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Local-scale Habitat Associations of Grassland Birds in Southwestern Minnesota

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Abstract.—Conservation of obligate grassland species requires not only the protection of a sufficiently large area of habitat but also the availability of necessary vegetation characteristics for particular species. As a result land managers must understand which habitat characteristics are important for their target species. To identify the habitat associations of eight species of grassland birds, we conducted bird and vegetation surveys on 66 grassland habitat patches in southwestern Minnesota in 2013 and 2014. Species of interest included sedge wren (*Cistothorus platensis*), Savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*Ammodramus henslowii*), dickcissel (*Spiza americana*), bobolink (*Dolichonyx oryzivorus*), and western meadowlark (*Sturnella neglecta*). We calculated correlation coefficients between vegetation variables and species density as measures of linear association. We assessed curvilinear relationships with loess plots. We found grassland birds on 95.5% of surveyed sites, indicating remnant prairie in southwestern Minnesota is used by grassland birds. In general individual species showed different patterns of association and most species were tolerant of a wide variety of habitat conditions. The most consistent pattern was a negative association with both the quantity and proximity of trees. Our findings that individual species have different habitat preferences suggest that prairie resource managers may need to coordinate management efforts in order to create a mosaic of habitat types to support multiple species, though tree control will be an important and ongoing management activity at the individual site level.

Introduction

The pressures of a growing global human population have increased rates of land conversion from native ecosystems to human use while the rate of habitat protection remains static (Hoekstra *et al.*, 2005). Land conversion has been particularly prevalent in temperate grasslands, resulting in precipitous declines in the extent of this habitat type across much of North America, Europe, and South America (Askins *et al.*, 2007). More than 50% of native temperate grasslands in North America have been converted to human use (Hoekstra *et al.*, 2005). In particular row-crop agriculture has replaced temperate grasslands in much of North America (Askins *et al.*, 2007). For example more than 84% of western Minnesota is dedicated to agricultural production (Minnesota Department of Natural Resources 2006).

The loss of grassland habitat has caused corresponding declines in the populations of grassland-specific species (Samson & Knopf, 1994). Obligate grasslandbreeding birds, which require grassland for all aspects of their life history (Vickery *et al.*, 1999), have experienced

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declines among the most severe seen for any avian group (North American Bird Conservation Initiative U.S. Committee, 2014).

The issue of habitat loss is further compounded in remnant grasslands by habitat degradation. Barriers to visibility (Eason & Stamps, 1992) or movement decrease the suitability of potential habitat for these grassland specialists (Harris & Reed, 2002; Hamer *et al.*, 2006), which are adapted to open habitats characterized by lack of vertical stratification (Mengel, 1970). For instance the vertical complexity added to the habitat by woody vegetation has a negative effect on obligate grassland bird occurrences (Grant *et al.*, 2004; Thompson *et al.*, 2014). Trees and shrubs have been introduced to the grassland landscape through intentional planting and unintended encroachment (Fuhlendorf *et al.*, 2002) due to fire suppression and modified grazing patterns (Samson & Knopf, 1994; Askins *et al.*, 2007). Such interference with natural disturbance regimes that have historically maintained grassland also has allowed the accumulation of litter, shrubs, and taller, denser vegetation through the process of succession (McCracken and Rowan, 2005; Holimon *et al.*, 2012). In addition some invasive species such as smooth brome (*Bromus inermis*) compound the structural issues of succession both through dense growth patterns that decrease the heterogeneity of the habitat and by reducing litter decomposition rates (Askins *et al.*, 2007). In particular these structural changes reduce the suitability of habitat for those species that require shorter, sparser vegetation (Powell, 2006).

For migratory grassland obligates, the threats of habitat loss and degradation in breeding regions have been exacerbated by similar threats experienced during other periods of the annual cycle (Faaborg *et al.*, 2010; Renfrew *et al.*, 2013). For example in Chihuahua, Mexico—a wintering ground for over 90% of migratory Great Plains grassland birds—a combination of agricultural conversion, desertification, and shrub encroachment has drastically reduced habitat extent and predicted carrying capacity (Pool *et al.*, 2014). Similarly, grasslands of southeastern South America have been severely impacted by the expansion of livestock, agriculture, and forestry (Azpiroz *et al.*, 2012). Additional threats on wintering grounds, staging grounds, and migratory routes include exposure to toxic agrichemicals, illegal capture, and lethal control (Azpiroz *et al.*, 2012; Renfrew *et al.*, 2013).

To conserve prairie biodiversity in general and sensitive grassland bird species in particular, researchers and management agencies frequently determine that large natural areas of open grassland need to be protected (Askins *et al.*, 2007). Given the vulnerability of grassland bird species throughout their annual cycle and their troubling population declines, we wonder if these protected breeding habitats are continuing to support the species. Furthermore, it is important to ensure not only the protection of sufficient area of habitat, but also that those protected areas provide the necessary vegetation characteristics for the suite of grassland species. Providing appropriate vegetation is critical for the success of grassland bird conservation because vegetation characteristics affect predation, brood parasitism, and food availability mechanisms that have repercussions for habitat use, survival, and reproductive success (Rodewald & Yahner, 2001; Dunford & Freemark, 2005; Koper & Schmiegelow, 2006). However, not all birds respond in the same way to these vegetation characteristics: vegetation preferences are species-specific (Scott *et al.*, 2002). With this in mind, land managers need to understand which habitat characteristics are important for their species of interest because management and monitoring are both expensive and labor intensive.

The objectives of this study are first, to assess breeding populations of grassland birds on remnant grasslands in southwest Minnesota to determine whether current available habitat continues to support these sensitive species, and second, to determine which vegetation characteristics are most important for the occurrence and density of obligate grassland bird species on these remnant grasslands. We focused on seven grassland bird species: sedge wren (*Cistothorus paltensis*), Savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*Ammodramus henslowii*), dickcissel (*Spiza americana*), bobolink (*Dolichonyx oryzivorus*), and western meadowlark (*Sturnella neglecta*). Of these seven species, U.S.G.S. Breeding Bird Survey (BBS) records show that six are declining in Minnesota (Sauer *et al.*, 2017) and the Minnesota Department of Natural Resources (MN DNR) has designated six of these as Species in Greatest Conservation Need (MN DNR, 2016a).

We chose habitat characteristics to measure based on a comprehensive review (Fisher & Davis, 2010) of vegetation measures studied in conjunction with grassland birds. This review showed nine variables were especially relevant to occurrence, abundance, and habitat selection. These nine variables include percent cover of bare ground, grass, dead vegetation, forbs, and shrubs, as well as vegetation density and volume, litter depth, and vegetation height. In addition woody vegetation is a landscape-scale vegetation characteristic that can influence habitat use and suitability (Grant *et al.*, 2004; Caplat & Fonderflick, 2009). We included measures of the distance to the nearest tree and the percentage of tree cover within 100 m.

METHODS

STUDY AREA

Breeding birds and vegetation were surveyed at 66 grassland sites within the Prairie Parkland Province of the MN DNR Southern Region in southwestern Minnesota (West: −96.835452; East: −93.394982; North: 45.649784; South: 43.440906; Fig. 1). This region of Minnesota is 41,970 km^2 in area and the region's climate is temperate, with average annual temperatures of 9 C (Minnesota Deparment of Natural Resources, 2016b). Average annual precipitation is between 50 and 75 cm (Hanson & Hargrave, 1996).

Historically this region was characterized by tallgrass prairie (Hanson & Hargrave, 1996) but only about 1% of the original prairie remains in the Prairie Parkland Province of Minnesota (MNDNR, 2006). The predominant land use was row-crop agriculture, with greater than 84% of the province dedicated to agricultural production (MNDNR, 2006). The elevation ranges from 185 to 530 m above sea level. The topography of this region is primarily level to gently rolling (MNDNR, 2006) However, steeper hillsides and rockier soils in the extreme southwestern Coteau and the Minnesota River Valley regions result in reduced agricultural conversion in this portion of the study area and hence a greater concentration of remnant grassland habitat.

Native vegetation of the region included grass species such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), green needlegrass (*Nassella viridula*), and porcupine grass (*Hesperostipa spartea*) (Niesar & Hubbard, 1997) interspersed with forbs such as narrowleaved purple coneflower (*Echinacea angustifolia*), purple prairie clover (*Dalea purpurea*), white prairie clover (*Dalea candida*) and shrubs such as leadplant (*Amorpha canescens*) and prairie rose (*Rosa arkansana*). Many sites that we visited were dominated by nonnative or invasive plant species such as smooth brome, Kentucky bluegrass (*Poa pratensis*), reed canary grass (*Phalaris arundinacea*), Canada thistle (*Cirsium arvense*), and yellow sweet clover (*Melilotus officinalis*).

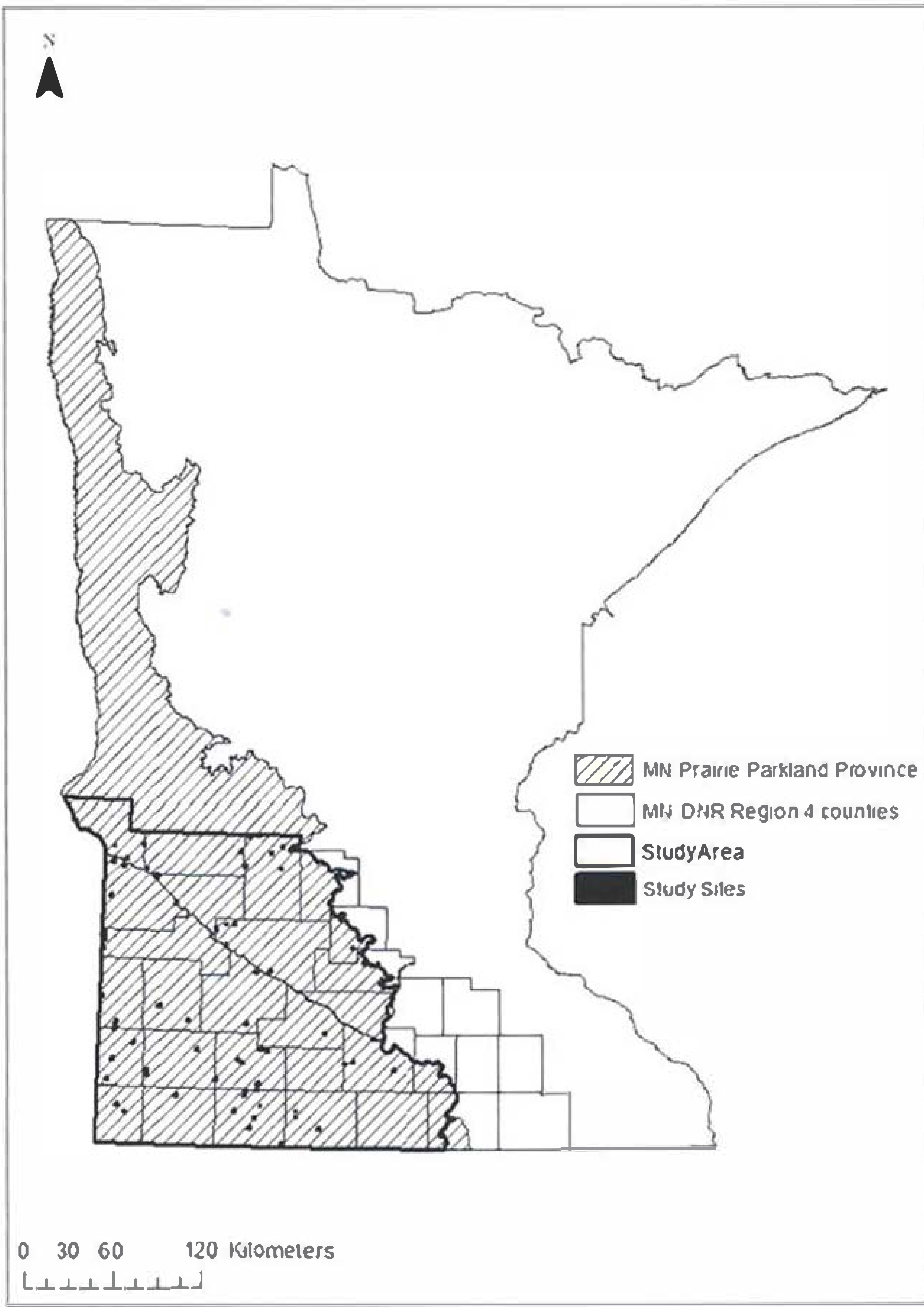

FIG. 1.—Locations of study sites within the Prairie Parkland Province ecoregion of Minnesota Department of Natural Resources Region 4 visited in 2013 and 2014

FIELD METHODS

Site selection.—During 2013 and 2014, we surveyed 66 sites within the study area. Sites were chosen in collaboration with MN DNR and The Nature Conservancy (TNC), on the basis that selected sites would have the potential to support breeding populations of grasshopper sparrows (a species of conservation concern in Minnesota) and other grassland birds. We used several sources of information to identify potential sites, including: (1) core areas and corridors identified in the Minnesota Prairie Landscape Conservation Plan (Minnesota Prairie Plan Working Group, 2011); (2) Grassland Bird Conservation Areas (Granfors, 2010a; Johnson *et al.*, 2010); (3) areas predicted by habitat models as likely to harbor grasshopper sparrows (*e.g.*, Quamen, 2007); (4) areas where grasshopper sparrows had been recorded consistently by the Minnesota Breeding Bird Atlas project, Minnesota Biological Survey, eBird, or the BBS; (5) additional areas with reported grasshopper sparrow occurrences and suitable habitat such as Important Bird Areas (IBAs); and (6) U.S. Department of Agriculture's Cropscape data files that identified remnant grassland. Forty acres (16.2 ha) was set as the minimum area threshold to represent the smallest area of grassland typically managed as a single unit within our study area. Sites were selected to represent a broad range of geographic extent, landscape types, habitat characteristics, anticipated abundance of grasshopper sparrows, and ownership.

Of the 66 sites visited, 45 were on public lands, 16 were privately owned, and five were owned by The Nature Conservancy. We visited 44 sites in 2013 and 45 sites in 2014, with 23 sites visited in both years. Each site was visited only once during a breeding season given occurrence rates for grassland bird species increase only marginally with a second visit (Quamen, 2007). Exceptions were made when the first visit occurred under marginal weather conditions (*i.e.*, higher than usual winds or light precipitation that did not exceed the thresholds for ending the survey) or during the first week of each field season, when observers were familiarizing themselves with survey methodology. When two surveys were conducted at a site, we used results from only one survey for each species. Whether we used the first or second visit was determined by whether the species of interest was considered an early-season breeder or a late-season breeder (as defined by Igl & Johnson, 1997).

Bird surveys.—Breeding bird surveys were conducted in 2013 and 2014 from late May to early July, which coincides with the peak breeding season of most breeding birds in this region. Surveys were conducted between 30 min before sunrise and 1000 to coincide with peak hours of bird activity. Counts of birds were based primarily on the number of breeding pairs on territories or home ranges. Generally, nearly all indicated pairs were observed as territorial males or as segregated pairs. We used the total-area count method for surveying breeding birds; this is a minor modification of the strip-transect procedures used by Stewart & Kantrud (1972) and Igl & Johnson (1997). Each site was surveyed by one or two observers walking slowly (1.0–1.5 km h^{-1}) on foot and documenting all birds encountered. This method allows one or two observers to efficiently cover one large field or several smaller fields within four hours after sunrise. Strip width varied depending on field size and shape but never exceeded 100 m on either side of the transect line. Transects were spaced 200 m apart so that there was no overlap in survey area. As recommended by Stewart & Kantrud (1972), deviations from the route were allowed and were sometimes necessary to adequately survey all portions of the fields (*e.g.*, in rolling topography, around large wetlands) or to track down elusive individuals to confirm identification. Large or wide-ranging birds (*e.g.*, raptors) that flush from the field upon the observer's arrival or during the survey were recorded as being within the field. In fields that were surveyed by two observers, observers compared field notes at the end of the survey to prevent duplication in the counts of large or wide-ranging birds.

Habitat measures.—We collected data on habitat characteristics to relate the occurrence and abundance of breeding grassland birds to a variety of habitat characteristics at several scales. We returned to sites for vegetation surveys after the initial bird surveys.

The number of points sampled along each transect was proportional to the square root of the transect length, with a starting density of two points for every 100 m. This method

TABLE 1.—Variables included in the analysis of habitat associations for each of the seven species of interest (sedge wren, Savannah sparrow, grasshopper sparrow, Henslow's sparrow, dickcissel, bobolink, and western meadowlark and brown-headed cowbird) in southwestern Minnesota. Ranges, means, medians, standard deviation (SD) and first and third quartiles are intended to give context to land managers for relative terms (denser, less, higher) used to describe species' habitat associations

Variable	Variable description	Range	Mean	Median	SD	1st Quartile	3rd Quartile
Litter	Depth of residual plant litter (cm)	0.00–16.67	5.00	4.75	2.50	3.40	6.17
Height	Height of vegetation (cm)	7.00–108.75	40.40	39.17	11.91	33.75	45.00
Grass	Percent cover of grass within 4 m	14.00–100.00	69.78	71.67	15.87	59.17	81.25
Forbs	Percent cover of forbs within 4 m	0.00–82.00	18.00	14.27	13.13	8.40	25.00
Shrub	Percent cover of shrubs within 4 m	0.00–30.25	3.13	0.50	4.99	0.00	4.88
DeadVeg	Percent cover of standing dead vegetation within 4 m	0.00–36.00	6.23	4.00	6.67	2.00	7.75
BareGround	Percent cover of bare ground within 4 m	0.00–22.03	2.08	1.00	3.79	0.00	2.00
VOR	Vegetation density estimated by visual obstruction reading	0.55–8.83	3.40	3.38	1.33	2.42	4.35
DistToTree	Distance to nearest tree (m)	16.67–480.50	147.43	151.81	74.12	92.45	188.41
Trees100	Estimated percent tree cover within 100 m	0.00–25.00	2.48	0.50	4.14	0.00	3.33

allowed for more sampling points at larger sites, while accounting for expected homogeneity within the site. The first sample point along each transect was determined randomly, with the first sampling point falling between 0 and 50 m from the start of the transect. The remaining points were spaced at equal intervals along the transect.

We assigned each transect to one of three broad habitat classes based on vegetation characteristics and other environmental factors (*e.g.*, MN DNR, 2009; Stewart and Kantrud, 1971, 1972): upland grassland, low grassland, or wet meadow. When more than one of these habitat classes was present, only the class that covered the greatest area was recorded. At each sampling point, we collected information on local features to assess habitat condition. Local features included height, height-density (Visual Obstruction Readings [VORs]; Robel *et al.*, 1970), litter depth, and visual estimates of the cover of dominant vegetation (grass, forb, shrub, dead vegetation [DeadVeg], and bare ground [BareGround]) in a 4 m radius circular plot around the sampling point, percent tree cover within 100 m of the point [Trees100], and distance to nearest tree [DistToTree]. Summary information for these vegetation variables is included in Table 1

Because birds were recorded along belt transects whereas vegetation measurements were recorded only for points along the center of each transect, and due to the heterogeneity of many of our sites, the conditions encountered by birds could vary appreciably from the recorded vegetation measurements. For instance we recorded some unusually high litter depths (above 15 cm) that may have been restricted to only a small portion of the total area surveyed.

Statistical Analysis

We ran statistical analyses in program R version 3.1.1 (R Core Team 2012) using the packages car (Fox & Weisberg 2011), zoo (Zeileis & Grothendieck 2005), and ggplot2 (Wickham and Chang 2014).

We calculated densities of individual species and grassland birds as a composite group by dividing the number of breeding pairs per transect survey area, which was calculated as transect length x width. We report densities as pairs per 100 ha.

As a measure of linear association between species and vegetation variables, we calculated correlation coefficients. We assessed curvilinear relationships by plotting density of each species of interest against each vegetation measurement and using locally weighted scatterplot smoothing to fit curves to the plots. We used loess.as from the fANCOVA package (Wang 2010) in R with the span for each plot chosen to minimize AIC_c. We also conducted unpaired two-sample *t*-tests to evaluate the differences in distance to nearest tree between transects with and without each species.

Results

On average, our sites contained a mean of 4.5 (±3.1 SD) transects. These transects were a mean length of 572.6 (±166.9 SD) m, representing a mean surveyed area of 37.4 (±20.3 SD) ha per site, though contiguous grassland area per site was considerably larger but difficult to quantify.

During the 2 y of our study we recorded a total of 2967 grassland birds: 293 sedge wrens, 212 Savannah sparrows, 610 grasshopper sparrows, 111 Henslow's sparrows, 255 dickcissels, 1190 bobolinks, 129 western meadowlarks, and 167 individuals of other grassland bird species. This resulted in mean abundances per site of 4.4 (±8.1 SD) sedge wrens, 3.2 (±6.0 SD) Savannah sparrows, 9.2 (±15.3 SD) grasshopper sparrows, 1.7 (±3.3 SD) Henslow's sparrows, 3.9 (±7.9 SD) dickcissels, 18.0 (±26.8 SD) bobolinks, and 2.0 (±3.6 SD) western meadowlarks.

Mean densities per 100 ha were as follows: 8.33 (±16.27 SD) sedge wrens, 5.80 (±12.04 SD) Savannah sparrows, 14.89 (±19.46 SD) grasshopper sparrows, 3.06 (±8.91 SD) Henslow's sparrows, 7.17 (±15.61 SD) dickcissels, 33.38 (±32.67 SD) bobolinks, 3.56 (±6.69 SD) western meadowlarks, and 66.11 (±50.26 SD) total grassland birds.

As a group grassland birds showed positive linear associations with greater distance to trees, fewer trees within 100 m, and less bare ground (Table 2). Grassland bird density was slightly higher at intermediate values of litter (Fig. 2A) and increased with increasing vegetation height up to 60 cm (Fig. 2B). Grassland bird density peaked at sites with about 1% bare ground (Fig. 2G). Grassland bird density was negatively related to trees (Figs. 2I, J). Grassland bird density was slightly higher at sites with very few shrubs (Fig. 2E). Grassland bird density decreased with increasing dead vegetation to about 10% dead vegetation (Fig. 2F). The overall density of all grassland birds was relatively unaffected by grass cover (Fig. 2C), forb cover (Fig. 2D), and VOR (Fig. 2H).

Sedge wren density showed linear correlations with taller, denser vegetation that included more standing dead vegetation, less bare ground, less shrubs, and more forbs and litter (Table 2). Sedge wren density increased slightly with increasing litter (Fig. 3A). Sedge wren density increased with increasing vegetation height to about 60 cm (Fig. 3B) and with increasing forb cover (Fig. 3D), dead vegetation (Fig. 3F), and VOR (Fig. 3H). Sedge wren density decreased with increasing grass cover (Fig. 3C) and was highest at sites with no shrub cover (Fig. 3E). Sedge wren density was relatively unaffected by bare ground (Fig. 3G),

TABLE 2.—Correlation coefficients between the densities of grassland birds of interest and the habitat variables. Grassland bird species are listed using standardized four-letter alpha codes (*see* Table 3) ALLGRASS refers to the composite of all grassland bird species. Statistically significant values (P < 0.05) are marked with an asterisk

Species	Litter	Height	Grass	Forbs	Shrub	DeadVeg	BareGround	VOR	DistToTree	Trees100
SEWR	0.12*	0.32*	−0.10	0.12*	−0.15*	0.17*	−0.14*	0.30*	0.06	−0.09
SAVS	0.00	−0.09	0.11*	−0.04	−0.16*	−0.07	−0.03	−0.12*	0.21*	−0.17*
GRSP	−0.08	−0.25*	0.00	0.03	0.03	−0.05	0.03	−0.22*	0.30*	−0.23*
HESP	0.01	0.05	0.03	0.06	−0.05	−0.08	−0.11	0.09	0.10	−0.09
DICK	0.04	0.03	−0.08	0.05	−0.03	0.14*	−0.14*	0.13*	0.12*	−0.08
BOBO	0.04 +	0.03	0.09	0.00	0.02	−0.18*	−0.10	−0.07	0.25*	−0.27*
WEME	−0.09	−0.06	0.12*	−0.01	−0.10	−0.20*	0.03	0.01	0.12*	−0.17*
ALLGRASS	0.07	0.10	0.05	0.06	−0.10	−0.08	−0.19*	0.07	0.32*	−0.30*

distance to trees (Fig. 3I), and trees within 100 m (Fig. 3J). Sites with and without sedge wrens did not differ significantly in terms of distance to trees ($t = -0.99$, df = 299, P = 0.326; Fig. 10).

Savannah sparrows had highest densities at sites farther from trees, and with less standing dead vegetation, fewer shrubs, and more grass cover (Table 2). Savannah sparrow density increased with increasing grass cover beyond about 70% grass cover (Fig. 4C) and with greater distance to trees (Fig. 4I). Savannah sparrow density peaked at about 5% dead vegetation (Fig. 4F) and 1% bare ground cover (Fig. 4G). Savannah sparrow density was highest where shrub cover was minimal (Fig. 4E). Savannah sparrow density decreased with increasing VOR (Fig. 4H) and with increasing forb cover to about 20% forb cover (Fig. 4D). Savannah sparrow density decreased slightly with increasing height (Fig. 4B). Savannah sparrows were almost always absent when tree cover exceeded 7% (Fig. 4J). Savannah sparrow density was relatively unaffected by litter depth (Fig. 4A). Sites with Savannah sparrows were significantly farther from trees than sites without Savannah sparrows ($t = -3.01$, df = 299, P = 0.003; Fig. 10).

Grasshopper sparrow densities showed linear correlations with distance from trees and shorter, sparser vegetation (Table 2). Grasshopper sparrow density peaked at about 4% shrub cover (Fig. 5E). Similarly, low cover by dead vegetation corresponded to higher grasshopper sparrow densities (Fig. 5F). The relationship between grasshopper sparrow density and bare ground was curvilinear, with grasshopper sparrow density peaking at about 8% bare ground (Fig. 5G). Because the relationship was curvilinear the linear correlation was not significant (Table 2). Whereas grasshopper sparrow density did not show a clear linear correlation with litter depth (Table 2), there was a noticeable pattern that, above about 5 cm of litter depth, grasshopper sparrow density declined slightly (Fig. 5A). Grasshopper sparrow density also declined with height, especially up to about 45 cm (Fig. 5B). Grasshopper sparrow density decreased with increasing Visual Obstruction Readings (Fig. 5H), consistent with the linear relationship (Table 2). Also grasshopper sparrow density decreased as the proportion of trees within 100 m increased (Fig. 5J) and analogously increased with increasing distance from nearest tree (Fig. 5I). Grass and forb coverage did not show any relationship with the density of grasshopper sparrows (Figs. 5C, D). Sites with grasshopper sparrows were significantly farther from trees than sites without grasshopper sparrows ($t = -7.48$, df = 299, P < 0.001; Fig. 10).

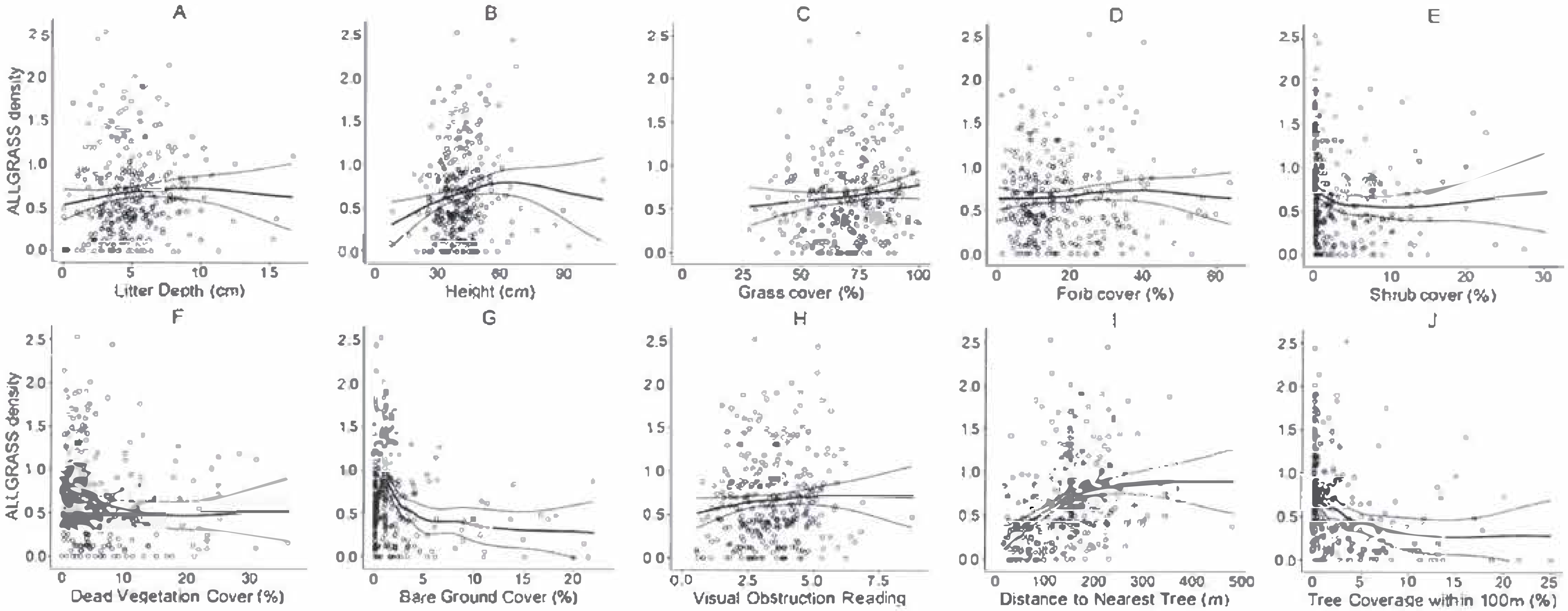

FIG. 2.—Loess plots of the density of all grassland birds (ALLGRASS) at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (A) litter depth, (B) vegetation height, (C) percent grass cover within 4 m, (D) percent forb cover within 4 m, (E) percent shrub cover within 4 m, (F) percent standing dead vegetation cover within 4 m, (G) percent bare ground cover within 4 m,(H) visual obstruction reading (VOR), I) distance to nearest tree, and (J) percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loessas from the FANCOVA package (Wang 2010) in R

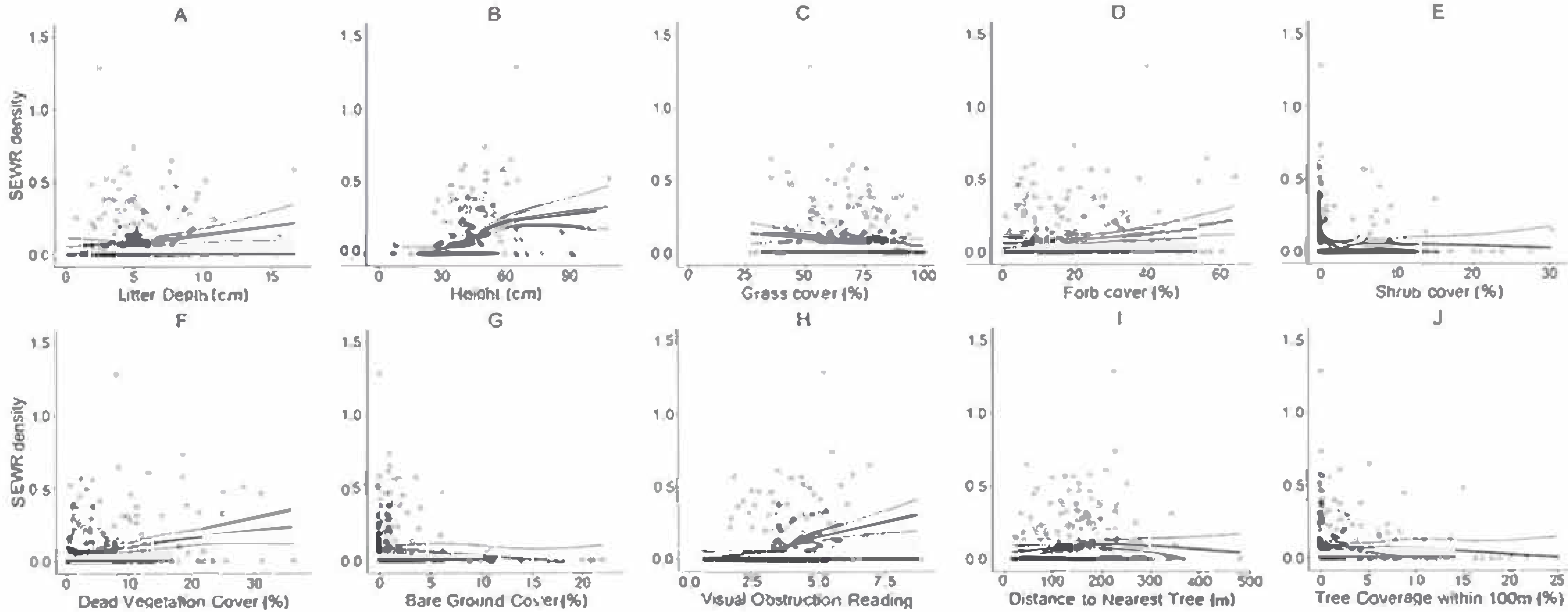

FIG. 3.—Loess plots of sedge wren (SEWR) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (A) litter depth, (B) vegetation height, (C) percent grass cover within 4 m, (D) percent forb cover within 4 m, (E) percent shrub cover within 4 m, (F) percent standing dead vegetation cover within 4 m, (G) percent bare ground cover within 4 m, (H) visual obstruction reading (VOR), (I) distance to nearest tree, and (J) percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R

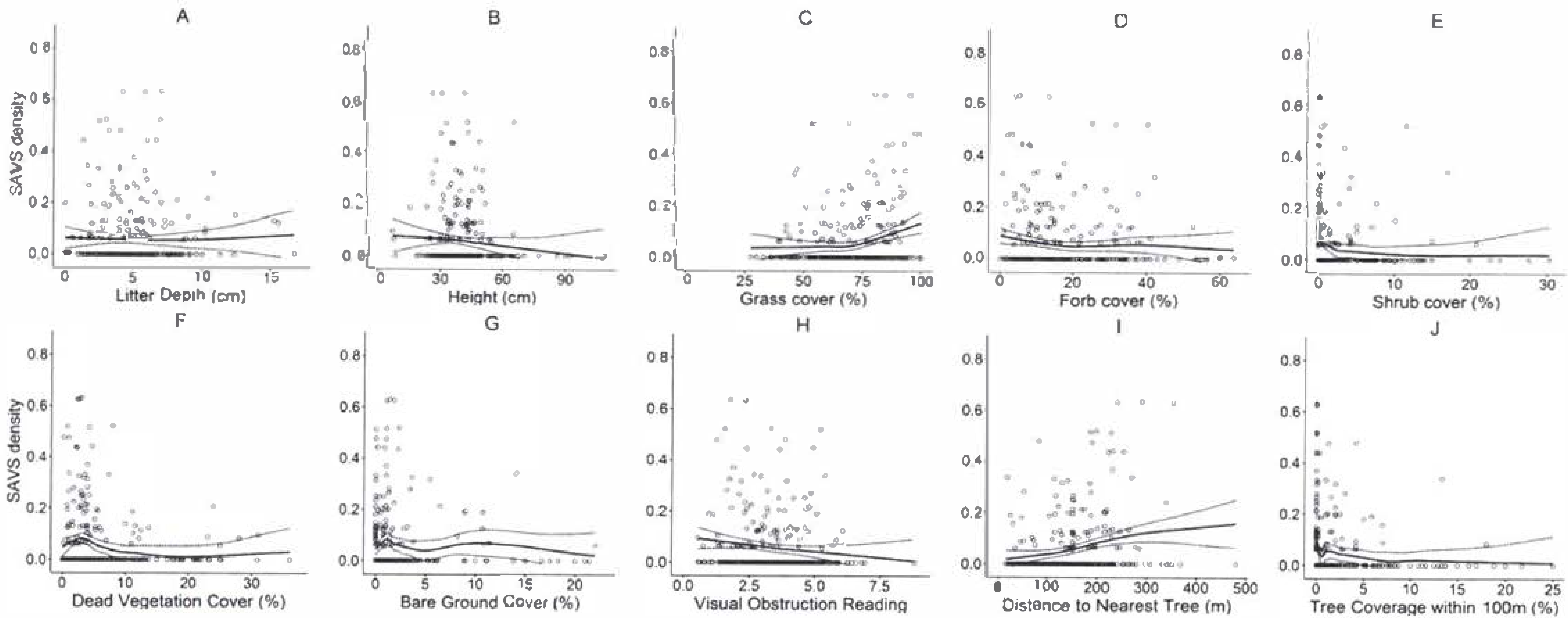

FIG. 4.—Loess plots of Savannah sparrow (SAVS) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (**A**) litter depth, (**B**) vegetation height, (**C**) percent grass cover within 4 m, (**D**) percent forb cover within 4 m, (**E**) percent shrub cover within 4 m, (**F**) percent standing dead vegetation cover within 4 m, (**G**) percent bare ground cover within 4 m, (**H**) visual obstruction reading (VOR), I) distance to nearest tree, and (**J**) percent tree cover within 100 meters. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R

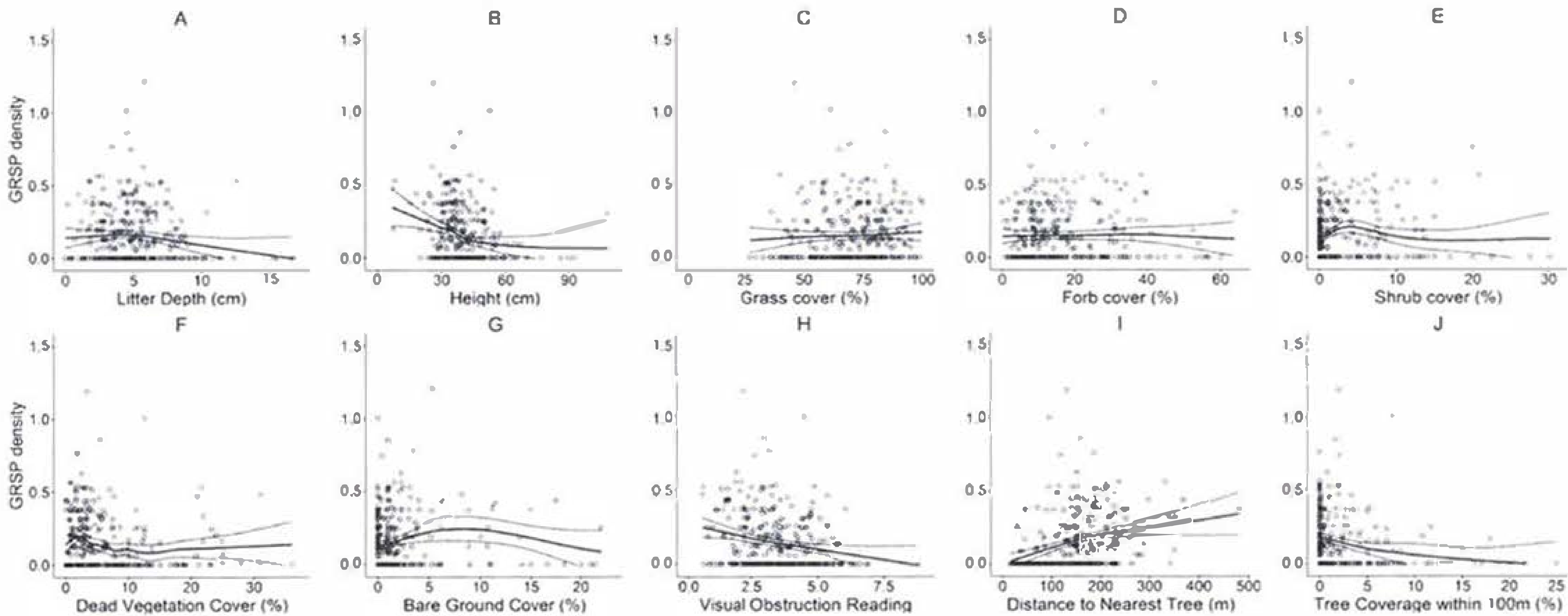

FIG. 5.—Loess plots of grasshopper sparrow (GRSP) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (**A**) litter depth, (**B**) vegetation height, (**C**) percent grass cover within 4 m, (**D**) percent forb cover within 4 m, (**E**) percent shrub cover within 4 m, (**F**) percent standing dead vegetation cover within 4 m, (**G**) percent bare ground cover within 4 m, (**H**) visual obstruction reading (VOR), (**I**) distance to nearest tree, and (**J**) percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R

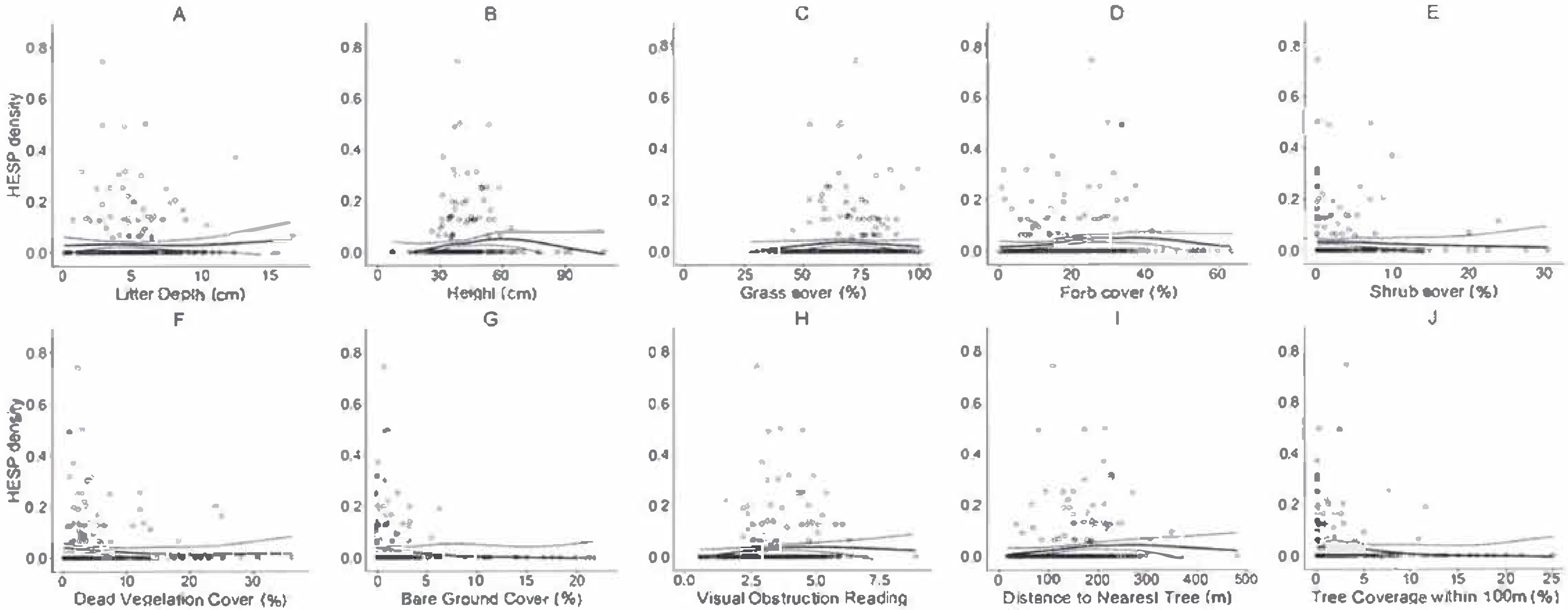

FIG. 6.—Loess plots of Henslow's sparrow (HESP) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (A) litter depth, (B) vegetation height, (C) percent grass cover within 4 m, (D) percent forb cover within 4 m, (E) percent shrub cover within 4 m, (F) percent standing dead vegetation cover within 4 m, (G) percent bare ground cover within 4 m, (H) visual obstruction reading (VOR), I) distance to nearest tree, and (J) percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R

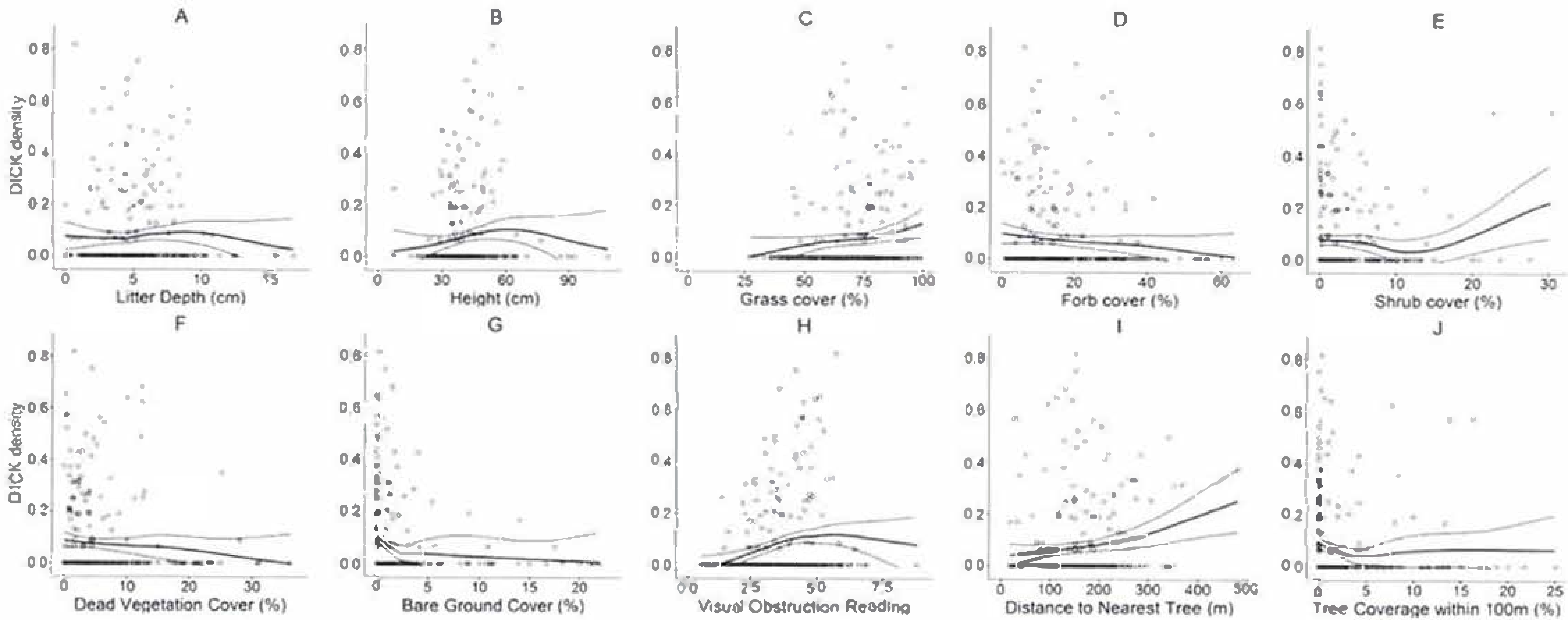

FIG. 7.—Loess plots of dickcissel (DICK) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to **(A)** litter depth, **(B)** vegetation height, **(C)** percent grass cover within 4 m, **(D)** percent forb cover within 4 m, **(E)** percent shrub cover within 4 m, **(F)** percent standing dead vegetation cover within 4 m, **(G)** percent bare ground cover within 4 m, **(H)** visual obstruction reading (VOR), I) distance to nearest tree, and **(J)** percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R

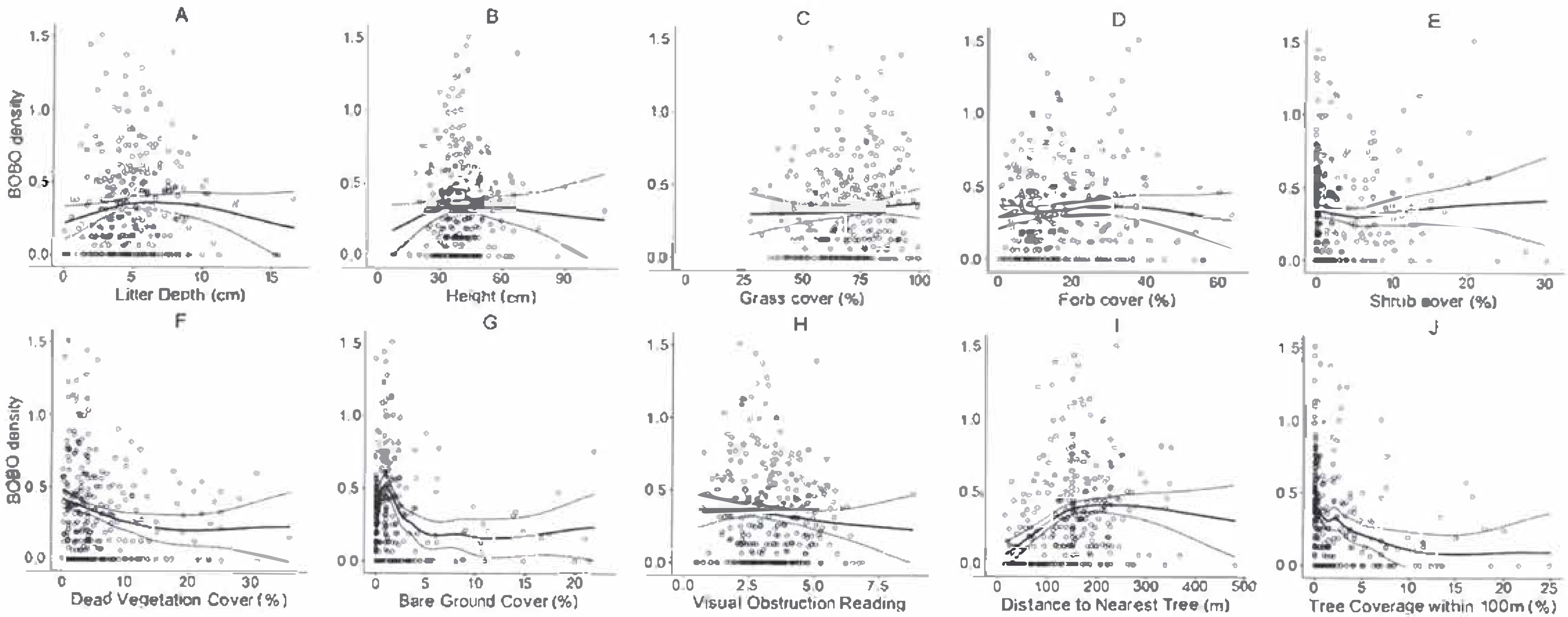

FIG. 8.—Loess plots of bobolink (BOBO) density at 66 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (A) litter depth, (B) vegetation height, (C) percent grass cover within 4 m, (D) percent forb cover within 4 m, (E) percent shrub cover within 4 m, (F) percent standing dead vegetation cover within 4 m, (G) percent bare ground cover within 4 m, (H) visual obstruction reading (VOR), (I) distance to nearest tree, and (J) percent tree cover within 100 m. Span was chosen to minimize AIC_c value using loess.as from the fANCOVA package (Wang 2010) in R.

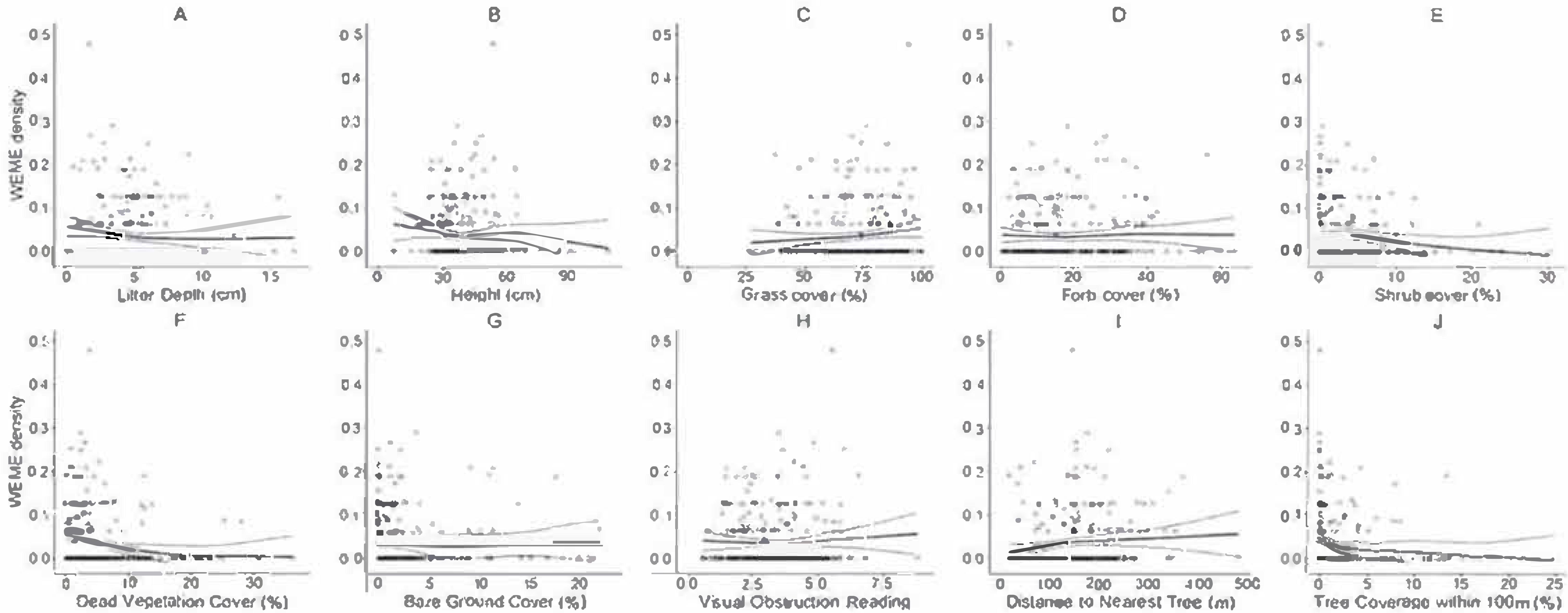

FIG. 9.—Loess plots of western meadowlark (WEME) density at 60 sites within the Prairie Parkland Province ecoregion of Minnesota in 2013 and 2014, in relation to (A) litter depth, (B) vegetation height, (C) percent grass cover within 4 m, (D) percent forb cover within 4 m, (E) percent shrub cover within 4 m, (F) percent standing dead vegetation cover within 4 m, (G) percent bare ground cover within 4 m, (H) visual obstruction reading (VOR), (I) distance to nearest tree, and (J) percent tree cover within 100 m. Span was chosen to minimize AICc value using loess.as from the fANCOVA package (Wang 2010) in R

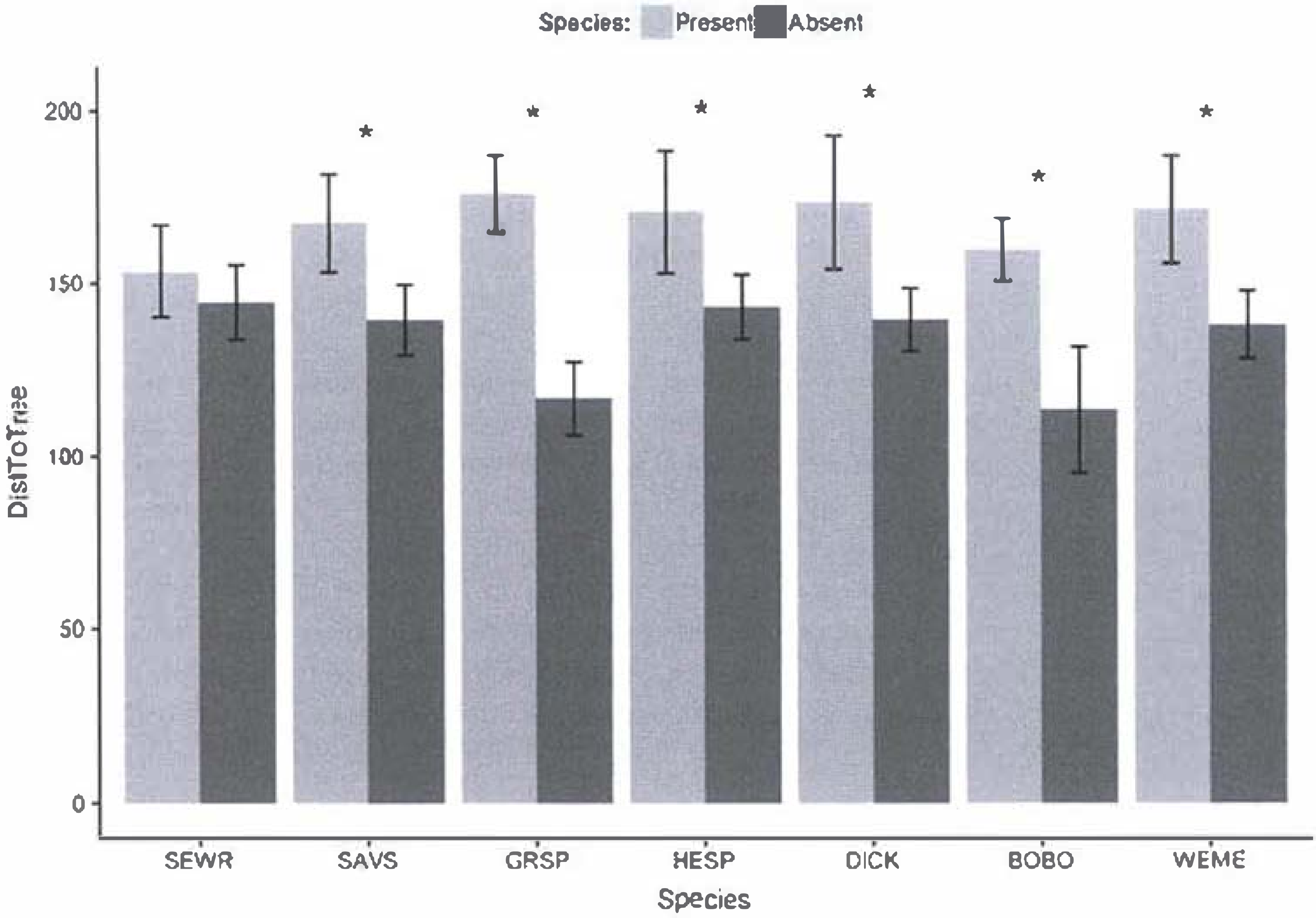

FIG. 10.—Mean distance to nearest tree (m) of transects with and without the indicated species of grassland bird at sites surveyed in 2013 and 2014 in southwestern Minnesota. Grassland bird species are listed using standardized 4-letter American Ornithological Society (formerly American Ornithologists' Union) alpha codes. Asterisks indicate a significant difference ($P < 0.05$) between the distances to nearest tree based on unpaired two-sample *t*-tests; error bars represent 95% confidence intervals.

We were unable to detect linear or nonlinear relationships between Henslow's sparrow density and our measures of vegetation, possibly as the result of small numbers of the species (Fig. 6). However, sites with Henslow's sparrows were significantly farther from trees than sites without Henslow's sparrows ($t = -2.38$, $df = 299$, $P < 0.018$; Fig. 10).

Dickcissel densities were highest at sites with a higher percentage of dead vegetation, denser vegetation, greater distance to trees, and less bare ground (Table 2). Dickcissel density was slightly higher at intermediate values of vegetation height (Fig. 7B). Dickcissel density increased slightly with greater grass cover (Fig. 7C) and with higher percentages of shrub cover (Fig. 7E) and bare ground (Fig. 7G). Dickcissel density increased with increasing VOR to a VOR value of about 5 (Fig. 7H). Dickcissel density increased with increasing distance to trees (Fig. 7I) and decreased with greater tree cover within 100 m up to 5% tree cover (Fig. 7J). Dickcissel density was relatively unaffected by litter depth (Fig. 7A), forb cover (Fig. 7D), and dead vegetation (Fig. 7F). Sites with dickcissels were significantly farther from trees than sites without dickcissels ($t = -3.45$, $df = 299$, $P = 0.001$; Fig. 10).

Bobolink densities showed a linear correlation with greater distance from trees and lower percentage of standing dead vegetation (Table 2). Bobolink density increased with increasing litter depth to about 5 or 10 cm, and possibly declined thereafter (Fig. 8A). Although the range in height was limited, there is some suggestion that bobolink density may increase to about 35 cm (Fig. 8B). Bobolink density increased up to about 2% bare ground cover, then decreased to about 4% bare ground, after which density remained constant (Fig. 8G). Bobolink density increased with increasing distance to nearest tree up to about 200 m (Fig. 8I). Bobolink density decreased with increasing proportion of trees within 100 m to about 10% tree cover (Fig. 8J). Bobolink density decreased with increasing dead vegetation to about 15% dead vegetation, after which the density was relatively stable (Fig. 8F). Bobolink density was relatively unaffected by grass cover (Fig. 8C), forb cover (Fig. 8D), shrub cover (Fig. 8E). Sites with bobolinks were significantly farther from trees than sites without bobolinks ($t = -4.87$, $df = 299$, $P < 0.001$; Fig. 10).

Higher densities of western meadowlark were most closely associated with greater distances to trees and less bare ground (Table 2). Slight positive relations were found with grass cover (Fig. 9C) and distance to trees (Fig. 9I). Western meadowlark density peaked with minimal tree cover (Fig. 9J). Western meadowlark density decreased slightly with greater litter depth (Fig. 9A), vegetation height (Fig. 9B), and dead vegetation (Fig. 9F). Western meadowlark density was lower where shrub cover exceeded 7% (Fig. 9E). Western meadowlark density was relatively unaffected by vegetation height (Fig. 9B), forb cover (Fig. 9D), bare ground (Fig. 9G), and VOR (Fig. 9H). Sites with western meadowlarks were significantly farther from trees than sites without western meadowlarks ($t = -3.58$, $df = 299$, $P < 0.001$; Fig. 10).

DISCUSSION

Our results demonstrate that obligate grassland birds are making use of remnant prairies in southwestern Minnesota. An earlier study by Quamen (2007) found somewhat higher densities of five of our seven species in 2003–2005 (*e.g.*, an average of 20–25 grasshopper sparrows per 100 ha), consistent with continued declines of grassland birds in the intervening decade. Densities of western meadowlarks were fairly comparable between the two studies with a mean of three to six birds per 100 ha in Quamen's study versus three and a half birds per 100 ha in our study. Densities of the seventh species—Henslow's sparrow—were not analyzed as part of Quamen's study. However, population levels of this species appear to respond to significant expansion and contraction of grassland acreage enrolled in the Conservation Reserve Program (CRP), which in turn has responded to crop prices (Cooper 2012). The period from 2007 to 2016 showed a marked contraction of CRP lands nationally (FSA 2016a), and Minnesota alone lost almost 37% of its CRP acreage (FSA 2016b). Thus we expect that our reported densities for Henslow's sparrows may be lower than densities in the years preceding our study (from roughly 2005 to 2012). Nonetheless, our observations provide evidence that the remaining remnant prairies that we visited continue to support this and other grassland breeding bird species.

We found evidence of both linear and curvilinear relationships between bird densities and vegetation characteristics. As expected these responses were species-specific. However, grassland bird density as a whole was representative in that it showed significant relationships with those vegetation characteristics most frequently important to individual species. Most notably, we found a uniform, negative response to trees. Densities of almost all species showed significantly negative correlations with percent tree cover within 100 m, and significantly positive correlations with distance to nearest tree. In addition sites that had a particular species of bird were, on average, farther from trees (Fig. 10) and had less tree cover. These site differences were consistent among species, though not significantly so in the case of sedge wrens (or for dickcissel, for percent tree cover). This finding, that the distance to trees or percent cover of trees are particularly closely associated with the density and occurrence of grassland birds, supports previous studies documenting the negative impacts of trees on grassland birds (Grant *et al.*, 2004; Thompson *et al.*, 2014) and the positive impacts of tree-removal on these species (Quamen, 2007; Thompson *et al.*, 2016).

Consistent with the summary by Shaffer *et al.* (2015b), we found that tall, dense vegetation with a high percentage of forb cover is important for the sedge wren. We found dead vegetation and litter depth were possibly more important than forb cover. This positive relationship with residual vegetation also was noted by Herkert *et al.* (2001).

Swanson's (2015) summary of the Savannah sparrow's habitat needs suggested that litter, height and density (VOR) are important for this species. We found Savannah sparrow density was negatively correlated with VOR but not affected by height or litter depth. Instead, we observed negative correlations with trees and percent shrub cover and a positive correlation with percent grass cover, all of which are correspondingly considered important in the Birds of North America account of this species (Wheelwright & Rising, 2008).

We found grasshopper sparrows were negatively associated with vegetation height, as did Shaffer *et al.* (2015a). This pattern also seems appropriate because, above a certain vegetation height, we typically did not encounter many obligate grassland bird species. Shaffer *et al.* (2015a) identified litter depth and shrub density to be particularly important vegetation characteristics for this species, and Vickery (1996) additionally noted a negative relationship with shrub density. In contrast our results showed a nonsignificant correlation with percent shrub cover, but a pattern of slightly higher densities of grasshopper sparrows at very low levels of shrub cover than at higher levels of shrub cover or no shrub cover. A few shrubs or other tall vegetation may provide males with singing perches necessary for territory establishment and defense, but more than that may be a deterrent for the species (Slater, 2004). In addition our results indicate that trees on the landscape are negatively correlated with grasshopper sparrow density. This finding supports previous suggestions (Vickery, 1996; Shaffer *et al.*, 2015a) that open grasslands are important for this species. Our results showed several individual transects that have much higher than expected grasshopper sparrow densities given the proximity to a tree (Fig. 5I), but a single small tree nearby could be less problematic than many trees farther away. Our examination of curvilinear relationships also indicates that a small amount of dead vegetation may be beneficial to the grasshopper sparrow (Fig. 5F), perhaps because it corresponds with a period length of time since last fire or other disturbance event (Dechant *et al.*, 2002). Similarly, some bare ground (about 7–9%) corresponds with higher grasshopper sparrow densities, probably because a small amount is good for foraging, but with too much the birds are exposed and may not have enough cover for nesting (Whitmore, 1981).

For Henslow's sparrows, our results showed no significant correlations with the vegetation characteristics that we measured, in contrast to Herkert (2015). However, the species has recently re- colonized our study area (Herkert *et al.*, 2002) and was uncommon in our surveys. We suspect that the species may be too uncommon to occupy all sites that provide preferred habitat, as is reflected by its endangered status within Minnesota (MNDNR, 2016a).

The vegetation characteristics that we found to be correlated with dickcissel density were dead vegetation, bare ground, VOR, and distance to trees. Similarly, Shaffer *et al.* (2015c) identified height and density (VOR) as important for this species. They also concluded that litter depth and forb cover are important habitat characteristics. Temple (2002) supported our finding that proximity to trees is negative for this species. However, Temple (2002) also identified density, height, litter, and forb cover as important vegetation characteristics.

For the bobolink, we found that the key vegetation characteristics correlated with breeding pair density were the absence of both trees and dead vegetation. In contrast the summary by Shaffer *et al.* (2015d) identifies vegetation height and density, and litter, forb, and shrub cover as key vegetation characteristics for this species. The Birds of North America account by Renfrew *et al.* (2015) was consistent with our findings and identified a high proportion of nonforested habitat as an important component of bobolink habitat. Furthermore, in agreement with the Shaffer *et al.* (2015d) summary, Renfrew *et al.* (2015) found density, litter, and forb cover to be important. In accordance with our finding that dead vegetation was negatively correlated with the density of grasshopper sparrows, Renfrew *et al.* (2015) identified hay fields more than eight years since plowing or reseeding as suitable habitat for this species, and such sites may be more likely to have residual dead vegetation if they were not mown during the previous fall or spring.

Consistent with Shaffer *et al.*'s (2015c) summary of the western meadowlark and Davis & Lanyon (2008), we found that absence of trees and a high percentage of grass cover are correlated with the density of this species. Although Shaffer *et al.* (2015c) and Davis & Lanyon (2008) concluded that a high litter component (litter depth and cover), is important for this species, we did not find this to be the case in our Minnesota study sites. However, we did find that residual dead vegetation, which often co- occurs with high litter, was negatively correlated with western meadowlark density.

In summary we were able to find breeding populations of obligate grassland birds on remnant prairie in southwestern Minnesota. Protecting prairie continues to be critical for the conservation of grassland birds; managing for different vegetation characteristics can allow natural resource professionals to favor selected species. Although our results are generally consistent with previous accounts of vegetation characteristics preferred by each of these species, the low correlation coefficients and the wide variation in our results indicate that most species tolerate a wide range of habitat conditions. The major exception, however, is that grassland birds generally responded negatively to the presence and proximity of trees.

Management implications

Because different species have different habitat associations (Scott *et al.*, 2002), local populations of different species are likely to respond differently to different management practices (Wiens & Rotenberry, 1981). Our findings support the idea that it is important to maintain a range of vegetation characteristics on the landscape in order to support the most grassland species (Vickery *et al.*, 1995). However, it is also important to note that such heterogeneity needs to be maintained at a landscape-level rather than within grassland plots to avoid patchiness that reduces grassland bird densities (Wiens, 1974). Therefore, we suggest coordination in the management of adjacent grassland patches to develop a mosaic of vegetation characteristics suitable for conservation of the full suite of grassland bird species. At a site-by-site level, the most critical management activity to support grassland biodiversity appears to be tree control or removal.

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LITERATURE CITED

ASKINS, R. A., F. CHÁVEZ-RAMÍREZ, B. C. DALE, C. A. HAAS, J. R. HERKERT, F. L. KNOPF, AND P. D. VICKERY. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. *Ornithol. Monogr.* 64:1–46.

AZPIROZ, A. B., J. P. ISACCH, R. A. DIAS, A. S. DI GIACOMO, C. S. FONTANA, AND C. M. PALAREA. 2012. Ecology and conservation of grassland birds in southeastern South America. *J. Field Ornithol.*, 83:217–246.

CAPLAT, P. AND J. FONDERFLICK. 2009. Area mediated shifts in bird community composition: a study on a fragmented Mediterranean grassland. *Biodivers. Conserv.*, 18:2979–2995.

COOPER, T.R. 2012. Status assessment and conservation plan for the Henslow's sparrow (*Ammodramus henslowii*). Version 1.0. U.S. Fish and Wildlife Service, Bloomington, MN. Available from https://www.fws.gov/midwest/es/soc/birds/pdf/HESP_SAandConsPlan11Oct2012.pdf. Accessed 8/29/16.

DAVIS, S. K. AND W. E. LANYON. 2008. Western meadowlark (*Sturnella neglecta*). *In:* A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/104. Accessed 8/29/16.

DECHANT, J. A., M. L. SONDREAL, D. H. JOHNSON, L. D. IGL, C. M. GOLDADE, M. P. NENNEMAN, AND B. R. EULISS. 2002. Effects of management practices on grassland birds: Grasshopper sparrow. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. Available from http://digitalcommons.unl.edu/usgsnpwrc/147. Accessed 8/29/16.

DUNFORD, W. AND K. FREEMARK. 2005. Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. *Landsc. Ecol.*, 20:497–511.

EASON, P. K. AND J. A. STAMPS. 1992. The effect of visibility on territory size and shape. *Behav. Ecol.*, 3:166–172.

FAABORG, J., R. T. HOLMES, A. D. ANDERS, K. L. BILDSTEIN, K. M. DUGGER, S. A. GAUTHREAUX, JR., P. HEGLUND, K. A. HOBSON, A. E. JAHN, D. H. JOHNSON, S. C. LATTA, D. J. LEVEY, P. P. MARRA, C. L. MERKORD, E. NOL, S. I. ROTHSTEIN, T. W. SHERRY, T. S. SILLETT, F. R. THOMPSON III, AND N. WARNOCK. 2010. Conserving migratory land birds in the New World: do we know enough? *Ecol. Appl.*, 20:398–418.

FARM SERVICES AGENCY (FSA). 2016a. Map of changes in CRP enrollment 2007–2016. U.S. Department of Agriculture. Available from https://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdafiles/Conservation/PDF/ChangeInCRPAcreagefrom2007_2016.pdf. Accessed 8/29/16.

_____. 2016b. CRP enrollment and rental payments by state, 1986-2016. U.S. Department of Agriculture. Available from https://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdafiles/Conservation/Excel/statepayments8616.xlsx. Accessed 8/29/16.

FISHER, R. J., AND S. K. DAVIS. 2010. From Wiens to Robel: A review of grassland-bird habitat selection. *J. Wildl. Manage.*, 74:265–273.

FOX, S. D. AND S. WEISBERG. 2011. An R companion to applied regression. Thousand Oaks, CA. Available from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Accessed 8/29/16.

FUHLENDORF, S. D., A. J. W. WOODWARD, D. M. L. JR. AND S. JOHN. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landsc. Ecol.*, 17:617–628.

GRANFORS, D. 2010a. Grassland Bird Conservation Area (GBCA) Maps. Habitat and Population Evaluation Team (Midwest Region), U.S. Fish and Wildlife Service, Anchorage, AK. Available from http://www.fws.gov/midwest/hapet/GrasslandBirdsConservationAreas.html. Accessed 8/29/16.

GRANT, T. A., E. MADDEN, AND G. B. BERKEY. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildl. Soc. Bull.*, 32:807–818.

HAMER, T. L., C. H. FLATHER, AND B. R. NOON. 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landsc. Ecol.*, 21:569–583.

HANSON, D.S. AND B. HARGRAVE. 1996. Development of a multilevel ecological classification system for the state of Minnesota. *Environ. Monit. Assess.*, 39:75–84.

Harris, R. J., and J. M. Reed. 2002. Behavioral barriers to non-migratory movements of birds. *Ann. Zool. Fennici*, 39:275–290.

Herkert, J. R. 2015. Henslow's sparrow. U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–10. Available from https://pubs.er.usgs.gov/publication/70159918. Accessed 9/18/2016.

———, D. E. Kroodsma, and J. P. Gibbs. 2001. Sedge wren. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/582/articles/habitat. Accessed 8/29/16.

———, P. D. Vickery, and D. E. Kroodsma. 2002. Henslow's sparrow (*Ammodramus henslowii*). *In:* A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/672. Accessed 8/29/16.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.*, 8:23–29.

Holimon, W. C., J. A. Akin, W. H. Baltosser, C. W. Rideout, and C. T. Witsell. 2012. Structure and composition of grassland habitats used by wintering Smith's longspurs: the importance of native grasses. *J. Field Ornithol.*, 83:351–361.

Igl, L. D. and D. H. Johnson. 1997. Changes in breeding bird populations in North Dakota: 1967 to 1992–1993. *Auk*, 114:74–92.

Johnson, R. R., D. A. Granfors, N. D. Niemuth, M. E. Estey, and R. E. Reynolds. 2010. Delineating grassland bird conservation areas in the U.S. Prairie Pothole Region. *J. Fish Wildl. Manag.*, 1:38–42.

Koper, N. and F. K. K. Schmiegelow. 2006. A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. *Landsc. Ecol.*, 21:1045–1059.

McCracken, J. D. and P. Rowan. 2005. Where the bobolinks roam: the plight of North America's grassland birds. *Biodiversity*, 6:20–29.

Mengel, R. M. 1970. The North American central plains as an isolating agent in bird speciation, p. 279–340. *In:* W. Dort Jr. and J. K. Jones Jr. (eds.). Pleistocene and recent environments of the central Great Plains. University Press of Kansas, Lawrence, KS.

Minnesota Department of Natural Resources (MN DNR). 2006. Tomorrow's habitat for the wild and rare: An action plan for Minnesota wildlife. Division of Ecological Services, Minnesota Department of Natural Resources, St. Paul, MN. p. 1–113. Available from http://files.dnr.state.mn.us/assistance/nrplanning/bigpicture/cwcs/tomorrows_habitat.pdf. Accessed 8/29/16.

———. 2016a. Minnesota's Wildlife Action Plan 2015–2025. Division of Ecological and Water Resources, Minnesota Department of Natural Resources, St. Paul, MN p. 1–240. Available from http://www.dnr.state.mn.us/mnwap/index.html. Accessed 8/29/16.

———. 2016b. Prairie Parkland Province. Available from http://dnr.state.mn.us/ecs/251/index.html. Accessed 8/29/16.

———. 2009. Upland Prairie System. Available from http://files.dnr.state.mn.us/natural_resources/npc/upland_prairie/ppatap_up_system.pdf. Accessed 8/29/16.

Minnesota Prairie Plan Working Group. 2011. Minnesota Prairie Conservation Plan. Minnesota Prairie Plan Working Group, Minneapolis, MN. p. 1–55. Available from http://files.dnr.state.mn.us/eco/mcbs/mn_prairie_conservation_plan.pdf. Accessed 8/29/16.

Niesar, S. L., and D. E. Hubbard. 1997. Breeding bird richness in the Prairie Pothole Region of Minnesota. *Prairie Nat.*, 29:81–92.

North American Bird Conservation Initiative U.S. Committee. 2014. The State of the Birds 2014 Report. p. 1–16. Available from http://www.stateofthebirds.org/2014/2014%20SotB_FINAL_low-res.pdf

Pool, D. B., A. O. Panjabi, A. Macias-Duarte, and D. M. Solhjem. 2014. Rapid expansion of croplands in Chihuahua, Mexico threatens declining North American grassland bird species. *Biol. Conserv.*, 170:274–281.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *Auk*, 123:183–197.

QUAMEN, F. R. 2007. A landscape approach to grassland bird conservation in the Prairie Pothole region of the Northern Great Plains. Dissertation. The University of Montana, Missoula. p. 1–150.

R CORE TEAM. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

RENFREW, R., D. KIM, N. G. PERLUT, J. SMITH, J. FOX AND P. P. MARRA. 2013. Phenological matching across hemispheres in a long-distance migratory bird. *Div. and Dist.*, 19:1008–1019.

_____, A. M. STRONG, N. G. PERLUT, S. G. MARTIN, AND T. A. GAVIN. 2015. Bobolink (*Dolichonyx oryzivorus*). *In:* A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/176. Accessed 8/29/16.

ROBEL, A. R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.*, 23:295–297.

RODEWALD, A. D. AND R. H. YAHNER. 2001. Influence of landscape composition on avian community. *Ecology*, 82:3493–3504.

SAMSON, F. AND F. KNOPF. 1994. Prairie conservation in North America. *BioScience*, 44:418–421.

SAUER, J. R., D. K. NIVEN, J. E. HINES, D. J. ZIOLKOWSKI, JR., K. L. PARDIECK, J. E. FALLON AND W. A. LINK. 2017. The North American Breeding Bird Survey, results and analysis 1966–2015. Version 2.07.2017. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD. Available from https://www.mbr-pwrc.usgs.gov/bbs/. Accessed 4/13/17.

SCOTT, P. E., T. L. DEVAULT, R. A. BAJEMA, AND S. L. LIMA. 2002. Grassland vegetation and bird abundances on reclaimed midwestern coal mines. *Wildl. Soc. Bull.*, 30:1006–1014.

SHAFFER, J. A., M. L. SONDREAL, D. H. JOHNSON, L. D. IGL, C. M. GOLDADE, M. P. NENNEMAN, T. L. WOOTEN, AND B. R. EULISS. 2015a. Grasshopper sparrow (*Ammodramus savannarum*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–17.

_____, _____, _____, _____, _____. B. D. PARKIN, T. L. WOOTEN, AND B. R. EULISS. 2015b. Sedge wren (*Cistothorus platensis*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–9.

_____, _____, _____, _____, _____. A. L. ZIMMERMAN, AND B. R. EULISS. 2015c. Dickcissel (*Spiza americana*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–14.

_____, _____, _____, _____, _____, _____. T. L. WOOTEN, AND B. R. EULISS. 2015d. Bobolink (*Dolichonyx oryzivorus*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–14.

_____, _____, _____, _____, _____, _____, _____, AND _____. 2015e. Western meadowlark (*Sturnella neglecta*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–16.

SLATER, G. L. 2004. Grasshopper sparrow: A technical conservation assessment. USDA Forest Service, Rocky Mountain Region, Mount Vernon, WA. Available from: http://www.fs.fed.us/r2/projects/scp/assessments/grasshoppersparrow.pdf. Accessed 8/29/16.

STEWART, R. E., AND H. A. KANTRUD. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish Wildl. Serv. Resour. Publ. 92. Available from http://esrd.alberta.ca/lands-forests/shorelands/documents/ClassificationPondsLakesPrairie-Part1.pdf. Accessed 8/29/16.

_____ AND _____. 1972. Population estimates of breeding birds in North Dakota. *Auk*, 89:766–788.

_____ AND _____. 1972. Vegetation of Prairie Potholes, North Dakota, in relation to quality of water and other environmental factors. Geological Survey Professional Paper 585-D. Available from http://pubs.usgs.gov/pp/0585d/report.pdf. Accessed 8/29/16.

SWANSON, D. A. 2015. Savannah sparrow (*Passerculus sandwichensis*). U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND. p. 1–17.

TEMPLE, S. A. 2002. Dickcissel (*Spiza americana*). *In:* A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/703. Accessed 8/29/16.

THOMPSON, S. J., T. W. ARNOLD, C. L. AMUNDSON. 2014. A multiscale assessment of tree avoidance by prairie birds. *Condor*, 116:303–315.

———, ———, J. FIEBERG, D. A. GRANFORS, S. VACEK, AND N. PALAIA. 2016. Grassland birds demonstrate a delayed response to largescale tree removal in central North America. *J. Appl. Ecol.*, 53:284–294.

VICKERY, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*). *In*: A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu/bna/species/239. Accessed 8/29/16.

———, J. R. HERKERT, F. L. KNOPF, AND C. E. KELLER. 1995. Grassland birds: an overview of threats and recommended management strategies. p. 73–77. *In*: R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles (eds.). Strategies for bird conservation: the Partners in Flight planning process; proceedings of the third Partners in Flight workshop. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT. Available from http://www.fs.fed.us/rm/pubs/rmrs_p016/rmrs_p016_074_077.pdf.

———, P. L. TUBARO, J. M. CARDOSA DA SILVA, B. G. PETERJOHN, J. R. HERKERT, AND R. B. CAVALCANTI. 1999. Conservation of grassland birds in the western hemisphere. *Stud. Avian Biol.* 19:2–26.

WANG, X. 2010. fANCOVA: Nonparametric analysis of covariance. Available from http://cran.r-project.org/package=fANCOVA.

WHEELWRIGHT, N. T. AND J. D. RISING. 2008. Savannah sparrow (*Passerculus sandwichensis*). *In*: A. Poole (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Online: http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/045. Accessed 8/29/16.

WHITMORE, R. C. 1981. Structural characteristics of grasshopper sparrow habitat. *J. Wildl. Manage.*, 45:811–814.

WICKHAM, H. AND W. CHANG. 2014. ggplot2. Available from http://ggplot2.org. Accessed 8/29/16.

WIENS, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. *Am. Midl. Nat.*, 91:195–213.

——— AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecol. Monogr.*, 51:21–42.

ZEILEIS, A. AND G. GROTHENDIECK. 2005. zoo: S3 infrastructure for regular and irreglar time series. *J. Stat. Softw.*, 14:1–27.

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