	AICc	ΔAICc	w_i
Observer	Year + Patch + (Year × Patch)	13	2719.16	2745.16	0.00	0.400
Constant	Year + Patch + (Year × Patch)	12	2721.47	2745.47	0.32	0.340
Observer	Year + Patch + Survey + (Year × Patch)	15	2718.08	2748.08	2.92	0.092
Constant	Year + Patch + Survey + (Year × Patch)	14	2720.46	2748.46	3.31	0.076
Observer	Year + Patch	9	2732.37	2750.37	5.21	0.029
Observer	Year + Patch + Survey + (Year × Patch) + (Year × Survey)	17	2717.14	2751.14	5.99	0.020
Constant	Year + Patch + Survey + (Year × Patch) + (Year × Survey)	16	2719.62	2751.62	6.46	0.016
Constant	Year + Patch	8	2735.62	2751.62	6.46	0.016

whether any differences in point estimates among treatments or other variables were significant by comparing 95% confidence intervals. To test the relation between territory size and male density, we restricted our data to June 2014, because we surveyed only a limited number of territories in 2013, and used general linear mixed models. To test whether territory size varied within-season for a subset of males, we used general linear mixed models and included bird ID as a random factor. All analyses were conducted with the "lme4" package or base functions of R (Bates et al. 2015, R Core Team 2017).

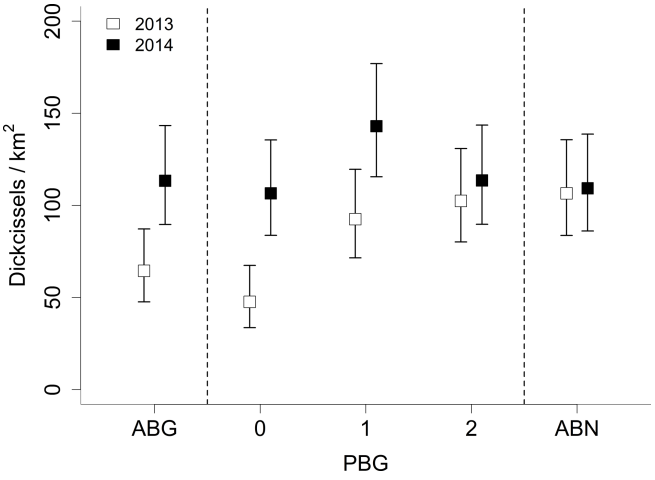
RESULTS

Densities of male Dickcissels

In 2013 and 2014, we completed 120 line transect surveys and recorded 744 observations of male Dickcissels to estimate local breeding densities. We found little support for treatment effects on the densities of male Dickcissels at our site, although densities tended to be lower on the annually burned and grazed unit (89.0 Dickcissels/km²; 95% CI = 73.3–108.1 Dickcissels/km²) compared to patch-burned and grazed (100.8; 95% CI = 88.6–114.7) and annually burned and ungrazed units (107.7; 95% CI = 89.9–128.9). Instead, our four highest ranked models all included effects of year, patch-within-treatment, and their interaction, with a combined model weight of 0.908 (Table 1).

Breeding densities of male Dickcissels in 2013 averaged 81.1 Dickcissels/km² (95% CI = 71.8–91.5). During that year, densities were lower in the most recently burned patch-burn grazing patch compared to the other two patch-burn grazing patches and the annually burned and ungrazed unit, while densities tended to be lower on the annually burned and grazed unit compared to those three treatment patches and units (Fig. 2). Compared to 2013, overall densities of male Dickcissels were 34% higher in 2014 (114.6; 95% CI = 103.5–126.9). We did not find any differences among our five treatment units in 2014. However, densities of male Dickcissels tended to be higher in the patch-burn grazing patch that was burned the previous year compared to the other treatment units (Fig. 2).

Fig. 2. Density of male Dickcissels (*Spiza americana*; ± 95% confidence intervals) at Konza Prairie, Kansas, for 2013 and 2014. Estimates were calculated separately by year for five rangeland management treatments: annual burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annual burned and not grazed (ABN). Overall densities of male Dickcissels on the patch-burn grazing treatment were 81.0 Dickcissels/km² (95% CI = 68.2–96.3) in 2013 and 120.9 Dickcissels/km² (95% CI = 104.0–140.4) in 2014.



When pooled across years, densities of male Dickcissels were lowest on the patch-burn grazing patch that was most recently burned (77.2 Dickcissels/km²; 95% CI = 62.9–94.8 Dickcissels/km²), and tended to be lower on the annually burned and grazed unit (88.9; 95% CI = 73.3–107.9) when compared to the patch-burn grazing patch that was burned the previous year (117.9; 95% CI = 99.0–140.4), with intermediate densities found on the annually burned and ungrazed unit (107.6; 95% CI = 89.9–128.7) and patch-burned grazing patch that had not been burned for two years (107.6; 95% CI = 89.9–128.7). We found weak support for an observer effect on the detection probability of Dickcissels (RI

Table 2. Model selection results for territory size of male Dickcissels (*Spiza americana*) based on 95% kernel density estimation for Konza Prairie, northeastern Kansas, for 2013 and 2014. We considered an intercept-only model, and models with possible effects of treatment, patch-within-treatment, time since last fire, the number of unique locations on territory collected for each bird (points), and a set of factorial and main effect models with effects of the number of unique points and any other variable. Model selection was based on the number of parameters (*K*), Deviance, AICc and ΔAICc values, and Akaike weights (w_i). We only show models where $w_i > 0.05$.

Model	*K*	Deviance	AICc	ΔAICc	w_i
Time Since Fire × Points	7	33.52	49.30	0.00	0.241
Time Since Fire	4	41.25	49.86	0.56	0.182
Time Since Fire + Points	5	39.46	50.38	1.08	0.140
Constant	2	46.29	50.46	1.17	0.134
Treatment	4	42.65	51.25	1.96	0.090
Patch	6	38.74	52.06	2.76	0.061
Points	3	45.78	52.13	2.84	0.058

= 0.549), but it introduced no bias in our estimates because the two observers alternated between transect lines. We did not find any effects of temperature, wind speed, cloud cover, year, treatment, and patch-within-treatment on detection probability of Dickcissels, presumably because we avoided surveying during unfavorable weather conditions (Table 1).

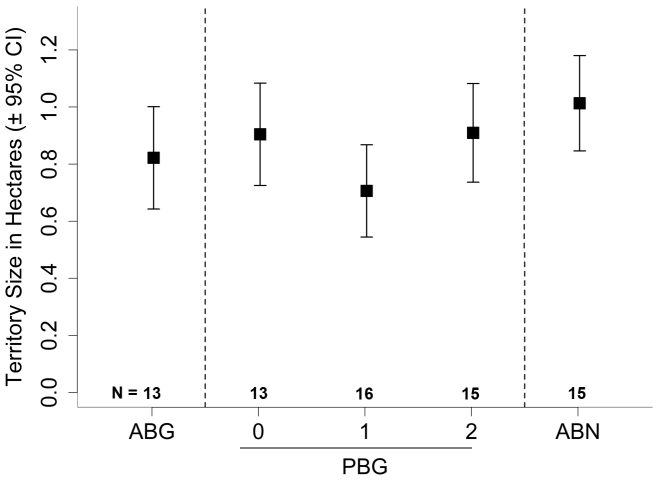
Territory size

During 2013 and 2014, we mapped at least 20 unique locations for the territories of 72 male Dickcissels across all management units (2013: N = 11, 2014: N = 61). Four male Dickcissels banded on our study area in 2013 returned in 2014 and their territories were mapped in both years. The territory sizes of all four males were highly variable between years (range = 0.22–0.67 ha), and our results remained unchanged if we selected one territory at random. We therefore accepted some pseudoreplication and included all estimates of territory size for these four birds in our analyses.

Overall, the average territory size of male Dickcissels was 0.87 ha based on 95% KDEs (95% CI = 0.79–0.95 ha; Fig. A1.2). Management treatment was not an important factor in explaining variation in territory size at our site (Table 2), but territory sizes tended to be smaller at the patch-burn grazing patch that was burned during the previous year compared to other patches and treatment units (Fig. 3). Variation in territory size was not well explained by any of our variables, although models containing time since fire as a factor had lower AICc values than the intercept-only model (Table 2). We found that territory size (TS) was negatively related to male density (TS = 1.75 - 0.008D, $P = 0.007$, Adj. $R^2 = 0.10$). Within the observed range of densities in 2014 (106–143 male Dickcissels/km²), there was a ~25% reduction in male territory size from 0.92 to 0.71 ha. However, no model explained much variation in territory size (max Adj. $R^2 = 0.100$).

In 2014, we mapped the territories of 26 male Dickcissels at the start of the season in early June and again later in the breeding season in mid-July. Average territory size based on 95% KDEs declined by 27% over the season (β = -0.215 ± 0.061SE), from 0.87 ha in June (0.73–1.01 ha) to 0.66 ha in July (0.53–0.78 ha; Fig. 4). Declines in territory sizes over the breeding season did not differ with prescribed fire (β = -0.122 ± 0.123), but tended to be greater in recently burned patches or units (0.28 ± 0.10SE ha; N = 13) than unburned patches (0.15 ± 0.07 ha; N = 13).

Fig. 3. Estimates of territory size for breeding male Dickcissels (*Spiza americana*; ± 95% confidence intervals) based on 95% kernel density estimates for Konza Prairie, Kansas, for 2013 and 2014, estimated separately for each treatment and patch-within-treatment. Treatments are labeled as followed: annual burned and grazed (ABG), patch-burned and grazed (PBG, 0–2 years since spring fire), and annual burned and not grazed (ABN).

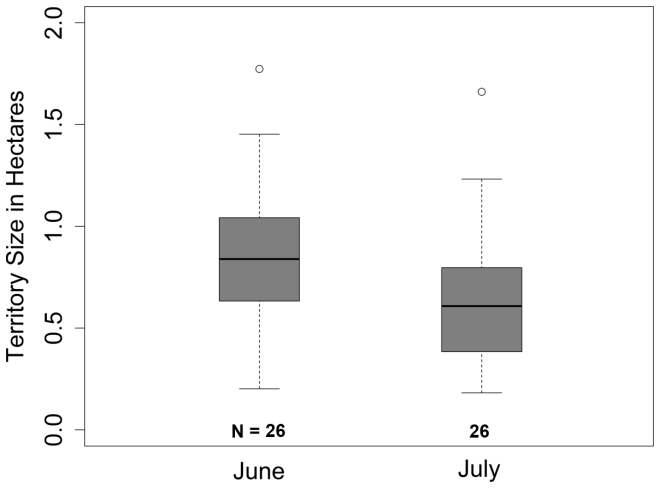


DISCUSSION

We provide some of the first estimates of local density and territory size for Dickcissels in managed tallgrass prairie. At our field site in northeastern Kansas, local densities of male Dickcissels were comparable across management treatments, but differed with grazing intensity and time since burning within the patch-burn treatment and among years. Territory sizes were inversely related to male density, but we found no effect of rangeland management on territory size, potentially because of

the large variation in territory size among individuals within management treatments. Last, we found that male Dickcissels had smaller territories in July than in June, but declines in territory size were not dependent on whether management units were recently burned or not.

Fig. 4. Within-season changes in the territory size of breeding male Dickcissels (*Spiza americana*; ± 95% confidence intervals) based on 95% kernel density estimates for Konza Prairie, Kansas, estimated separately for June and July 2014.



Management effects on density and territory size

Although densities of male Dickcissels were relatively comparable among treatments, densities were 33% higher at the patch-burn grazing patch that was rested from fire for one growing season and 21% higher at the patch that was rested for two growing seasons compared to the annually burned and grazed unit. Higher densities of male Dickcissels on rested patches could potentially be explained by the high forb cover due to the lack of fire (Ricketts and Sandercock 2016, Verheijen 2017), thereby creating high quality breeding habitat that might attract breeding Dickcissels (Zimmerman 1971, Finck 1984, Fuhlendorf et al. 2006, Weir et al. 2013). Earlier work on patch-burn grazing by Churchwell (2005) supports our findings that forb cover is an important driver of the density of male Dickcissels. At the Tallgrass Prairie Preserve in Oklahoma, Dickcissel densities were highest and territories were smallest in traditionally grazed pastures that, because of a lack of spraying, had higher forb cover than patch-burned and grazed pastures (Churchwell 2005).

The uneven distribution of males within the patch-burn grazing pasture might benefit the population dynamics of Dickcissels. Unburned patches within patch-burn grazing pastures could provide habitat that improves reproductive success of grassland songbirds by decreasing rates of nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016). If Dickcissels preferentially settle in patches with the potential for higher reproductive success, overall population growth would be higher in pastures that are managed with patch-burn grazing, despite local densities of Dickcissels being similar to annually burned and grazed pastures. Moreover, the lack of negative effects of patch-burn grazing on local densities of breeding Dickcissels compared to annually burned and grazed pastures complements previously described benefits of heterogeneous land-use on the diversity of plants, small mammals, and grassland songbirds (Fuhlendorf et al. 2006, Powell 2006, Coppedge et al. 2008, Ricketts and Sanderock 2016).

Although territory size of Dickcissels declined with local breeding density, our density models only explained 10–13% of variation in territory size, and we did not find any effects of rangeland management on territory size. One possible explanation could be that territory size showed large variation among individual males within management units at our site (range = 0.20–3.10 ha). Furthermore, we only observed a ~25% decrease in average territory size (0.92–0.71 ha) with density, while Zimmerman (1971) surveyed a larger variety of habitats and reported much stronger density-dependent reductions in territory size of ~50% (0.72–0.36 ha based on 95% minimum convex polygons) over the same range of densities, reaching a minimum threshold of 0.32 ha at a density of 148 male Dickcissels/km^2. If variation in habitat quality across rangeland management units is relatively small compared to the variation in habitat quality of patches within management regimes, the relationships between territory size and density, and territory size and management treatments, might be hard to observe.

Within-season variation in territory size

We found that territory sizes of Dickcissels at Konza Prairie declined by 22–27% over the breeding season. Territory sizes might be predicted to increase late in the breeding season after densities of male Dickcissels are reduced by territorial break-down and departure on migration (Zimmerman 1966). However, changes in territory sizes were not coupled to within-season variation in male densities, which remained constant throughout the breeding season. Instead, within-season variation in territory size of male Dickcissels might be a direct result of changes in food availability, and therefore habitat quality. Williams (2016) found that arthropod biomass in tallgrass prairie increases over the breeding season, especially in burned areas. Higher food availability in July could allow males to defend smaller areas with necessary resources later in the season (Stenger 1958, Wilson 1975, Smith and Shugart 1987, Marshall and Cooper 2004). At Konza Prairie, declines in territory size during the breeding season tended to be greater in recently burned units or patches, indicating that seasonal changes in food availability might affect territory size, but our sample sizes for comparisons were limited.

Annual variation in management effects

Densities of male Dickcissels in management units that were burned and grazed were lower in 2013 than 2014, whereas bird densities on other treatments were only slightly depressed. In burned units, the amount of standing biomass that is available for breeding is based on new vegetative growth, and grazed units will naturally have less standing biomass than ungrazed units (Ricketts and Sandercock 2016, Verheijen 2017). Weather conditions at out site were relatively similar between 2013 and 2014, and the average temperature and amount of precipitation during the growing season in either year were comparable to the long-term average (NOAA 2017, Verheijen 2017). However,

vegetation height of new growth was shorter and the amount of dead vegetation from previous years was lower in 2013 than 2014, possibly because of the legacy effects of drought conditions at our site in 2011 and 2012 (Verheijen 2017). Large-scale droughts could cause considerable annual variation in local population densities by displacing Dickcissels out of their core breeding range (Temple 2002). Contrastingly, Rahmig et al. (2009) found higher densities of breeding Dickcissels during dry conditions, suggesting that other factors such as annual variation in food availability or the local abundance of nest predators or Brown-headed Cowbirds as brood parasites could also play a role. Nevertheless, our results imply that at our site in northeastern Kansas, patch-burn grazing might benefit Dickcissel populations by providing suitable breeding habitat in unburned patches during or following drought conditions.

CONCLUSION

Our field study is the first test of the effects of patch-burn grazing management on the breeding density and territory size of grassland songbirds. Although densities and territory sizes of male Dickcissels were comparable between annually burned and grazed and patch-burn grazed pastures, we found positive effects of unburned patches within patch-burn grazing units on densities of male Dickcissels, while territory sizes tended to be smaller on unburned patches. Management-specific estimates of territory size are essential for the conservation of grassland songbirds because territory size and competition among males could limit population densities in high-quality breeding habitat. Moreover, because conspecific attraction plays an important role in the colonization of grasslands by grassland songbirds, prairie fragments need to be large enough to contain multiple breeding territories (Ahlering et al. 2006, Andrews et al. 2015). Rangeland management that leads to smaller territories could therefore reduce the minimum patch size that is necessary for breeding grassland songbirds to successfully colonize prairie fragments. Although the scope of our study is limited to one site in northeastern Kansas, we show that patch-burn grazing management does not limit breeding densities of Dickcissels compared to annually burned and grazed pastures. Furthermore, Dickcissels preferentially settle in unburned patches, which complements previously described benefits of patch-burn grazing on the population dynamics of breeding Dickcissels (Churchwell et al. 2008, Hovick et al. 2012, Davis et al. 2016, Verheijen 2017). Patch-burn grazing management might therefore benefit Dickcissel populations by providing higher quality breeding habitat in some patches, while supporting similar or higher breeding densities than on more intensively managed pastures, especially during or following drought conditions.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1343

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Fig. A1.1. Three representative examples of territories of male Dickcissels (designated by unique four-letter codes corresponding to their colored leg bands) that illustrate how a variable smoothing parameter selected by the h_{ref} function is better than one overall smoothing parameter for all birds, because the individual-specific h_{ref} successfully avoids under- and over-smoothing by taking the location density of each individual into account. Shown are kernel densities of three birds with a smoothing parameter of $h = 5$, $h = 10$, and $h = 15$ as well as the selected smoothing parameter by the h_{ref} function. Black dots indicate observation locations and dashed lines show a 100% minimum convex polygon overlaid on each kernel density estimate.

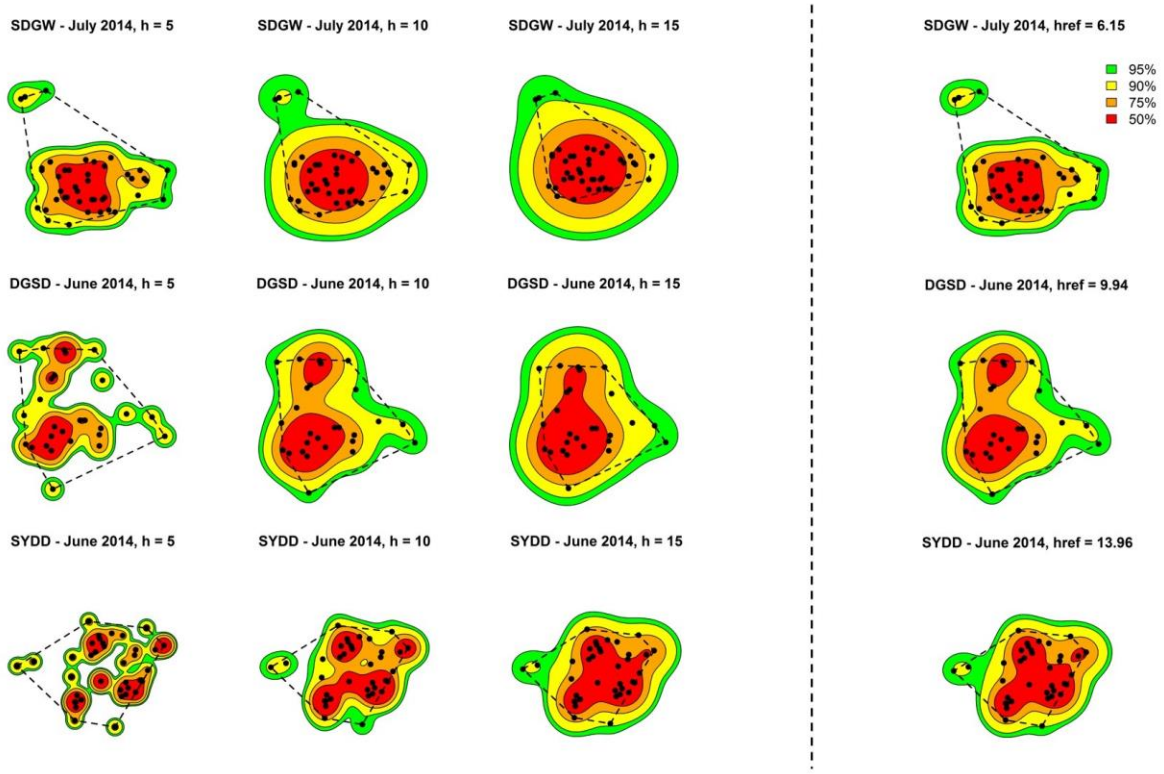

Fig. A1.2. Maps of territories of male Dickcissels at Konza Prairie, Kansas, for June 2013 and 2014. Bird were individually marked with color bands or had distinctive vocalizations or plumage markings. Territories are based on 95% minimum convex polygons (A: 2013, B: 2014) and 95% kernel density estimates (C: 2013, D: 2014). Most of the unoccupied area in our maps included unmarked males that were defending territories but were not mapped.