Grassland fragmentation affects declining tallgrass prairie birds most where large amounts of grassland remain

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Mark R. Herse · **Kimberly A. With** · **W. Alice Boyle**

Abstract

Context Habitat fragmentation can exacerbate the negative effects of habitat loss for some species. Mitigating fragmentation is difficult, however, because population responses depend on species-level traits (e.g., dispersal ability, edge sensitivity) and landscape context (e.g., habitat amount). Thus, conservation requires determining not only if, but also where and why, fragmentation matters.

Objectives We aimed to determine if and where grassland fragmentation affects tallgrass prairie birds, which have declined precipitously due to land-use change. We surveyed four edge-sensitive species at 2250 sites (10,291 total surveys) across eastern Kansas, USA, over two breeding seasons. We assessed how the occurrence of each species varied with different levels of fragmentation in local landscapes comprising different grassland amounts.

Results Fragmentation clearly mediated positive relationships between occurrence probability and grassland area for all four species. The direct effect of fragmentation was greater than that of grassland area for two species. Moreover, fragmentation reduced the occurrence of each species by at least half in some contexts. Fragmentation effects were most pronounced in landscapes comprising $\sim$ 50–90% grassland, and less pronounced or absent in landscapes comprising < 50% grassland, which were occupied relatively infrequently.

Conclusions Conservation efforts should minimize 'perforation' of large grasslands by woody vegetation and land development, which not only replace grassland, but also often create disproportionately large amounts of grassland edge. Identifying mechanisms responsible for edge effects could further inform species-level conservation. Our results counter assertions that fragmentation does not matter or only matters when habitat is scarce or for species that are dispersal limited.

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Introduction

Humans have "severely altered" more than three-quarters of Earth's terrestrial environments and now use more than one-third of land surface for crop or livestock production (IPBES 2019). Temperate grasslands and savannas have been particularly hard hit; globally, nearly half (46%) have been replaced by crop agriculture and other land uses (Hoekstra et al. 2005). In North America, more than 97% of tallgrass prairie—an ecosystem that once covered 160 million hectares throughout the Great Plains—has been lost (Samson and Knopf 1994), and most of what remains is either managed intensively for cattle production or unmanaged (With et al. 2008; Rahmig et al. 2009). Shrubs and trees are encroaching on unmanaged grasslands due to fire suppression, climate change, and surrounding land development (Briggs et al. 2005; Kulmatiski and Beard 2013; Ratajczak et al. 2014; Scholtz et al. 2018). Additionally, ever-increasing energy demands mean that oil and gas wells and wind turbines are now common within grasslands (Hovick et al. 2014; Shaffer and Buhl 2016). Only 2% of remaining native grasslands in the USA are publicly owned and managed for conservation (NABCI 2011), reflecting the generally low level of protection that temperate grasslands receive worldwide (Hoekstra et al. 2005).

The widespread loss and fragmentation (e.g., increased edge-to-area ratio; Ewers and Didham 2006; Hargreaves 2019) of grasslands has caused drastic declines of grassland-dependent taxa (Samson and Knopf 1994; Brennan and Kuvlesky 2005; Azpiroz et al. 2012; Grand et al. 2019). Grassland birds have declined more rapidly than any other bird group in North America, and one-third of all grassland bird species are of conservation concern (NABCI 2016). Many grassland bird species have large habitat area requirements and thus do not occur in landscapes without expansive grassland (Ribic et al. 2009; Patten et al. 2011; Winder et al. 2014). Grassland birds also often avoid edges of grassland patches, particularly near woodlands or energy facilities, where they may experience greater risk of adult mortality (Hovick et al. 2014), nest depredation (With 1994; Renfrew and Ribic 2003; Klug et al. 2010), and/or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Winter et al. 2000). Likewise, empirical studies have found that the occurrence and abundance of some tallgrass prairie birds correlate more strongly with interior or 'core' grassland area away from edges than total grassland area per se (e.g., Helzer and Jelinksi 1999; Renfrew and Ribic 2008; Herse et al. 2018). However, few of these studies have assessed the importance of fragmentation while accounting for habitat amount (i.e., area), which could further inform management decisions about when to prioritize increasing total habitat area versus increasing core habitat area (Collinge 2009; Herse et al. 2018).

Empirical studies of population and community responses to habitat amount and fragmentation have mostly focused on determining which of these two landscape factors has a greater overall effect (Fahrig 2003, 2017; Hadley and Betts 2016), and in recent years, divergent views have emerged regarding the importance of fragmentation (Didham et al. 2012; Fahrig 2013; Hanski 2015; Fletcher et al. 2018a; Fahrig et al. 2019). For example, the 'habitat amount hypothesis' posits that within local landscapes, relationships between species richness and habitat distribution are determined primarily by habitat amount irrespective of fragmentation (Fahrig 2013). Nevertheless, numerous theoretical and empirical studies indicate that both population and community responses to habitat amount can be mediated by fragmentation, and responses depend on species-level traits (e.g., dispersal ability, sensitivity to habitat edges) and landscape context (e.g., amount of habitat present, edge type) (Ewers and Didham 2006; With 2016; Haddad et al. 2017; Martin 2018; Valente and Betts 2019). For instance, species with small habitat-area requirements and/or low sensitivity to habitat edges may only be affected by fragmentation in landscapes where habitat is scarce (With and King 2001; Villard and Metzger 2014). In contrast, fragmentation may affect species with large habitat area requirements and/or high sensitivity to habitat edges in landscapes where habitat is relatively abundant (With and King 2001; Villard and Metzger 2014). Importantly, it is not always clear whether edge-sensitive species will exhibit landscape-scale responses to fragmentation, because the amount of edge habitat in a landscape is partially a function of the total amount of habitat present, and edge effects could reflect indirect responses to either habitat amount (Ruffell et al. 2016) or fragmentation (With and Pavuk 2012). Thus, understanding if and where populations are affected by fragmentation requires assessing

responses to different levels of fragmentation while accounting for habitat amount (Didham et al. 2012; Villard and Metzger 2014).

We adopted a landscape-scale approach to test whether variation in the occurrence of four species of declining, edge-sensitive tallgrass prairie birds is driven by grassland area irrespective of fragmentation (consistent with the habitat amount hypothesis; Fahrig 2013) versus grassland area and fragmentation in combination. We further assessed where along a grassland amount gradient (i.e., 20–90% grassland) fragmentation effects occurred by comparing species occurrence probabilities across landscapes containing different levels of grassland fragmentation while accounting for grassland amount. We predicted that grassland area and fragmentation would influence tallgrass prairie birds in one of four possible ways: (A) fragmentation has no effect, such that only grassland amount affects species occurrence (Fig. 1a); (B) fragmentation only matters at low habitat amounts (e.g., < 30%) (Fig. 1c; Andrén 1994; Fahrig 1997); (C) fragmentation only matters at intermediate habitat amounts, where the amount of edge habitat is greatest and varies most (Fig. 1c; Villard and Metzger 2014); or, (D) fragmentation matters across a range of habitat amount, with population responses depending on a species' edge sensitivity (Fig. 1d; With and King 1999, 2001). We assessed these relationships and tested predictions by modelling the effects of grassland area and fragmentation on species occurrence probabilities across thousands of local landscapes in eastern Kansas, USA.

Fig. 1 Plots illustrating predictions about how tallgrass prairie birds would respond to variation in habitat amount (i.e., area) and fragmentation. If total grassland amount irrespective of fragmentation determines species occurrence, we predicted that **A** responses to a given amount of grassland would not vary between landscapes containing aggregated versus fragmentated grassland configurations. Alternatively, if fragmentation mediates grassland area effects, we predicted that responses to a given amount of grassland would depend on fragmentation **B** only in landscapes where habitat is scarce, or **C** only in landscapes containing intermediate amounts of grassland (where fragmentation varies most), or **D** within a range of habitat amount that depends on a species' edge sensitivity (grey lines indicate low edge sensitivity whereas black lines indicate high edge sensitivity). We illustrated species-habitat relationships as non-linear functions to make them clearer, but they could also be more linear

Methods

Focal species

We surveyed Grasshopper Sparrows (*Ammodramus savannarum*), Henslow's Sparrows (*Ammodramus henslowii*), Upland Sandpipers (*Bartramia longicauda*), and Greater Prairie-Chickens (*Tympanuchus cupido*) because all four species exhibit sensitivity to grassland area and edges (Johnson and Temple 1990; Helzer and Jelinski 1999; Winter et al. 2000; Ribic et al. 2009) and are currently declining across all or most of their geographic ranges (Houston et al. 2011; Rosenberg et al. 2016; Sauer et al. 2017). Both sparrow species are migratory and have male-
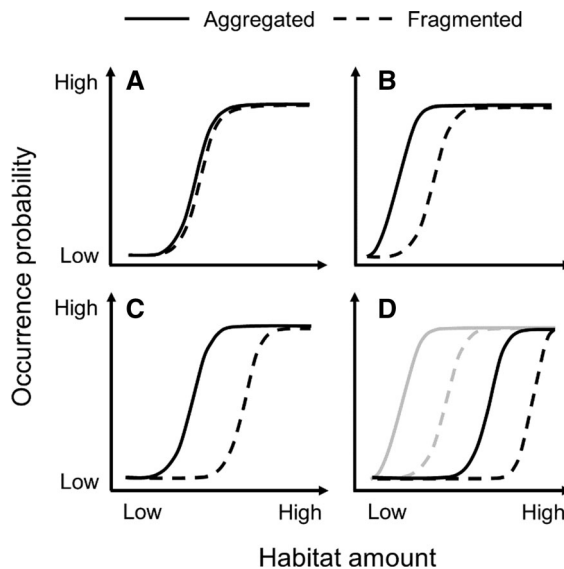
territorial breeding systems. Grasshopper Sparrows are widely distributed, nesting in both arid and mesic grasslands characterized by moderate vegetative cover (Vickery 1996). Grasshopper Sparrows are recognized as a Common Bird in Steep Decline by Partners in Flight (PIF) because populations have declined by > 60% since 1970 (Rosenberg et al. 2016). Henslow's Sparrows favor undisturbed mesic grasslands with tall native vegetation and dense litter (Zimmerman 1988). Henslow's Sparrow population trends are uncertain due to their rarity and elusiveness, but the species is recognized as a Species of Continental Concern (SCC) by PIF because their preferred habitat is extremely scarce (Rosenberg et al. 2016). The Greater Prairie-Chicken is also considered a SCC by PIF and listed as Vulnerable by the International Union for

Conservation of Nature because populations have declined by > 50% over the past half-century (Bird-Life International 2016; Rosenberg et al. 2016). Prairie-chickens require expansive and heterogeneous grasslands as they use different prairie habitats for lekking (competitive mating displays), nesting, and brood-rearing (Patten et al. 2011). Upland Sandpipers are listed as a species of conservation concern in 22 states and provinces in North America (Houston et al. 2011). A long-distance migrant, the species has a male-territorial breeding system and nests in temperate grasslands in North America characterized by low vegetative cover (Houston et al. 2011).

Study area and bird surveys

Our study area covered ∼ 65,000 km² of eastern Kansas, USA, including most of the Flint Hills ecoregion and parts of the Central Irregular Plains and Western Corn Belt Plains ecoregions (Omernik 1987) (Fig. 2). Approximately 80% (2 million ha) of North America's remaining tallgrass prairie is in the Flint Hills, where rocky soils prevent crop agriculture and native perennial grasses are managed for cattle production (With et al. 2008). Areas outside the Flint Hills are dominated by crop agriculture, but also contain hayfields and pastures.

We conducted point-count bird surveys during the breeding seasons of 2015 and 2016 along North American Breeding Bird Survey (BBS) transects and new transects that we established (Supplementary Material) (Herse et al. 2017, 2018). Both BBS and new transects were primarily along unpaved, infrequently-traveled secondary roads (Supplementary Material), which cause minimal bias in grassland bird surveys (Lituma and Buehler 2016). Eastern Kansas is almost entirely privately owned, and secondary roads provide an efficient means to survey extensive areas while minimizing potential survey bias (Lituma and Buehler 2016). During each 6-min survey, observers recorded presence or absence of each focal species detected within an unlimited radius. In total, we surveyed 1425 points located along 57, 19.2-km transects in 2015. In 2016, we added additional points to all transects, and 18 new 30-point transects, resulting in a total of 2250 survey points located along 75, 23.2-km transects (Fig. 2). Each year we began surveying in early April, which corresponds with sparrow and sandpiper arrival and peak prairie-chicken lekking activity. We finished
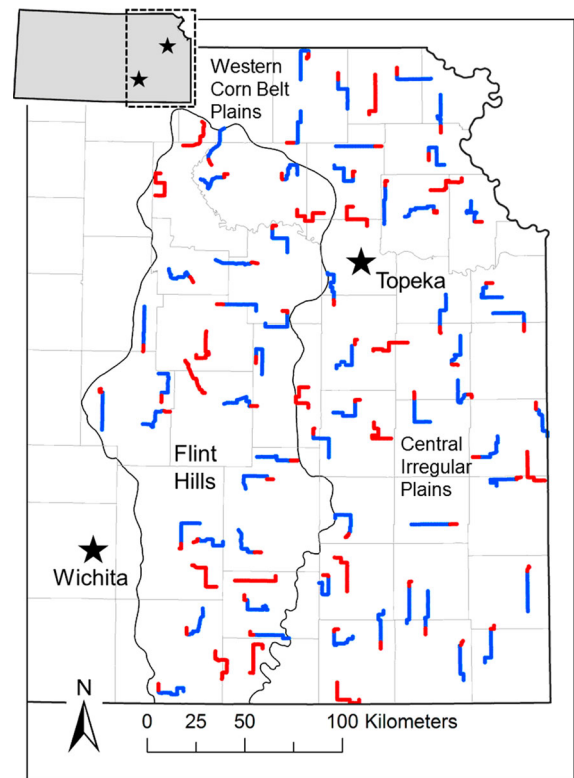

Fig. 2 Map of our study area and the 75, 30-point (23.2-km) transects we surveyed for tallgrass prairie birds in eastern Kansas, USA. Blue lines represent portions of transects we surveyed in 2015 and 2016, whereas red lines represent portions we surveyed only in 2016. Thin black and grey lines are boundaries of the Flint Hills ecoregion and state counties, respectively. The rectangular shape in the upper left inset is Kansas, which is in central USA

surveys in late July when most breeding ends. We aimed to survey all transects three times per season during successive 'rounds' of surveys. Start and end dates of each survey round overlapped by < 1 week when heavy rains constrained survey schedules. We separated consecutive visits to the same transect by ≥ 2 weeks. 'Early season' began 7 April in 2015 and 9 April in 2016, 'mid season' began 13 May in 2015 and 20 May in 2016, and 'late season' began 15 June in 2015 and 27 June in 2016. Late-season surveys ended by 23 July in 2015 and 29 July in 2016. We describe survey protocols and observer training in more detail in the Supplementary Material.

Landscape factors and spatial scales

Given the study objectives, we considered total grassland area and fragmentation around point-count stations as sources of variation in the occurrence of each species. The broad spatial extent of our study region, coupled with the inherent dynamics of tallgrass prairie ecosystems and private land ownership, precluded mapping finer-scale distributions of each species' preferred prairie habitat, which varies locally and seasonally with weather and rangeland management (Fuhlendorf et al. 2006; With et al. 2008). Thus, using land-cover data developed by the Kansas Applied Remote Sensing Lab from classified satellite imagery (Peterson et al. 2010), we calculated grassland area as the percent area comprising grassland at different spatial scales (described below; Table S1), combining both warm- and cool-season grasslands because all study species breed in both types (Vickery 1996; Houston et al. 2011; Jaster et al. 2013; Matthews et al. 2013). We used grassland edge density as a measure of grassland fragmentation at each scale (Table S1) because focal species in this study are known to be edge-sensitive (Johnson and Temple 1990; Helzer and Jelinski 1999; Winter et al. 2000; Ribic et al. 2009), and because alternative metrics such as number of grassland patches could obscure variation among landscapes in their proportion of edge habitat. We calculated edge density as the length (m) of grassland edge abutting trees or shrubs, croplands, waterbodies, or developed areas (i.e., commercial, industrial, or residential zones) per ha grassland. The overall accuracy of land-cover classifications was 86.2% (Peterson et al. 2010).

We summarized percent grassland and grassland edge density within spatial scales corresponding with the dispersal distances and space-use areas of the focal species (McGarigal et al. 2016; Fletcher et al. 2018b) using ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA) and Fragstats 4.2 (McGarigal et al. 2012). We defined the most local scale as the area within 400-m radii ($\sim$ 50 ha) of each survey point, which encompassed within-season dispersal distances of $>$ 50% of individuals of each sparrow species (Young 2017; Williams and Boyle 2018), as well as observers' maximum detection radius ($\sim$ 250 m) measured previously (Herse et al. 2017, 2018). Because individuals of both sparrow species sometimes disperse over larger distances within breeding

seasons (Young 2017; Williams and Boyle 2018), we doubled the extent while holding the resolution of land-cover data (30 m $\times$ 30 m) unchanged, summarizing land cover within 800-m ($\sim$ 200 ha) and 1600-m ($\sim$ 800 ha) radii. Due to larger detection distances of some prairie-chickens and sandpipers (estimated by observers to sometimes be $>$ 400 m away), we only considered intermediate (800-m radii) and broad (1600-m radii) scales when modelling habitat associations for these species. The intermediate scale corresponds with the minimum patch-area requirements of sandpipers in fragmented landscapes ($\sim$ 200 ha; Vickery et al. 1994), whereas the broad scale corresponds with mean breeding-season home range size of sandpipers in the Flint Hills (8.4 km^2; Sandercock et al. 2015). Breeding-season home ranges of prairie-chickens are similar or larger in size ($>$ 7–12 km^2), with space use and nesting concentrated near leks (Patten et al. 2011; Winder et al. 2014). Thus, because we almost always detected prairie-chickens while lekking, these two scales represent potential core breeding-season home-range areas for this species.

Statistical models

Ecologists often estimate species occurrence probabilities using occupancy models designed to account for imperfect detection (e.g., MacKenzie et al. 2002, 2003). We did not use occupancy models for two main reasons. First, occupancy models estimate site occupancy and detection probabilities by assuming that sites are closed to immigration and emigration between secondary sampling periods within primary sampling periods (e.g., between individual surveys within breeding seasons, such as in this study; Mackenzie et al. 2002, 2003). Thus, if we fit occupancy models to our data, we would have to assume that birds did not move in or out of sites (described below) over entire breeding seasons. However, both focal sparrow species are highly dispersive within breeding seasons (Herse et al. 2017; Williams and Boyle 2018), and sandpipers and prairie-chickens often utilize multiple core areas within large breeding home ranges (Patten et al. 2011; Winder et al. 2014; Hill et al. 2019), which violates the closure assumption of occupancy models and would likely lead to biased estimates (Mackenzie et al. 2002, 2003, 2005; Hayes and Monfils 2015).

Second, this study aimed to assess how patterns of species occurrence varied with grassland area and fragmentation, and we did not expect potential imperfect detection to vary systematically with these landscape factors. Thus, we modelled the apparent occurrence of each species using binomial generalized linear mixed models (GLMMs; Bolker et al. 2009), including a random effect of transect in all models to account for spatial non-independence in the survey design. We defined 'sites' as areas within which observers could detect each species and classified a site 'occupied' by a given species if we detected the species during ≥ 1 survey of either study season or 'unoccupied' otherwise. Despite minimizing imperfect detection by hiring seven trained observers (3–4 per season in addition to MRH), rotating observers among transects, surveying each site five times on average (detailed below), and following standardized protocols (see Supplementary Material), we expected that survey effort and timing could have affected detection. Thus, we included fixed effects of survey effort (number of surveys) and the time of morning when we conducted surveys (represented analytically by survey point number because we surveyed points in a consistent order during each visit; Supplementary Material) in all models to account for these potential sources of variation in apparent occurrence. We defined 'landscapes' as areas within 400-, 800-, and 1600-m radii of survey points. We only considered landscape factors assayed within 800- and 1600-m radii scales for models of sandpipers and prairie-chickens due to their large detection distances, as described above.

For each species, we first compared alternative models to determine (i) the spatial scale over which percent grassland and grassland edge density affected apparent occurrence most strongly, (ii) whether effects of percent grassland and grassland edge density were interactive versus additive only, and (iii) whether the relationship between apparent occurrence and percent grassland was linear versus non-linear. Constraining individual models to include only landscape variables assayed at a single spatial scale ("pseudo-optimized single scale" approach; McGarigal et al. 2016), we considered alternative models representing all possible combinations of (i) spatial scale, (ii) interactive versus non-interactive effects of landscape variables, and (iii) linear versus quadratic versus logarithmic (i.e., pseudo-threshold) effects of percent grassland.

Each model also included fixed effects of survey effort and survey point number, as described above. Correlations among fixed predictor variables (percent grassland, grassland edge density, survey effort, and survey point number) used together were low ($r \leq 0.38$; Supplementary Fig. S1). We scaled all predictors to allow direct comparisons of slope estimates (i.e., partial regression coefficients or effect sizes), which are based only on the variation attributed to a given predictor after holding all the others constant (Abdi 2004). Therefore, the slope estimate for a given predictor provides a measure of its relative overall importance for estimating apparent occurrence probability. We fit models using 'lme4' package in software R (Bates et al. 2019; R Core Team 2019) and compared competing models using corrected Akaike's information criterion (ΔAICc; Burnham and Anderson 2002). Next, we removed uninformative parameters (i.e., those with slope estimate confidence intervals overlapping zero) from the most parsimonious model if doing so reduced AICc. We then validated the resulting 'final' model of each species by verifying that standardized residuals were not spatially autocorrelated (Supplementary Fig. S2) using correlograms ('ncf' pacakge; Bjørnstad 2019) and that overdispersion was negligible using χ^2 tests (Bolker et al. 2009). As additional measures of fit, we estimated the proportion of variance in apparent occurrence explained by fixed effects only and by each final model including the random effect of transect (Table 1) ('MuMIn' package; Barton 2019; Nakagawa et al. 2017).

Assessing where fragmentation affected species occurrence

To determine where fragmentation per se influenced species occurrences most strongly along the grassland-area gradient, we used the final model for each species to assess the predicted relationship between apparent occurrence and percent grassland when grassland configurations were aggregated (i.e., contained small proportions of grassland edge) versus fragmented (i.e., contained large proportions of grassland edge) (Figs. 1, 3). We only predicted relationships across the range of grassland area where fragmentation varied considerably (20–90% grassland; Fig. 3; Supplementary Fig. S1). We used a single value of grassland edge density to represent each configuration

Table 1 Slope parameter estimates ($\hat{\beta}$) and standard errors (SE) for predictor variables in the most parsimonious (i.e., lowest AICc) models of species apparent occurrence

Statistic	Grasshopper Sparrow	Henslow's Sparrow	Greater Prairie-Chicken	Upland Sandpiper
Sites occupied	1004/2250 (45%)	99/2250 (4%)	195/2250 (9%)	576/2250 (26%)
Transects occupied	74/75 (99%)	36/75 (48%)	30/75 (40%)	58/75 (77%)
Model fixed effects	Slope estimate (SE)			
Intercept	0.03 (0.16)	− 3.77 (0.31)***	− 6.01 (0.63)***	− 1.90 (0.18)***
Grass	1.21 (0.10)***	0.89 (0.30)**	1.10 (0.23)***	0.58 (0.13)***
Grass^2	− 0.47 (0.10)***	− 0.84 (0.33)*		
Edge	− 0.71 (0.09)	− 1.17 (0.25)***	− 0.76 (0.18)***	− 1.36 (0.11)***
Grass × edge				− 0.21 (0.10)*
Number of surveys	0.46 (0.09)***	0.42 (0.15)**	0.59 (0.30)§	0.53 (0.10)***
Survey point	− 0.15 (0.07)*		− 1.57 (0.16)***	
Variance explained				
Conditional R^2	0.51	0.16	0.61	0.48
Marginal R^2	0.39	0.13	0.24	0.30

Percent grassland ('Grass') and grassland edge density ('Edge') were measured within 400-m radii in models of Grasshopper Sparrows and Henslow's Sparrows, and 1600-m radii for Greater Prairie-Chickens and Upland Sandpipers. Estimates are based on scaled variables and thus directly comparable. Asterisks indicate significance level (***< 0.001, **< 0.01, *< 0.05, §< 0.1). The proportion of the variance in apparent occurrence explained by each full model versus only fixed effects are indicated by conditional R^2 and marginal R^2, respectively, and based on the delta method

type (aggregated versus fragmented) for modelling predictions, basing values on those observed in our study region (Fig. 3). Interdependence between percent grassland and grassland edge density precluded using the overall minimum and maximum observed edge densities to represent aggregated and fragmented configurations, respectively, in all contexts, because grassland edge density varied with grassland amount (Fig. 3; Supplementary Fig. S1). Thus, we chose edge density values that reflected extreme configurations which we observed across the entire gradient of 20–90% grassland. To that end, we identified the minimum and maximum edge densities observed within each 10%-grassland increment from 20–90% grassland at each spatial scale, and then used the highest minimum value of grassland edge density observed across all increments at a given spatial scale to represent 'aggregated' configurations, and the lowest maximum edge density to represent 'fragmented' configurations (Fig. 3). This approach allowed us to assess the effect of grassland fragmentation on the apparent occurrence of each species in landscapes comprising a given amount of grassland

while accounting for the effect of that amount of grassland.

Results

We completed 10,291 point-count bird surveys over two breeding seasons (3656 in 2015 and 6635 in 2016) at 2250 sites, visiting most sites 4–5 times in total (mean 4.5, median 5, range 2–6). Henslow's Sparrows and Greater Prairie-Chickens were each recorded at < 10% of sites and on fewer than half of the transects (Table 1). Upland Sandpipers and Grasshopper Sparrows were each recorded at approximately one-quarter and one-half of sites, respectively, and on most transects. Holding grassland area and fragmentation effects constant, apparent occurrence of all species increased with survey effort. Apparent occurrence of Grasshopper Sparrows and Greater Prairie-Chickens was also higher at sites surveyed earlier in the morning (Table 1). Having accounted for variation in apparent occurrence caused by effects of survey effort and timing, we subsequently regarded residual variation as representing an index of true occurrence.
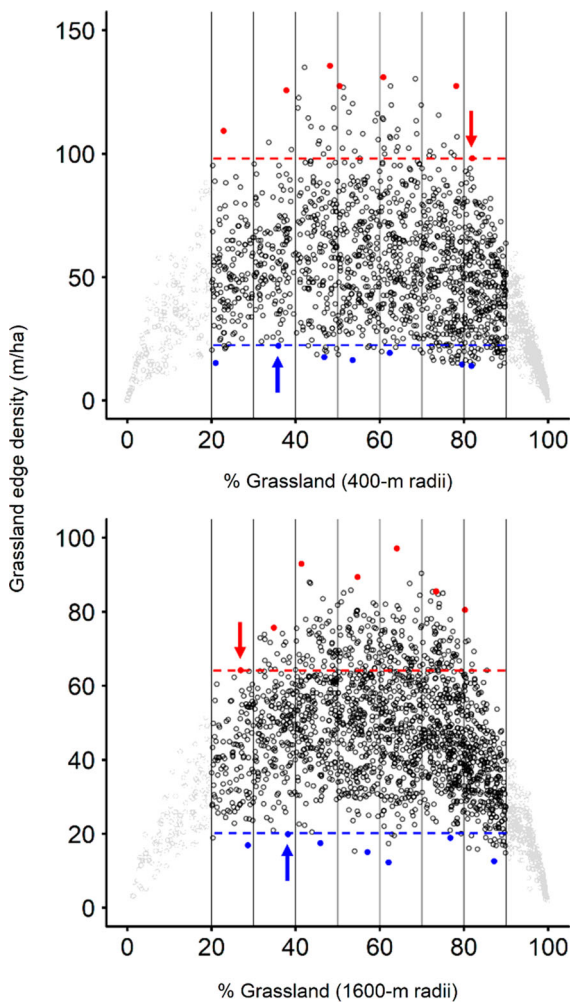
Fig. 3 Plot illustrating how we selected edge density values to define aggregated versus fragmented grassland configurations for model predictions. Each circle represents one of 2250 local landscapes (centered on individual survey sites) and the corresponding values of percent grassland and grassland edge density. Black circles represent landscapes comprising 20–90% grassland (the range of percent grassland over which modelled predictions), whereas light grey circles represent landscapes that fall outside that range. Solid blue and red dots indicate minimum and maximum edge densities, respectively, within each 10%-grassland increment from 20 to 90% grassland (marked by black vertical lines). Arrows and dashed lines indicate the highest minimum and lowest maximum values of grassland edge density observed across all increments, which we used to define 'aggregated' and 'fragmented' configurations, respectively, in model predictions

The occurrence of Grasshopper Sparrows and Henslow's Sparrows correlated most strongly with landscape factors within 400-m radii, whereas Greater Prairie-Chicken and Upland Sandpiper occurrence

correlated with landscape factors most strongly within 1600-m radii (Supplementary Tables S2–S5). Occurrence of all species increased with percent grassland, with both sparrow species responding non-linearly (Table 1; Fig. 4). Grassland edge density was negatively associated with the occurrence of all four focal species (Table 1; Fig. 4). Overall, the direct effect of grassland edge density on species occurrence was greater than that of percent grassland for Grasshopper Sparrows and Upland Sandpipers (Table 1). Moreover, the magnitude of the fragmentation effect on sandpipers depended strongly on percent grassland, as indicated by a significant interaction term (Table 1). Grassland fragmentation reduced the occurrence of sandpipers in landscapes comprising 20–90% grassland, with fragmentation effects being most pronounced in landscapes containing 90% grassland (Fig. 4). Even in the absence of significant interactions, fragmentation reduced the occurrence of the other species by at least half in some contexts (Fig. 4). Fragmentation effects on the occurrence of sparrows were most pronounced in landscapes comprising ~ 50–90% grassland. Confidence limits for the occurrence of prairie-chickens within aggregated versus fragmented grasslands overlapped across the entire grassland-area gradient, but the estimates differed most at 90% grassland (Fig. 4).

Discussion

Fragmentation clearly mediated the effects of grassland area on the occurrence of four declining tallgrass prairie bird species. Fragmentation effects were most pronounced in landscapes comprising ~ 50–90% grassland (Fig. 4), reflecting the focal species' strong preferences for large tracts of grassland and high sensitivity to grassland edges (Johnson and Temple 1990; Helzer and Jelinski 1999; Winter et al. 2000; Ribic et al. 2009). Conversely, fragmentation effects were less pronounced or absent in landscapes comprising < 50% grassland as these landscapes were occupied relatively infrequently regardless of the level of fragmentation (Fig. 4). This result suggests that when grassland is scarce, edge habitat is unavoidable for focal species and modifying grassland configuration to reduce habitat edge-to-area ratio may not attract more birds. It could also explain why the focal species are absent from many of North America's
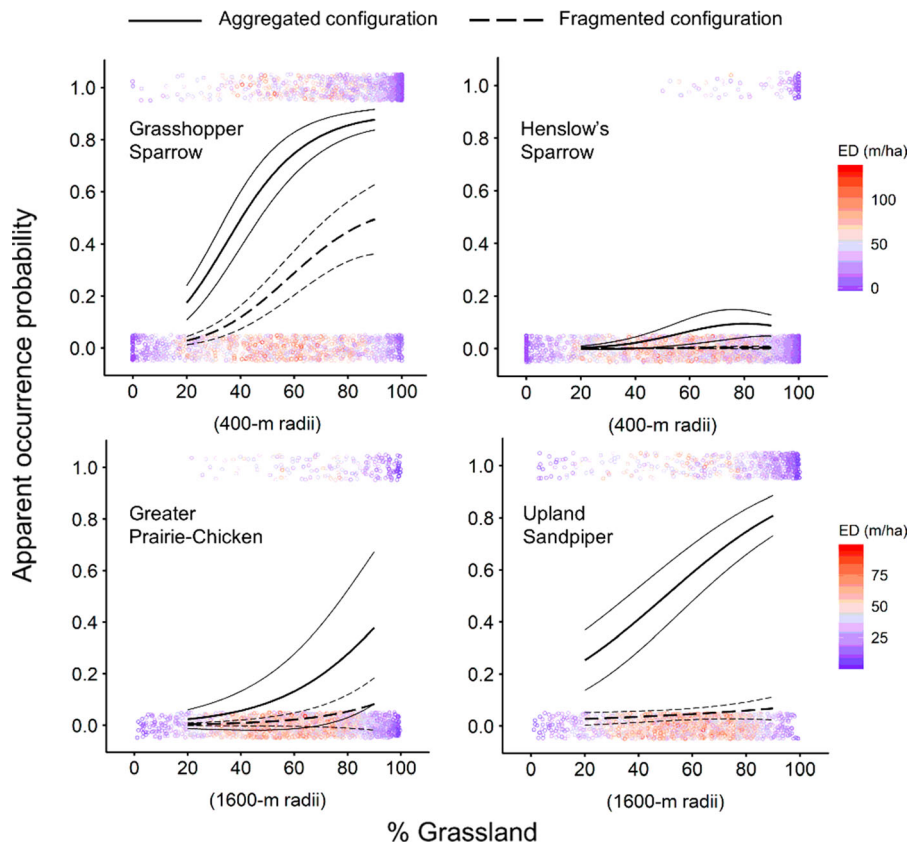
Fig. 4 Grassland fragmentation mediated relationships between apparent occurrence and percent grassland for four tallgrass prairie bird species. To illustrate where fragmentation effects were most pronounced, we plotted relationships between apparent occurrence and percent grassland in landscapes containing 'aggregated' versus 'fragmented' grassland configurations. We defined 'aggregated' configurations as having low edge density (400-m radii landscapes = 22.2 m/ha; 1600-m radii landscapes = 19.9 m/ha) and 'fragmented' configurations as having high edge density (400-m radii landscapes = 98.2 m/ha; 1600-m radii landscapes = 64.2 m/ha). Circles are the raw presence-absence data for each species, offset slightly along the y axis to make them more visible and colored to show variation among landscapes in grassland edge density (ED). Thin lines around estimates indicate 95% confidence limits for fixed effects only. Estimates are based on the most parsimonious model (i.e., lowest AICc) for each species and account for variation in apparent occurrence that is attributable to differences among sites in survey effort and timing

remaining tallgrass prairies, which tend to be confined to relatively small fragments (Herkert 1994; Ribic et al. 2009). Theoretical models have predicted that a species' response to habitat amount and fragmentation should be influenced more by edge-sensitivity than area-sensitivity (With and King 2001). However, many grassland birds are apparently both edge- and area-sensitive (Ribic et al. 2009; Winter et al. 2000), which has undoubtedly contributed to population collapses following landscape change (Brennan and Kuvlesky 2005; NABCI 2016).

The landscape-scale models developed in this study tended to be better at explaining variation in the occurrence of species that were relatively common

(Table 1). The low proportion of variance explained by models of Henslow's Sparrow occurrence (Table 1) likely reflects both their rarity and stringent habitat preferences that are not simply reflected in total grassland area and grassland edge density. Despite strongly favoring sites embedded in large grasslands with low edge density, Henslow's Sparrows were absent from hundreds of such sites. Some apparent absences of Henslow's Sparrows could be due to imperfect detection. However, the remarkable rarity of Henslow's Sparrows in expansive prairie must be at least partially explained by intensive rangeland management practices in eastern Kansas (Reinking 2005; With et al. 2008), where annual fires,

heavy grazing, and frequent haying reduce vegetation height and density in ways that reduce habitat quality for Henslow's Sparrows (Reinking 2005). Thus, preserving or increasing core grassland area without simultaneously reducing the intensity of management of those grasslands is unlikely to benefit this species (Fuhlendorf et al. 2006; With et al. 2008; Hovick et al. 2015b).

Greater Prairie-Chickens were like Henslow's Sparrows in that they strongly favored expansive grasslands and were frequently absent from such grasslands, probably due in part to the intensity of rangeland management and resulting lack of vegetative cover. Another aspect of the prairie-chicken results hints that fragmentation effects may depend on edge context; grassland edge negatively affected prairie-chicken occurrence (Table 1), but confidence limits for estimates in aggregated versus fragmented landscapes overlapped over the entire gradient of grassland amount (Fig. 4). This could be caused by prairie-chickens responding differently to grassland-to-cropland versus grassland-to-woodland edges, which collectively comprise most grassland edges in the study region. Although prairie-chickens consistently avoid woody edges (Matthews et al. 2011; McNew et al. 2014), they sometimes select areas near crop fields, which may provide suitable combinations of vegetative cover for nesting and bare ground for feeding (Matthews et al. 2011). Thus, treating cropland and woody edges as equivalent may obscure finer-scale responses to landscape features. We recommend that land managers recognize the potential threats and values associated with different edge types (Winter et al. 2000; Ries et al. 2004; Herse et al. 2018).

Most temperate grasslands worldwide have already been lost to, or fragmented by, agricultural development (Hoekstra et al. 2005). Remaining grasslands are still subject to an array of anthropogenic threats and disturbances. One such threat is the pervasive spread of buildings and energy infrastructures that intersect and dot, or 'perforate,' grassland patches (Hovick et al. 2014, 2015a). Because patterns of grassland perforation are spatially irregular, small amounts of grassland loss via perforation can disproportionately increase the edge-to-area ratio of grassland to levels typically associated with greater loss via agricultural development. Thus, for edge-sensitive species with large habitat-area requirements, habitat fragmentation may only matter in landscapes comprising large amounts of

habitat (e.g., > 50%) where habitat perforation is the main cause of habitat loss. Conversely, fragmentation may matter less for species such as those we studied where, regardless of spatial configuration, habitat area is insufficient to attract viable numbers of individuals. Thus, future development should avoid expansive tracts of habitat, and when development is unavoidable, minimize the amount of perforation and resulting edge that it creates.

Another major source of habitat perforation in grasslands is woody encroachment. In mesic tallgrass prairies, fire-free periods of > 3 years allow shrubs and trees to establish and grow large enough to survive subsequent fires and ultimately transition to shrublands or woodlands within a few decades (Ratajczak et al. 2014). Furthermore, agricultural development can contribute to woody encroachment by increasing edge area where young shrubs and trees are less susceptible to fires (Scholtz et al. 2018). Thus, woody encroachment can be both a product and driver of grassland loss and fragmentation, and undoubtedly contributed to the fragmentation effects we found. Likewise, preventing woody encroachment, particularly in expansive grasslands such as the Flint Hills of eastern Kansas, is necessary for reversing grassland bird declines in North America (Fuhlendorf et al. 2017; Tack et al. 2017).

Rethinking expectations
about where fragmentation matters

Ecologists often expect fragmentation to matter most when habitat is scarce (Fahrig 1998; Hanski and Gaggiotti 2004; Hanski 2015; Supplementary Fig. S3). For example, Hanski (2015) stated, "everybody agrees that in the case of land-coverings such as forests, fragmentation makes little or no difference if the amount of habitat is large, [covering] more than 20–30% of the landscape." This notion is rooted in island biogeography and metapopulation theories wherein fragmentation negatively affects populations by inhibiting dispersal (MacArthur and Wilson 1967; Levins 1969; Hanski 1998). Indeed, dispersal-limited populations become increasingly vulnerable to isolation as habitat becomes confined to distant patches that are too far away to reach, which often does not occur until more than half of the habitat in a landscape is lost (With and Crist 1995; King and With 2002; Swift and Hannon 2010). However, this is not always the case;

theoretical models have shown that species with weak dispersal ability can be influenced by fragmentation where habitat covers as much as 80% of a landscape (King and With 2002). Habitat can also become effectively isolated for vagile species if individuals are unwilling to disperse. For example, some tropical understory birds avoid dispersing across forest clearings despite being able to (Van Houtan et al. 2007). Thus, when fragmentation inhibits dispersal, the range of habitat amount where fragmentation matters depends on a species' dispersal propensity, which may be influenced by characteristics of the intervening matrix between habitat patches (Ewers and Didham 2006; Boesing et al. 2018).

Importantly, dispersal is not the only mechanism via which fragmentation can negatively affect populations. The focal species of this study are not dispersal-limited within the spatial scales we considered, eliminating dispersal as a mechanism that could explain the negative responses we observed to fragmentation. Instead, fragmentation in local landscapes probably affected grassland birds via negative edge effects (Winter et al. 2000; Herse et al. 2018; Lockhart and Koper 2018). For instance, in expansive North American prairies, energy infrastructure can displace adult Greater Prairie-Chickens and/or increase their mortality via collisions (Hovick et al. 2014). Similarly, the presence of woody vegetation within or beside grasslands can increase nest predation rates by snakes and mid-sized carnivores for Henlsow's Sparrows, Grasshopper Sparrows, and other grassland-obligate birds such as Dickcissel (*Spiza americana*) (Winter et al. 2000; Klug et al. 2010). Negative edge effects such as these and others are not unique to tallgrass prairie birds and have been documented in places ranging from North America to Borneo and in taxa ranging from ants to ungulates (Suarez et al. 1998; Ewers and Didham 2006; Brodie et al. 2015; Pérez-Rodríguez et al. 2018). Thus, edge-mediated fragmentation effects can occur in landscapes comprising small, intermediate, and/or large amounts of habitat and depend on edge context and species' responses to different edge types (Ewers and Didham 2006; Herse et al. 2018).

Conclusions

The results of this study run counter to assertions that fragmentation does not matter (Fahrig 2013) or only matters when habitat is scarce (Fahrig 1998; Hanski and Gaggiotti 2004; Hanski 2015). Fragmentation mediated the effects of habitat area on declining tallgrass prairie birds, likely by increasing proportions of edge habitat, which the focal species often avoid. Fragmentation effects were most pronounced in landscapes comprising large amounts of grassland and less pronounced or absent in landscapes comprising small amounts of grassland as they were inhabited relatively infrequently. In expansive prairie, small amounts of grassland perforation can create disproportionately large amounts of edge habitat that deter birds from settling. Thus, large grasslands are not necessarily suitable if they lack enough core habitat away from edges. Consequently, preventing further land development and woody encroachment in remaining large prairies is crucial to reversing the rapid declines that grassland birds are currently experiencing. Additional research is needed to identify the species-level traits that determine if, where, and why fragmentation matters, to help guide species-level conservation.

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