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RESEARCH ARTICLE

Territory and nest site selection patterns by Grasshopper Sparrows in southeastern Arizona

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ABSTRACT

Grassland bird populations are showing some of the greatest rates of decline of any North American birds, prompting measures to protect and improve important habitat. We assessed how vegetation structure and composition, habitat features often targeted for management, affected territory and nest site selection by Grasshopper Sparrows (*Ammodramus savannarum ammolegus*) in southeastern Arizona. To identify features important to males establishing territories, we compared vegetation characteristics of known territories and random samples on 2 sites over 5 years. We examined habitat selection patterns of females by comparing characteristics of nest sites with territories over 3 years. Males selected territories in areas of sparser vegetation structure and more tall shrubs (>2 m) than random plots on the site with low shrub densities. Males did not select territories based on the proportion of exotic grasses. Females generally located nest sites in areas with lower small shrub (1–2 m tall) densities than territories overall when possible and preferentially selected native grasses for nest construction. Whether habitat selection was apparent depended upon the range of vegetation structure that was available. We identified an upper threshold above which grass structure seemed to be too high and dense for Grasshopper Sparrows. Our results suggest that some management that reduces vegetative structure may benefit this species in desert grasslands at the nest and territory scale. However, we did not assess initial male habitat selection at a broader landscape scale where their selection patterns may be different and could be influenced by vegetation density and structure outside the range of values sampled in this study.

Keywords: Ammodramus savannarum ammolegus, Arizona, desert grassland, Grasshopper Sparrow, grassland bird, habitat selection, nest site, territory

Patrones de selección de territorios y sitios de anidación de *Ammodramus savannarum ammolegus* en el sureste de Arizona

RESUMEN

Las poblaciones de aves de pradera están mostrando algunas de las tasas de disminución poblacional más altas de las aves norteamericanas, lo que promueve medidas para proteger y mejorar el hábitat importante para ellas. Determinamos cómo la estructura y composición de la vegetación, características del hábitat que usualmente son el enfoque de los planes de manejo, afectan la selección de territorios y sitios para anidar por parte de *Ammodramus savannarum ammolegus* en el sureste de Arizona. Para identificar las características que son importantes para los machos que están estableciendo territorios comparamos las características de la vegetación de territorios conocidos y muestras al azar en 2 sitios durante 5 años. Examinamos los patrones de selección de hábitat de las hembras comparando las características de los sitios de anidación con las de los territorios por 3 años. Los machos seleccionaron territorios en áreas con una estructura de vegetación más dispersa y con más arbustos altos (>2 m) que en las parcelas ubicadas al azar en el sitio con bajas densidades de arbustos. Los machos no seleccionaron territorios con base en la proporción de pastos exóticos. Las hembras generalmente ubicaron los nidos en áreas con densidades más bajas de arbustos pequeños (1–2 m de alto) cuando fue posible y seleccionaron preferiblemente pastos nativos para construir los nidos. La selección de hábitat solo fue aparente cuando había un gradiente en la estructura de la vegetación. Identificamos un límite superior por encima del cual la estructura de los pastos parecía ser muy alta y densa para *A. s. ammolegus*. Nuestros resultados sugieren que un nivel de manejo que reduzca la estructura vegetativa podría beneficiar a esta especie en las praderas desérticas a escala de los nidos y los territorios. Sin embargo, no evaluamos la selección inicial del hábitat por los machos a escala del paisaje, a la cual los patrones de selección pueden ser diferentes y podrían verse afectados por la densidad y estructura de la vegetación por fuera del rango de valores muestreados en este estudio.

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Palabras clave: Ammodramus savannarum ammolegus, Arizona, aves de pradera, praderas desérticas, selección de hábitat, sitio de anidación, territorio

INTRODUCTION

Characteristics of habitats selected by birds for territories and nest sites have consequences for reproduction and adult and juvenile survival (Misenhelter and Rotenberry 2000, Davis 2005, Fisher and Davis 2011). Vegetation structure and composition can affect food availability, foraging behavior, predation, and nest parasitism (Hovick and Miller 2013, Lyons et al. 2015), and can provide cues regarding food resources and risks of predation or other threats (Fisher and Davis 2011). Therefore, characteristics of habitat used by birds may differ from the habitat that is available (Misenhelter and Rotenberry 2000, Davis 2005, Fisher and Davis 2011). In general, songbird males establish and defend territories and females select nest sites and construct nests. Nest concealment and suitable nest microclimate are presumed to drive female nest site selection (Davis 2005, Fisher and Davis 2011). Territories are defended for purposes of mating, nesting, and foraging (Anich et al. 2009, Fisher and Davis 2011). This wider range of activities may mean that males select from a different set of vegetation cues. Nest site selection and territory site selection also occur at different spatial scales (Misenhelter and Rotenberry 2000). Therefore, the vegetation characteristics associated with nest sites may differ from those of the territory (Misenhelter and Rotenberry 2000, Fisher and Davis 2011).

Identifying vegetation characteristics associated with known territories and nest sites of grassland birds presents the most accurate information about territory and nest site selection (Dieni and Jones 2003, Davis 2005). However, many habitat selection studies measure bird abundance or occurrence and associate those bird measures with general measures of vegetation on the sites. Although they provide helpful information about general bird habitat requirements, the results provide limited information about the specific vegetation characteristics selected by territorial and nesting individuals. Among the studies that do measure specific bird territory or nest sites, fewer studies report territory than nest site vegetation characteristics, and even fewer compare characteristics between territories and nest sites.

Grassland bird populations are showing some of the greatest rates of decline of any North American birds, prompting measures to protect and improve important habitat (Knopf 1996, Berlanga et al. 2010, Sauer et al. 2014). These declines are attributed to habitat loss, degradation, and fragmentation, grassland management practices (e.g., grazing, burning, mowing, shrub encroachment, exotic plants), and natural forces (e.g., predation and nest parasitism) (Vickery et al. 1999, Askins et al. 2007, Rosenberg et al. 2016). Grasshopper Sparrow (*Ammodramus savannarum*), one of the most abundant species of grassland birds in the plains and desert grasslands of southeastern Arizona, may function as an indicator for the habitat needs of other grassland species as well (Bock and Webb 1984, Elliott 2016). Determining Grasshopper Sparrow nest and territorial habitat selection patterns will provide resource managers with critical information about how environmental and anthropogenic changes in habitat characteristics affect the abundance and distribution of this subspecies of conservation concern (U.S. Fish and Wildlife Service 2008).

We assessed how vegetative structure and composition, habitat features often targeted for management, affected territory and nest site selection by Grasshopper Sparrows on 2 grassland study sites in southeastern Arizona. We compared territory characteristics with characteristics of available vegetation structure measured on randomly located transects within the study sites, and compared nest plot characteristics with territories. Our objectives were to (1) identify the vegetation characteristics of Grasshopper Sparrow territories and nest sites; (2) determine whether Grasshopper Sparrows selected territories and nest sites that differed from what was available, based on the vegetation structure and composition characteristics that we measured, assuming that this constituted habitat selection; and (3) determine whether those choices were affected by variation in vegetation structure between sites and among years.

METHODS

Study Sites

In North America, desert grasslands stretch from the southwestern United States into northern Mexico at elevations of 1,100–1,800 m (McClaran and Van Devender 1995, Brown and Makings 2014). The climate is dry, hot, and sunny. Mean annual precipitation in the U.S. portions of the desert grasslands ranges from 230 to 460 mm; ~60% of precipitation occurs between July and September in southeastern Arizona, and there is significant spatial and temporal variation (McClaran and Van Devender 1995). Mean annual temperature is 13–16°C, and the region typically experiences 20 summer days hotter than 40°C. The main ecological driver is drought/precipitation; secondary drivers are fire and grazing (Askins et al. 2007).

We worked on 2 sites ~13 km apart in the semidesert and plains grasslands of Santa Cruz County, southeastern Arizona: Audubon Appleton-Whittell Research Ranch

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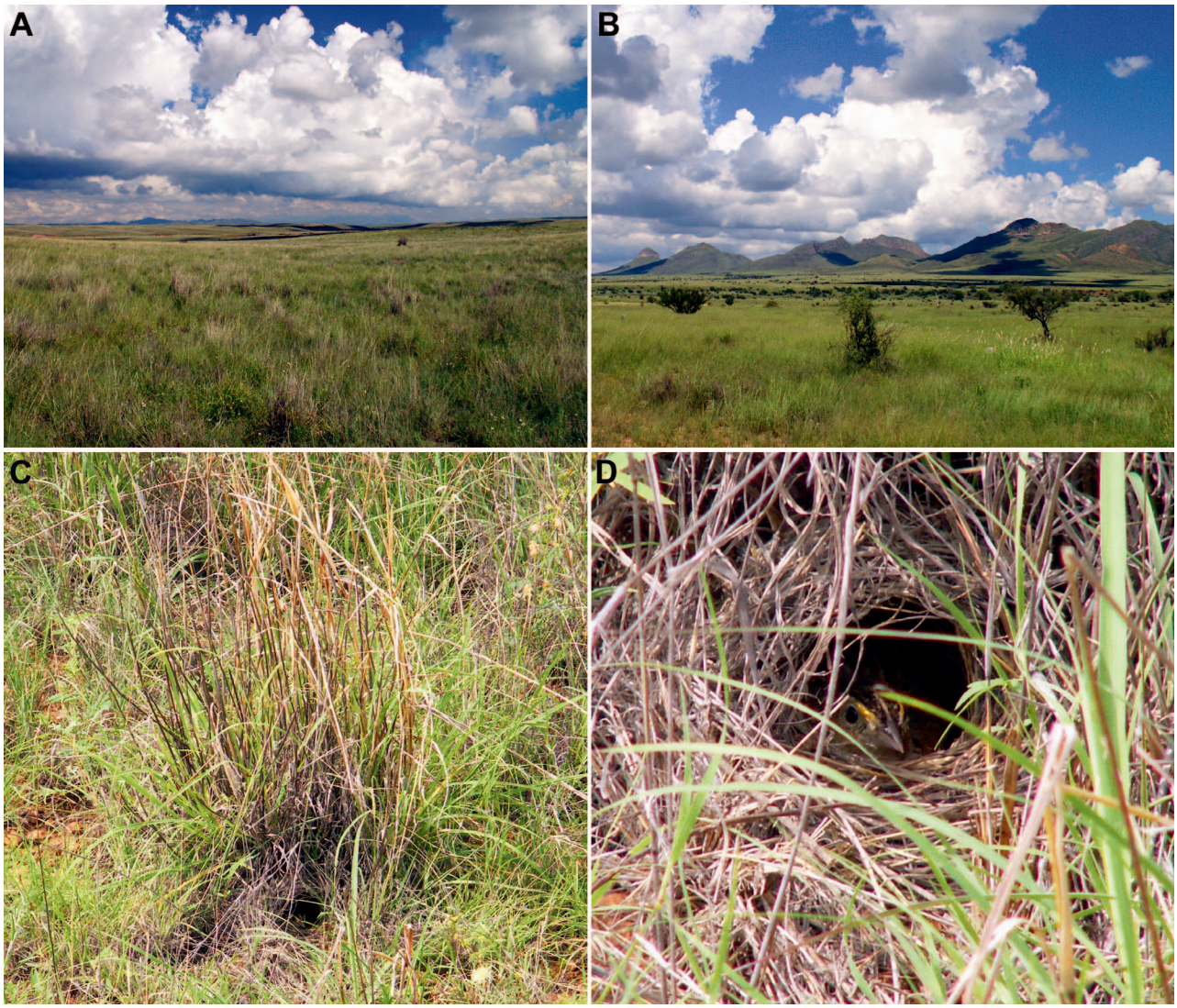


FIGURE 1. Grasshopper Sparrow study sites in southeastern Arizona (August 2012). (**A**) Davis pasture on Las Cienegas National Conservation Area has lower shrub density than (**B**) Audubon Appleton-Whittell Research Ranch. Female Grasshopper Sparrow on her nest (**C** and **D**) constructed beneath a native cane bluestem (*Bothriochloa barbinodis*) clump (July 2012).

(Audubon; 3,200 ha, 31.60°N, 110.51°W, elevation 1,497 m) and Davis pasture (Davis) on the Bureau of Land Management (BLM) Las Cienegas National Conservation Area (NCA) (1,560 ha, 31.70°N, 110.60°W, elevation 1,430 m; Figure 1A,B). These study sites were 2 of 7 sites located throughout the desert grasslands of southeastern Arizona that were studied previously for grassland bird winter habitat use (Ruth et al. 2014). These 2 sites were selected because land managers provided access for breeding ecology studies and because the density of Grasshopper Sparrows ensured the necessary sample sizes for territory and nest plots. We considered these sites to be representative of Grasshopper Sparrow habitat based on distribution surveys conducted throughout the U.S. range of the subspecies (Ruth 2008).

The upland grasslands on these sites are dominated by a variety of native annual and perennial bunchgrasses including gramas (*Bouteloua* spp.), cane bluestem (*Bothriochloa barbinodis*), threeawns (*Aristida* spp.), bristly wolfstail (*Lycurus setosus*), curly-mesquite (*Hilaria belangeri*), and plains lovegrass (*Eragrostis intermedia*), as well as exotic grasses, predominantly Lehmann lovegrass (*Eragrostis lehmanniana*) and some Boer lovegrass (*E. chloromelas*). These grasslands also support varying densities of shrubs, succulents, and low trees, predominantly velvet mesquite (*Prosopis velutina*) (McClaran and Van Devender 1995). Although both sites include some areas with higher densities of trees, our studies focused on the relatively open grassland portions of both sites. Audubon is managed as a desert grassland research facility

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and has been ungrazed since 1968; it is occasionally exposed to unplanned wildfires (e.g., 2002 Ryan Wildfire). Davis, as part of the Las Cienegas NCA, is managed for multiple uses including grazing; during the period of this study, cattle were only grazed on Davis for one month in 2012.

Study Species

The Grasshopper Sparrow is a widely distributed open grassland bird with 4 recognized subspecies that breed in North America (Vickery 1996). Although a common species in North American grasslands, Grasshopper Sparrow populations show continent-wide long-term declines (Sauer et al. 2014), and it is designated a Common Bird in Steep Decline (Berlanga et al. 2010, North American Bird Conservation Initiative 2014, Rosenberg et al. 2016). It is also designated as a focal species by U.S. Fish and Wildlife Service (USFWS) with a status assessment and conservation plan (Ruth 2015). Southeastern Arizona is the core breeding range for *Ammodramus savannarum ammolegus* (commonly referred to as the Arizona Grasshopper Sparrow), the subspecies we studied. The breeding range of this subspecies extends from southeastern Arizona and southwestern New Mexico south to northern Sonora, Mexico (Vickery 1996), and likely northwestern Chihuahua (Ruth 2015). The subspecies is considered a Bird of Conservation Concern for USFWS Region 2 (U.S. Fish and Wildlife Service 2008) and is listed as endangered in the state of New Mexico. The limited information about habitat preferences of *A. s. ammolegus* is based on general vegetation measures taken in association with surveys of occurrence, abundance, and observation rates (Mills 1982, Bock and Webb 1984, Strong 1988, Block and Morrison 2010). Consistent with our interest in comparing territory habitat with nest site habitat, male Grasshopper Sparrows establish and defend breeding territories, but females construct the nest, incubate the eggs, and brood the young (Vickery 1996, J. M. Ruth personal observation). Females construct domed nests on the ground beneath bunch grasses (Vickery 1996; Figure 1C,D).

Field Methods

We conducted summer fieldwork, including nest searching, territory mapping, and vegetation measurements on territory and nest plots and random transects, from late June/early July through August in 2009–2013. We worked on randomly selected representative portions of the 2 study sites: ~50 ha on Audubon and ~67 ha on Davis. We observed similar densities of Grasshopper Sparrows throughout the grassland portions of these sites.

Territory mapping and vegetation measurements. We used the flushing territory mapping protocol (Wiens 1969) on both sites in all years to document 223 territories of male Grasshopper Sparrows. Using global positioning system (GPS) units, we followed a territorial male, recording waypoints for every position of a perched (singing and nonsinging) or flushed individual until we compiled 20–30 observation points. In most cases, we recorded all observation points on a single day. On a few occasions, if fewer than 20 observations were compiled in 1 day, the observer returned as soon as possible to complete the mapping.

We measured the vegetation within territories by locating the centroid of the territory. We intersected the centroid with 15-m transects in the 4 cardinal directions, and took measurements at the centroid and at 5-, 10-, and 15-m intervals outward along each transect, resulting in 13 sample points per territory.

Nest searching and vegetation measurements. We conducted nest searches and monitoring from 2011 to 2013. We searched sites for active nests 3–5 times per week from early July through the end of August. Search techniques included rope dragging (Labisky 1957, Davis 2003, Dieni and Jones 2003), opportunistic foot flushing, behavioral observation (Martin and Geupel 1993), and occasional visual sighting of nests. Rope dragging was conducted by 2 people pulling a single 28-m length of heavy rope weighted at each end with a 30-mm length of pipe, and with aluminum or tin cans attached at 1-m intervals; in some cases a third person walked immediately behind the rope at the middle to help in sighting flushed birds. The rope was pulled systematically across the study sites.

Once a nest was found, we marked it for relocation; in addition to the GPS location, we attached a small piece of colored flagging to vegetation ~3 m from the nest in the direction that the nest entrance faced, and another at ~3 m in the opposite direction. Following fledging or nest failure, we sampled vegetation at the nest and in the nest plot (5-m radius centered on the nest). We typically measured nest vegetation within a week of fledging or failure, with the exception of 17 nests in the first year of nest monitoring that were measured later. For vegetation measurements at and near the nest, we intersected each nest with 5-m transects in the 4 cardinal directions and took measurements at the nest (center of plot) and at 1-, 3-, and 5-m intervals outward along each transect, resulting in 13 sample points per nest plot. On 2 sites over 3 years we measured vegetation on 121 nests.

We could not always associate a particular nest with a specific territorial male and his mapped territory because some discovered nests were found outside of any mapped territory and other nests were found along the boundary between 2 territories.

Random transect vegetation measurements. To document available vegetation structure by site and year, we randomly located one 1,000-m transect to bisect the study

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area on each site in each year. We used a random numbers table each year to identify the transect's starting point and direction, with the requirement that the resultant transect fit within the area of mapped Grasshopper Sparrow territories and monitored nests. We sampled vegetation at 25-m intervals along the transect, resulting in 40 samples per transect.

Vegetation measurement protocols. We selected vegetation variables based on relevant variables associated with grassland bird occurrence, abundance, and density as reported and summarized in the literature (Vickery 1996, Dieni and Jones 2003, Fisher and Davis 2010, Ruth 2015). Our vegetation variables included measures of vegetation structure (visual obstruction, vertical vegetation density, litter depth, standing dead litter, bare ground), composition (proportion native hits, proportion native points, proportion exotic points), and distribution (shrub density, distance to nearest shrub).

Measurement protocols were the same as those used on these sites for wintering grassland bird research (Ruth et al. 2014). We measured visual obstruction by holding a 6-mm diameter pole vertically at each sample point. The observer stood perpendicular to the transect at a distance of 4 m from the pole and viewed the pole from 1 m above ground level; we recorded the height at which the pole was completely obscured by vegetation from both sides of the transect (Robel et al. 1970). We measured vertical vegetation structure on the same 6-mm diameter pole; the observer identified live vegetation to species (or genus if necessary), dead litter, and estimated the number of contacts by each (Wiens 1969). At the same time, the observer recorded the depth of ground litter at the base of the vertical pole. We gathered shrub data using point-centered quarter (PCQ) measurements (Bonham 1989); from the center point of the plot (territory or nest) we divided the surrounding area into 4 quadrants defined by the cardinal directions. For the random transect, we established PCQ quadrants at both ends and at the midpoint of the transect. In each quadrant we identified the nearest shrub 1–2 m tall, and the nearest shrub or tree >2 m tall. We recorded distance from the central point using distance categories (0–5 m; >5–15 m; >15–30 m; >30–50 m; >50–100 m; >100–200 m; >200 m).

Data Analysis

Vegetation variable calculations. We calculated visual obstruction by averaging the 2 obstruction measurements at each point and then averaging over all points on territory, nest, and random plots. We calculated the following variables from the vertical vegetation structure measurements. Vertical vegetation density: sum of total number of contacts on the vertical pole in first (lowest), second, third, and fourth decimeters at a sampling point and averaged over all points on a plot. Standing dead litter: sum of total number of contacts with standing dead litter on the vertical pole in all decimeter intervals at a point and averaged over all points on a plot. Percent bare ground: percentage of points on a plot where the vertical pole had no contacts with vegetation. Litter depth: averaged the litter depth over points on a plot.

We expressed proportion of native grass on each plot as 2 variables representing different perspectives on the proportions of native and exotic grass (excluding unknown grasses). The first variable, proportion native hits, presents the proportion of grass contacts on the pole (hits) that were native, averaged over all points on the plot. Any points that had no hits of known grass species (e.g., had only unknown grass hits, only hits by forbs, woody vegetation, or standing dead litter, or no hits at all) received a value of zero. By definition, sites with a higher proportion of native grass hits had lower proportions of exotic grasses. Because the calculation uses total number of hits on the pole at each point, resulting values are affected by the structure of grasses. The second variable, proportion native points, presents the proportion of points on a plot that intersected with any native grass. We also calculated the proportion exotic points in the same manner, as it was not necessarily the inverse of the grass value in this case, because both native and exotic grass could occur at a point. Resulting values are primarily affected by the distribution of natives and exotics across the plot rather than grass structure.

For calculating territory means for the above variables, each plot had a sample size of 13, including the point at the center of the plot. In contrast, when calculating nest plot means, each plot had a sample size of 12, because we excluded the point at the center (the nest site). We chose to exclude the center point from nest plot structure calculations because Grasshopper Sparrows always construct their nests under grass clumps and, therefore, including the center point would bias the vegetation means upward. We did use vegetation structure measures from the center point of nest plot arrays to calculate proportion of nests that were constructed under native or exotic grass plants (NestPlant).

We calculated density (m) of shrubs 1–2 m and density of shrubs >2 m using the PCQ methodology (Bonham 1989)

$$m = \frac{4(4n-1)}{(\pi \sum_{i=1}^{n} \sum_{j=1}^{4} r_{ij}^2)}$$

where n is the number of randomly located points (or territories, or nests), and r is the individual distances to the nearest shrub in a given quadrant. We evaluated 2 different variables representing different aspects of shrub distribution: shrub density and distance to the nearest shrub. We thought that birds might respond differently to these 2

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features and to tall versus short shrubs. We calculated distance to the nearest shrub 1–2 m and distance to the nearest shrub >2 m using PCQ measurements as the shortest distance to a shrub of the pertinent height category in any of the 4 quadrants in a nest or territory plot or averaged over the 3 PCQ points along the random transect. We assumed no change in shrub density (and distance to nearest shrub) on a site over the study period; thus for random site values, we calculated the shrub metrics combining all 5 years of data.

Habitat selection comparisons. We consider that the characteristics of territories represent selection by males, whereas the characteristics of nest plots and nest sites represent selection by females. There are 2 issues to consider in accurately describing habitat selection for comparison. Measuring characteristics of random plots on study sites, rather than "unused" plots, provides the best assessment of available habitat to compare with characteristics of territories (Jones 2001). Given the lack of species-specific information (Vickery 1996), we assumed that Grasshopper Sparrow females locate nests within their mate's territory (Misenhelter and Rotenberry 2000, Jones 2001, Fisher and Davis 2011). Therefore, using territory characteristics, rather than random plot characteristics, provides the best assessment of habitat available to females with which to compare characteristics of nest plots (Jones 2001).

For territory selection by males, we compared random and territory features over all 5 years. For nest site selection, we compared territory and nest plot features over the 3 years with available nest data. Means and 95% confidence intervals (CI) of vegetation variables were calculated for each site and year. Hereafter these are referred to as site-years, and references to particular site-years are formatted as A12 = Audubon 2012, D09 = Davis 2009. Initial comparisons of random vegetation among years and between sites were made using ANOVA and two-sample *t*-tests for unequal samples using Systat 13 (Systat 2009) as appropriate. To detect habitat selection, we compared vegetation means using two-sample *t*-tests to determine whether vegetation on male sparrow territories differed from what was available within the study sites (random), or whether vegetation on female sparrow nest sites differed from what was available within territories. We compared nest plant(s) means with nest plot means because females could only select plants under which to place their nests from the habitat within their selected nest plot. For comparisons of proportion of native grass between nest plots and nest plants, we report whether the proportion of nest plants that were native fell within the 95% confidence intervals for nest plots.

In addition, because birds could be selecting from a narrower range of values than what is available even if the means are found to be similar, we also examined variation around the means. We considered total variation by pooling across all site-years as well as variation within each site-year. Where possible, we used Levene's test to compare the variability between random and territory, and between nest plots and territories, to identify whether birds were using a narrower range of vegetation structure, litter, and bare ground than was available. Levene's test is frequently recommended for comparing variation within ecological studies because it is more robust to departures from normality assumptions than alternative approaches (Donnelly and Kramer 1999, Jacobs and Podolsky 2010). To evaluate variation in shrub density values, we calculated variance after Bonham (1989:163), then used the variance ratio test to determine whether birds were using a narrower range of shrub densities than was available. Unless stated otherwise, we report values in tables and appendices as means and 95% confidence intervals; we report differences as statistically significant when $P \leq 0.05$.

We include 2 points of clarification. First, territory values for all 10 site-years were compared to random values for those site-years; but nest plot values were only available for 3 years, so they were compared to territory values for those same 6 site-years. Second, mean vegetation values for all territories for a site-year were compared to mean values for all nest plots for the same site-year; individual nest plots were not compared with individual territories. In order that comparisons between random transects (a single transect per site per year) and multiple territory or nest plots be made at a similar scale and sample size, for the random transect, we calculated means for vegetation variables unrelated to shrubs for each 2 adjacent points along the transect (e.g., points 1 and 2, points 3 and 4) for a sample size of $n = 20$. Assuming that shrub density and the related distance to nearest shrub did not change at the site level over such a short time span (5 years), we calculated the random site means pooled across years for these 2 variables.

RESULTS

We found notable annual and between-site differences in vegetation over the study period (Tables 1–3, Figures 2 and 3). Visual obstruction differed significantly over years at both sites (Audubon $F_{4,195} = 6.0$; $P < 0.001$; Davis $F_{4,195} = 19.4$; $P < 0.001$) as did vertical vegetation density (Audubon $F_{4,195} = 3.0$; $P = 0.02$; Davis $F_{4,195} = 3.0$; $P = 0.02$), but not litter and bare ground variables (Table 1). Davis had a higher proportion of native grass and a lower proportion of exotic grass than the Audubon site (Table 2, Figure 3A). In addition, mean shrub density was higher on Audubon than Davis for shrubs 1–2 m ($t_{28} = 17.9$; $P < 0.001$) and for shrubs >2 m ($t_{28} = 9.4$; $P < 0.001$) (Table 3, Figures 1 and 3). In connection with this pattern, distance to the nearest shrub was less on Audubon than on Davis

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TABLE 1. Mean and 95% confidence intervals (CI) of vegetation variables for random transects, Grasshopper Sparrow territory plots, and nest plots by site and year. Nest plots were only measured in 2011–2013. Any confidence interval with a negative value was truncated at zero. Symbols following the mean indicate significant results of two-sampled *t*-tests between values in that category and the previous category (e.g., random vs. territory, or nest vs. territory); symbols following the CI indicate significant results of Levene's test of variance between values in that category and the previous category; * indicates $P \leq 0.05$.

		Random transect			Territory			Nest plot		
Site	**Year**	***n***	**mean**	**CI**	***n***	**mean**	**CI**	***n***	**mean**	**CI**
(A) Visual obstruction (dm)										
Davis	2009	20	2.9	2.4, 3.4	22	1.5 *	1.3, 1.8 *			
Audubon	2010	20	1.9	1.5, 2.2	20	1.1 *	1.0, 1.2			
Audubon	2012	20	1.5	1.3, 1.7	22	0.8 *	0.7, 0.9 *	10	0.9	0.7, 1.2
Audubon	2009	20	1.2	0.9, 1.4	22	1.5	1.2, 1.9			
Davis	2010	20	1.2	1.0, 1.4	20	0.7 *	0.6, 0.9 *			
Davis	2011	20	1.1	0.9, 1.4	28	0.6 *	0.5, 0.7 *	22	1.0 *	0.8, 1.1 *
Audubon	2013	20	1.1	0.9, 1.3	20	1.0	0.9, 1.2 *	31	1.1	1.0, 1.2
Davis	2013	20	1.0	0.7, 1.2	25	0.6 *	0.5, 0.7	28	0.8	0.7, 0.9 *
Audubon	2011	20	0.9	0.7, 1.2	24	0.8	0.7, 0.9 *	13	0.7	0.6, 0.8
Davis	2012	20	0.4	0.3, 0.6	20	0.5	0.4, 0.6	17	0.4	0.3, 0.5
(B) Vertical vegetation density (# hits in 4 dm)										
Audubon	2012	20	8.4	7.1, 9.8	22	6.6 *	6.1, 7.1 *	10	6.6	5.6, 7.7
Audubon	2010	20	8.3	7.0, 9.6	20	7.2	6.4, 9.0			
Audubon	2013	20	7.7	6.2, 9.1	20	6.2	5.6, 6.7 *	31	6.5	6.2, 6.8
Davis	2011	20	7.4	6.1, 8.7	28	6.4	5.9, 6.8 *	22	7.4 *	6.8, 8.1 *
Davis	2009	20	6.7	5.6, 7.9	22	6.5	5.6, 7.4			
Audubon	2011	20	6.4	5.3, 7.5	24	6.5	5.9, 7.2 *	13	5.4 *	4.8, 6.0
Davis	2010	20	6.3	5.4, 7.2	20	6.4	5.8, 7.0			
Audubon	2009	20	6.2	4.9, 7.6	22	6.4	5.8, 6.9			
Davis	2012	20	5.6	4.4, 6.7	20	6	5.4, 6.6 *	17	5.7	5.0, 6.4
Davis	2013	20	5.1	3.9, 6.3	25	4.9	4.3, 5.5	28	5.7 *	5.4, 6.1
(C) Standing dead litter (# hits on pole)										
Davis	2012	20	1.1	0.6, 1.6	20	0.9	0.7, 1.0 *	17	0.8	0.6, 1.1
Davis	2009	20	1.0	0.4, 1.6	22	1.2	0.9, 1.5			
Audubon	2009	20	0.8	0.2, 1.4	22	0.8	0.6, 1.1			
Davis	2013	20	0.7	0.3, 1.1	25	1	0.8, 1.2 *	28	0.9	0.7, 1.1
Audubon	2013	20	0.6	0.1, 1.1	20	0.7	0.5, 0.9 *	31	0.8	0.6, 1.0
Audubon	2010	20	0.5	0.1, 1.0	20	0.8	0.6, 0.9			
Audubon	2012	20	0.5	0, 1.0	22	0.5	0.3, 0.8 *	10	0.9	0.9, 1.3
Davis	2010	20	0.3	0, 0.7	20	0.8 *	0.6, 1.0			
Davis	2011	20	0.3	0, 0.6	28	0.7 *	0.5, 0.9	22	0.5	0.3, 0.7
Audubon	2011	20	0.2	0, 0.5	24	0.5	0.3, 0.6	13	0.4	0.2, 0.6
(D) Litter depth (cm)										
Davis	2012	20	1.3	1.0, 1.7	20	1.1	0.9, 1.4	17	1.0	0.8, 1.3
Davis	2013	20	1.1	0.7, 1.5	25	1.2	1.0, 1.4	28	1.0	0.9, 1.2 *
Audubon	2013	20	1.1	0.6, 1.6	20	1.0	0.8, 1.2 *	31	1.0	0.8, 1.2
Davis	2010	20	0.9	0.4, 1.5	20	0.9	0.8, 1.1 *			
Davis	2011	20	0.9	0.5, 1.3	28	1	0.8, 1.2	22	1.1	0.9, 1.4 *
Davis	2009	20	0.8	0.5, 1.1	22	1.3 *	0.9, 1.7			
Audubon	2012	20	0.6	0.2, 1.0	22	0.8	0.5, 1.1	10	0.9	0.5, 1.4
Audubon	2009	20	0.5	0.2, 0.8	22	0.6	0.4, 0.8			
Audubon	2010	20	0.5	0.3, 0.6	20	0.5	0.4, 0.6			
Audubon	2011	20	0.5	0.3, 0.8	24	0.5	0.4, 0.6	13	0.4	0.3, 0.6 *
(E) Percent bare ground										
Audubon	2009	20	8	0, 16	22	6	3,9			
Davis	2009	20	5	0, 12	22	4	1, 6			
Davis	2011	20	5	0, 12	28	2	1, 4	22	0.4 *	0, 1
Audubon	2011	20	5	0, 12	24	7	4, 11	13	5	1, 9
Audubon	2012	20	5	0, 12	22	5	2, 8	10	3	0, 7 *
Davis	2010	20	3	0, 8	20	7	2, 12			
Davis	2012	20	3	0, 8	20	5	2, 8	17	3	0, 7 *
Davis	2013	20	3	0, 8	25	6	4, 9 *	28	3 *	1, 4
Audubon	2010	20	0	0, 0	20	8 *	5, 12			
Audubon	2013	20	0	0, 0	20	6 *	3, 9	31	4	1, 6

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TABLE 2. Mean and 95% confidence intervals (CI) of proportion of native and exotic grass for random transects, Grasshopper Sparrow territory plots, nest plots, and nest site plants by site and year. Nest plant mean is designated with a + or − if the value lies above or below the nest plot CI. Analysis and symbols as in Table 1.

		Random transect			Territory			Nest plot			Nest plant(s)	
Site	**Year**	***n***	**mean**	**CI**	***n***	**mean**	**CI**	***n***	**mean**	**CI**	***n***	**mean**
(A) Proportion native grass hits												
Davis	2011	20	0.87	0.76, 0.99	28	0.74	0.63, 0.85	22	0.77	0.64, 0.90	22	0.72
Davis	2013	20	0.78	0.59, 0.96	25	0.84	0.75, 0.94	28	0.86	0.78, 0.95	28	0.72 −
Davis	2010	20	0.76	0.60, 0.93	20	0.80	0.68, 0.93					
Davis	2012	20	0.75	0.58, 0.93	20	0.78	0.65, 0.91	17	0.81	0.65, 0.97	17	0.79
Davis	2009	20	0.64	0.41, 0.86	22	0.60	0.44, 0.76					
Audubon	2013	20	0.58	0.38, 0.78	20	0.50	0.38, 0.62	31	0.57	0.47, 0.67	31	0.93 +
Audubon	2010	20	0.54	0.35, 0.73	20	0.33	0.21, 0.45					
Audubon	2012	20	0.46	0.29, 0.63	23	0.34	0.25, 0.44	10	0.48	0.30, 0.65	10	0.84 +
Audubon	2011	20	0.35	0.17, 0.52	24	0.29	0.20, 0.39	13	0.45	0.30, 0.61	13	0.63 +
Audubon	2009	20	0.32	0.12, 0.52	22	0.48	0.33, 0.62					
(B) Proportion of points with native grass												
Davis	2011	20	0.85	0.74, 0.96	28	0.60 *	0.51, 0.69	22	0.73 *	0.63, 0.83	22	0.78
Davis	2013	20	0.75	0.59, 0.91	25	0.63	0.54, 0.73	28	0.72	0.65, 0.78	28	0.86 +
Davis	2010	20	0.73	0.56, 0.89	20	0.49 *	0.39, 0.59					
Davis	2012	20	0.63	0.48, 0.77	20	0.59	0.48, 0.69	17	0.65	0.53, 0.78	17	0.82 +
Audubon	2010	20	0.58	0.40, 0.75	20	0.30 *	0.21, 0.39					
Audubon	2013	20	0.55	0.37, 0.73	20	0.44	0.35, 0.54	31	0.57 *	0.49, 0.65	31	0.97 +
Davis	2009	20	0.50	0.30, 0.70	22	0.41	0.32, 0.50					
Audubon	2011	20	0.50	0.29, 0.72	24	0.30	0.21, 0.38	13	0.42	0.27, 0.57	13	0.69 +
Audubon	2012	20	0.48	0.31, 0.64	23	0.36	0.29, 0.44	10	0.44	0.28, 0.61	10	0.90 +
Audubon	2009	20	0.30	0.12, 0.48	22	0.30	0.23, 0.38					
(C) Proportion of points with exotic grass												
Audubon	2011	20	0.68	0.50, 0.85	24	0.63	0.53, 0.73	13	0.53	0.40, 0.65	13	0.23 −
Audubon	2012	20	0.55	0.38, 0.72	23	0.59	0.50, 0.68	10	0.51	0.33, 0.69	10	0.30 −
Audubon	2010	20	0.55	0.35, 0.75	20	0.52	0.41, 0.62					
Audubon	2009	20	0.50	0.30, 0.70	22	0.45	0.33, 0.58					
Audubon	2013	20	0.33	0.12, 0.50	20	0.45	0.36, 0.55	31	0.36	0.27, 0.44	31	0.16 −
Davis	2009	20	0.28	0.10, 0.45	22	0.23	0.13, 0.34					
Davis	2013	20	0.20	0.06, 0.34	25	0.12	0.05, 0.20	28	0.13	0.05, 0.21	28	0.21
Davis	2010	20	0.20	0.06, 0.34	20	0.13	0.05, 0.22					
Davis	2012	20	0.15	0.04, 0.26	20	0.19	0.09, 0.30	17	0.15	0.03, 0.26	17	0.35 +
Davis	2011	20	0.15	0.02, 0.28	28	0.19	0.11, 0.27	22	0.28	0.14, 0.43	22	0.35

for shrubs 1–2 m ($t_{28} = 5.7$; $P < 0.001$) and shrubs >2 m ($t_{28} = 2.4$; $P = 0.24$) (Table 3).

Evidence for Territory Selection

We found evidence that Grasshopper Sparrow males selected for sparser vegetation structure on territories as measured by visual obstruction. When random visual obstruction values averaged 1.0 dm or greater, mean visual obstruction on territory plots was significantly lower than random in 6 of 8 site-years (D09, A10, A12, D10, D11, and D13; Table 1), suggesting a potential threshold effect (Figure 2). For the 2 site-years with the lowest random visual obstruction measurements (A11 and D12), visual obstruction on territories was not different. In addition, total variation in visual obstruction within territories was significantly lower than total variation on random plots ($F_{1,421} = 34.3$; $P < 0.001$). Further, in 5 of 10 individual site-years, variation around territory means was also significantly smaller than around random means (D09, D10, D11, A13, A11; Table 1).

Evidence for territory selection based on the vegetation density variable was weaker. Vertical vegetation density on territories was significantly lower than random only at the highest mean value (A12; Table 1). In addition, total variation in vertical vegetation density within territories was significantly lower than total variation in random plots ($F_{1,421} = 44.9$; $P < 0.001$). In 4 of 10 individual site-years, variation around territory means was significantly smaller than around random means (A13, D11, A11, D12; Table 1).

There was only weak evidence for territory selection based on standing dead litter. Above a mean of 0.5 hits on the pole, there were no differences between random and territory plots, although in 2 of the 3 site-years with the lowest random standing dead litter, territories had

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TABLE 3. Mean and 95% confidence intervals (CI) of shrub density and distance to nearest shrub for random transects, Grasshopper Sparrow territory plots, and nest plots by site and year. Analysis and symbols as in Table 1, except that symbols following the CI indicate significant results of variance ratio test between that category and the previous category.

	Random transect				Territory			Nest plot		
Site	***n***	**mean**	**CI**	**Year**	***n***	**mean**	**CI**	***n***	**mean**	**CI**
(A) Density of shrubs 1–2 m tall (shrubs per ha)										
Audubon	15	0.51	0.47, 0.54	2009	22	0.56 *	0.53, 0.58			
				2010	20	0.47	0.45, 0.50			
				2011	24	0.33 *	0.31, 0.34 *	13	0.45 *	0.41, 0.49 *
				2012	23	0.65 *	0.62, 0.68	10	0.63	0.56, 0.70
				2013	20	0.43 *	0.41, 0.46	31	0.38 *	0.36, 0.39
Davis	15	0.17	0.16, 0.19	2009	22	0.24 *	0.23, 0.25			
				2010	20	0.18	0.17, 0.19			
				2011	28	0.19	0.18, 0.19	22	0.17 *	0.17, 0.18
				2012	20	0.20 *	0.19, 0.21	17	0.18 *	0.17, 0.20
				2013	25	0.17	0.17, 0.18	28	0.16 *	0.15, 0.17
(B) Density of shrubs >2 m tall (shrubs per ha)										
Audubon	15	0.29	0.27, 0.31	2009	22	0.39 *	0.37, 0.41			
				2010	20	0.29	0.28, 0.31			
				2011	24	0.29	0.28, 0.31	13	0.34 *	0.31, 0.37 *
				2012	23	0.28	0.27, 0.29	10	0.32 *	0.28, 0.36 *
				2013	20	0.24 *	0.23, 0.26	31	0.24	0.24, 0.25
Davis	15	0.18	0.17, 0.19	2009	22	0.23 *	0.22, 0.24			
				2010	20	0.22 *	0.21, 0.23			
				2011	28	0.23 *	0.22, 0.24	22	0.22	0.21, 0.23
				2012	20	0.25 *	0.23, 0.26	17	0.24	0.23, 0.26
				2013	25	0.22 *	0.21, 0.23	28	0.21 *	0.20, 0.21
(C) Distance to nearest shrub 1–2 m tall (m)										
Audubon	15	32	21, 44	2009	22	42	34, 51			
				2010	20	45	27, 63 *			
				2011	24	63	35, 92 *	13	34	11, 56 *
				2012	23	31	17, 44	10	31	13, 48
				2013	20	36	26, 45	31	45	26, 64 *
Davis	15	168	118, 217	2009	22	92 *	69, 115 *			
				2010	20	166	114, 218			
				2011	28	145	101, 188	22	166	121, 211
				2012	20	110	71, 149	17	139	86, 192
				2013	25	156	106, 206	28	217	174, 260
(D) Distance to nearest shrub >2 m tall (m)										
Audubon	15	81	55, 107	2009	22	80	57, 103			
				2010	20	89	54, 124			
				2011	24	78	57, 99	13	63	32, 94
				2012	23	77	50, 104	10	66	30, 101
				2013	20	97	70, 123	31	124	87, 161 *
Davis	15	152	94, 210	2009	22	126	99, 153 *			
				2010	20	103	58, 148			
				2011	28	115	80, 151	22	116	81, 151
				2012	20	92	51, 133	17	127	84, 169
				2013	25	105	72, 137	28	135	100, 170

significantly higher values than random (D10 and D11; Table 1). Total variation in standing dead litter within territories was significantly lower than total variation in random plots ($F_{1,421} = 71.6$; $P < 0.001$). However, the results for individual site-years were mixed (Table 1), with 2 of 10 site-years showing significantly less variation in territories than random (A13, D12) and 2 site-years showing significantly more variation in territories than random (A12, D13).

There was little to no evidence for territory selection based on litter depth. In only 1 site-year was there a significant difference between mean litter depth on territories (greater) than random (D09; Table 1). Total variation in litter depth within territories was significantly lower than total variation in random plots ($F_{1,421} = 16.0$; $P < 0.001$). However, in only 2 of 10 site-years was there significantly less variation in territories than in random (A13 and D10; Table 1).

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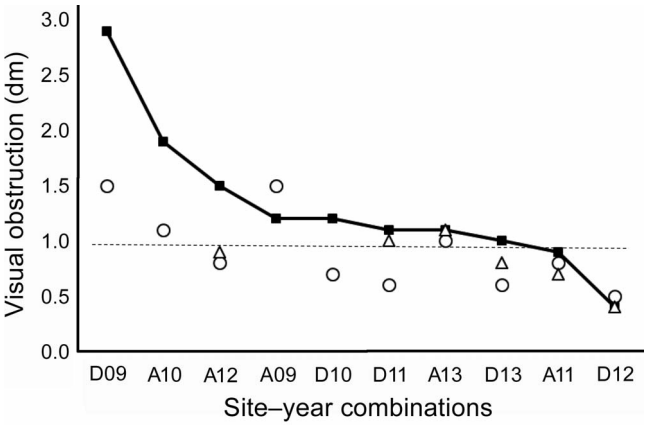


FIGURE 2. Comparison of mean visual obstruction (VO) among random transect (closed square and black line), Grasshopper Sparrow territory plot (open circle), and nest plot (open triangle), in descending order of random values for all site-year combinations (e.g., D09 = Davis 2009). Horizontal dotted line represents a threshold in random values above which territory values are significantly different from random.

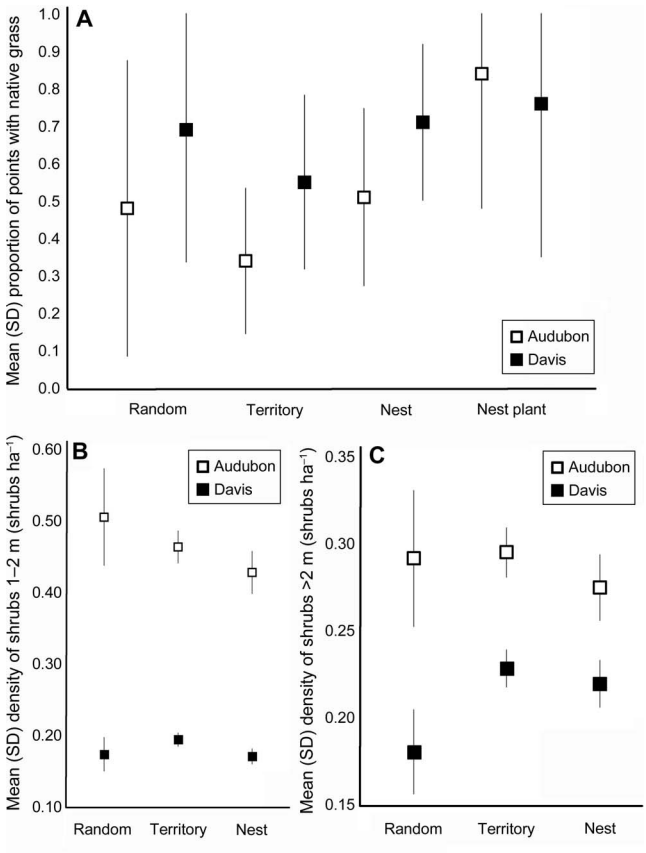


FIGURE 3. Site differences and habitat selection for territories, nest sites, and nest plants pooled across years in (**A**) proportion of plot points (or nest plants) that had native grasses (any SD that exceeded 1.0 was truncated at 1.0), (**B**) density of shrubs 1–2 m tall, and (**C**) density of shrubs >2 m tall.

Similarly there was little evidence for territory selection based on amount of bare ground. For site-years with random plot bare ground at 3% or more, there was no significant difference between territory plots and random, but for the 2 site-years when mean available bare ground approached zero, territory plots had significantly more bare ground (A10, A13; Table 1). In contrast to previous variables, total variation in bare ground within territories did not differ from total variation in random plots ($F_{1,421} = 1.3$; $P = 0.26$), and in only one site-year (D13) was there less variation in territories than random.

The evidence for territory selection based on vegetation composition (proportion of native and exotic grass) was mixed. There was no evidence of significant differences in proportion of native grass hits (the variable affected by grass structure) between territories and random plots (Table 2). However, for proportion native points (the variable affected more by plant distribution) in 3 of 10 site-years, territories had significantly lower proportions of natives than random (D10, D11, and A10; Table 2); the same general pattern is seen when site data are pooled over years (Figure 3A). There was also no evidence of territory selection based on proportion of exotic grass (Table 2).

We found relatively strong evidence that males selected territories based on vegetation distribution (shrub density), but this pattern differed somewhat depending on the height of the shrubs and seemed to demonstrate a threshold based on site differences (Table 3; Figures 1, 3B, 3C). On Audubon, where mean density of shrubs of 1–2 m exceeded 0.50 shrubs per ha, and mean density of shrubs >2 m exceeded 0.28 shrubs per ha, comparisons with shrub density on Grasshopper Sparrow territories were mixed. Some years showed greater shrub density on territories than random (shrub 1–2 m: A09 and A12; shrub >2 m: A09), some years had lower shrub density on territories (shrub 1–2 m: A11 and A13; shrub >2 m: A13), and some years showed no difference (shrub 1–2 m: A10; shrub >2 m: A10, A11, A12) (Table 3). In contrast, on Davis, where densities of both 1–2 m and >2 m shrubs were less than 0.20 shrubs per ha, a more consistent pattern emerged. In 2 of 5 years, density of shrubs 1–2 m on territories was significantly greater than random (D09 and D12), and in all 5 years, density of shrubs >2 m on territories was greater than random (Table 3). In addition, total variation in shrub density on territories was significantly lower than total variation on random plots (Figure 3B,C; Audubon: $F_{15,109} = 9.1$; $P < 0.001$ and $F_{15,109} = 7.5$; $P < 0.001$ for shrubs 1–2 m and shrubs >2 m, respectively; Davis: $F_{15,115} = 6.5$; $P < 0.001$ and $F_{15,115} = 5.1$; $P < 0.001$ for shrubs 1–2 m and shrubs >2 m, respectively). However, in only one site-year for shrubs 1–2 m was there lower variance among territories than random plots (A11; Table 3).

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As expected, where shrub density was higher (Audubon), distance to the nearest shrub was lower. However, unlike with shrub density, there was no evidence of territory selection based on distance to the nearest shrub on either site (Table 3). In only one site-year (D09) was there a significant difference between territories and random, where distance to nearest 1–2 m shrub was significantly less on territories than random.

Evidence for Nest Site Selection

We found little to no evidence that female Grasshopper Sparrows selected nest sites within territories based on vegetation structure. Mean visual obstruction on nest plots did not differ significantly from visual obstruction on territories (Table 1, Figure 2), with one site-year exception (nest plots in D11 had greater visual obstruction than territories). Neither did total variation around mean visual obstruction on nest plots differ from total variation on territories ($F_{1,258} = 3.7$; $P = 0.06$).

Evidence for nest site selection based on vertical vegetation density was inconclusive. In 3 of 6 site-years, nest plot vertical vegetation density was significantly different from territories (Table 1). However, in 2 of these, nest plot density was higher than on territories (D11 and D13), and in the third, nest plot density was lower than on territories (A11). In addition, total variation around mean vertical vegetation density at nest plots did not differ from total variation on territories ($F_{1,258} = 0.8$; $P = 0.37$).

There was no evidence of nest site selection based on litter (neither standing dead litter nor litter depth). In none of the 6 site-years did average standing dead litter or litter depth in nest plots differ from territories (Table 1). In addition, total variation around the means on nest plots did not differ from total variation on territories for either standing dead litter ($F_{1,258} = 0.4$; $P = 0.56$) or litter depth ($F_{1,258} = 0.1$; $P = 0.72$).

There was little evidence of nest site selection based on amount of bare ground. In only 2 of 6 site-years (D11 and D13) was mean percent bare ground on nest plots significantly lower than on territories (Table 1). However, in contrast to the previous variables on nest plots, total variation in bare ground on nest plots was lower than on territories ($F_{1,258} = 6.8$; $P = 0.01$). In only 2 site-years was nest plot variation less than on territories (A12 and D12; Table 1).

Similar to male territory selection above, the evidence for female nest site selection based on vegetation composition (proportion of native and exotic grass) was mixed. There were no significant differences in proportion of native grass hits between nest plots and territories (Table 2). For proportion native points, there was again only limited evidence (Figure 3A). In 2 of 6 site-years, proportion native points on nest plots was significantly higher than for territories (D11 and A13; Table 2). There was also no evidence of differences in proportion exotic points between nest plots and territories (Table 2).

The strongest evidence for nest site selection based on vegetation composition arose when comparing nest plots and the specific plant(s) under which the nests were placed. On Davis the proportion of native hits for nest plants fell within or below the 95% confidence intervals of the nest plots (Table 2). But on Audubon, the proportion of native hits for nest plants fell outside and above the 95% confidence intervals for nest plot means (Table 2). A similar pattern was seen at both sites for the proportion native points variable. Proportion native points for nest plants was greater than on nest plots, and in 5 of 6 site-years, the proportion of native points for nest plants fell above the 95% CI for the nest plot mean (Table 2); the same general pattern is seen when site data are pooled over years (Figure 3A). A similar but reverse pattern held for the proportion exotic points variable (Table 2). On Davis, where mean proportions of exotic points on random transects were low, only D12 had a greater proportion of exotic nest plants than at the nest plot scale. For Audubon, where random proportion of exotic points was relatively high, in all 3 years proportions of exotic points for nest plants were lower than nest plot means and the nest plant values fell below the 95% CI for the nest plots.

We also found relatively strong evidence that females selected nest plots based on vegetation distribution (shrub density). As with male territory selection, this pattern differed somewhat between sites and depending on the height of the shrubs (Table 3; Figures 1A, 1B and 3B, 3C). On Davis, where shrub densities were lower, in all 3 years 1–2 m shrub density surrounding nests was significantly lower than for territories. Also, in one year (D13), shrub >2 m density on nest plots was significantly lower than for territories. On Audubon, where shrub densities were higher, results were mixed. In one year (A11), 1–2 m shrub density surrounding nests was significantly higher than on territories, while in another year (A13) shrub density around nests was significantly lower. In 2 of 3 years, shrubs >2 m density surrounding nests was significantly higher than territories (A11 and A12). In addition, total variation around shrub density means on nest plots did not differ from total variation on territories (Figure 3B, 3C; Audubon: $F_{54,67} = 1.2$; $P > 0.5$ and $F_{54,67} = 1.3$; $P > 0.5$ for shrubs 1–2 m and shrubs >2 m, respectively; Davis: $F_{73,67} = 1.1$; $P > 0.5$ and $F_{67,73} = 1.0$; $P > 0.5$ for shrubs 1–2 m and shrubs >2 m, respectively). Again, similar to male territory selection, there was no evidence of female nest site selection based on mean distance to the nearest shrub (Table 3). We did not attempt to interpret patterns of variation around the mean distance to nearest shrubs because variation was so large (Table 3).

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DISCUSSION

Our results are based on specific habitat characteristics on individual mapped Grasshopper Sparrow territories and plots surrounding monitored nests, in contrast to much of the literature which reports on less specific bird and habitat data. We suggest that different, and sometimes conflicting, factors are driving selection of Grasshopper Sparrow territories and nest sites, and that as a result, there are differences in the vegetation structure, composition, and shrub density between male-selected territories and female-selected nest sites.

Male Grasshopper Sparrows establish and defend territories, while the female constructs the nest, and presumably also selects the nest site (Vickery 1996, J. M. Ruth personal observation). This "division of labor" between males and females results in these territory and nest site differences. In selecting territories, males are driven by the need for food resources, cover, singing perches, and vigilance for predators; in selecting nest sites, females are driven by the need for cover and suitable microclimate (Misenhelter and Rotenberry 2000, Davis 2005, Fisher and Davis 2011). Both males and females are faced with spatial and temporal variation in vegetation structure due to the primary ecological drivers in desert grasslands—precipitation/drought, fire, and grazing—which in turn result in variation in prey abundance and availability. Primary productivity in grasslands is positively associated with previous seasonal precipitation (Sala et al. 1988, Mowll et al. 2015), and vegetation structure is at least temporarily reduced by both fire and grazing. In a region with great annual and seasonal variation in these factors, one would expect annual variation in measures of vegetation structure, as we found. Evidence that Grasshopper Sparrow males select territory features is strongest when considering visual obstruction and vertical vegetation density. Males generally placed territories within sparser vegetation structure, except under certain thresholds (1.0 dm of visual obstruction and possibly 7 vegetation hits in 4 dm for vertical vegetation density). Therefore, even in these relatively sparse desert grasslands, we suggest that grass structure can be too high or dense for Grasshopper Sparrow territories. In contrast, these metrics were not important to females selecting nest sites, suggesting that visual obstruction and vertical vegetation density in male territories were suitable for nest placement.

In open grassland habitats, distribution and density of vertical structural components, most frequently represented by shrubs and trees, can have important impacts on avian communities and habitat selection. We suggest there was a lower threshold of shrub density that was important for Grasshopper Sparrows, and that males and females exhibit a balancing act when it comes to selecting territories and nest sites in relation to shrub density. When selecting territories, male Grasshopper Sparrows may prefer sites with some shrubs to use for singing perches, a pattern that was more obvious at low shrub densities. Territorial males regularly used taller shrubs in their territories as favored singing perches; in fact, despite inter-territorial aggression, the edges of adjacent territories often shared a favored mesquite singing perch where shrub density was low (J. M. Ruth personal observation). In contrast, female sparrows are likely driven to locate nest sites that will protect their eggs and nestlings. In open grassland habitats, shrubs and trees provide perches for prospective predators such as ravens (*Corvus* spp.) and Loggerhead Shrikes (*Lanius ludovicianus*). Small mammal and snake nest predators also use vertical cover in the form of shrubs for protective cover, location of burrows, and favorable microclimates (With 1994, Klug et al. 2010). In response, Grasshopper Sparrow females may prefer to locate nests so as to minimize nearby shrubs. Therefore, the balancing act our findings suggest may involve males selecting territories that have some shrubs for singing perches, whereas the females select nest sites that, within the options provided in those territories, minimize shrubs. Lack of the same patterns on Audubon may be because the entire site provides sufficient shrubs for male perch sites, and given the higher density of shrubs overall, it may be impossible for the female to select nest sites that show any significant difference in shrub density from what is available on the territory.

There was no clear evidence that the proportion of native grass was an important factor for Grasshopper Sparrow male territory selection. The most notable selection for native grasses was at the nest plant scale, with females strongly selecting native grasses under which to construct nests. The selection of native grasses may be related to the evolution of nest building, specifically to nest construction behaviors that may have evolved in response to the structures of plants to which the species was commonly exposed (Collias and Collias 1984, Hansell 2000). The lack of evidence in our study for the importance of proportions of native and exotic grass for Grasshopper Sparrow territories or nest sites is not consistent with other regional studies that found Grasshopper Sparrows to be more abundant on sites dominated by native grasses than on sites dominated by exotic grasses (Bock et al. 1986, Bock and Bock 1992). Across its range, however, Grasshopper Sparrow responses to native and exotic grasses are mixed (Ruth 2015). At the territory scale, vegetation structure may be more important than species composition (Davis and Duncan 1999, Ruth 2015), as suggested by our findings regarding visual obstruction and vertical vegetation density.

Our findings of the importance of vegetation structure are consistent with literature for this subspecies (Mills 1982, Bock and Webb 1984, Strong 1988, Block and Morrison 2010). Across the Grasshopper Sparrow's

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breeding range, it is found in grasslands with intermediate grass structure (height and density) (Vickery 1996, Ruth 2015), resulting in varying occupancy patterns depending on the height and density of available grasslands (e.g., they occur in shorter, sparser grass in tallgrass prairie, and in taller, denser grass in shortgrass prairie).

Our findings about the importance of habitat characteristics selected for territories and nest sites have broader implications for bird conservation. Habitat characteristics can have consequences for productivity and survival (Misenhelter and Rotenberry 2000, Davis 2005, Fisher and Davis 2011, Davis et al. 2016). In addition, because primary productivity, and therefore vegetation structure, in grasslands has been positively associated with previous seasonal precipitation (Sala et al. 1988, Mowll et al. 2015), climate may have both direct and indirect impacts on avian populations as well as productivity and survival (Morrison and Bolger 2002, Skagen and Yackel Adams 2012, Öberg et al. 2015, Gorzo et al. 2016). There is evidence that Grasshopper Sparrow nest survival is associated with both seasonal precipitation and nest site habitat characteristics (J. M. Ruth personal observation).

Management Implications

Our findings may be used as guidelines for evaluating the suitability of specific grasslands within the region for Grasshopper Sparrows. Based on the properties of normal distributions, we assume that ~68% of new observations will fall within 1 SD of the mean for normally distributed variables such as visual obstruction, vertical vegetation density, and shrub density. Therefore, based on our measurement protocols, Grasshopper Sparrows may find suitable habitat for territories (and nest sites) where visual obstruction readings fall between 0.4 and 1.4 dm (between 0.5 and 1.2 dm for nest sites), vertical vegetation density is between 4.8 and 7.8 hits in 4 dm of a pole (between 5.0 and 7.6 hits on the pole for nest sites), there is a sufficient proportion of native grasses (> 0.40) available for nest construction, densities of small shrubs (1–2 m) are between 0.2 and 0.5 shrubs per ha (slightly lower for nests), and densities of large shrubs (>2 m) are between 0.2 and 0.3 shrubs per ha (Tables 1–3, Figures 2 and 3).

We suggest a few cautionary notes. First, evidence for habitat selection can vary with the position of study sites along a continuum of available habitat characteristics, and comparisons between studies may be difficult and potentially misleading. For example, if a species prefers intermediate levels of a given habitat characteristic (e.g., shrub density), studies at the high end of the continuum may contradict studies at the low end (Ruth 2000). An example from this study is Grasshopper Sparrow response to shrubs. Most literature for this broadly distributed species indicates a negative response to woody cover (Ruth 2015), and most breeding season studies in the desert grassland region showed similar results (Bock and Webb 1984, Block and Morrison 2010). As suggested by our study, apparent contradictions in responses of Grasshopper Sparrows to woody cover on different sites may be a function of where the study sites were located along the available continuum of shrub cover in the region (Ruth 2000, 2015).

Second, desert grasslands in southeastern Arizona exhibit a broader range (higher and lower than Audubon and Davis) of vertical vegetation density and shrub density, based on previous winter studies (Ruth et al. 2014). Although our results suggest that some management that reduces vegetative structure may benefit this species in desert grasslands at the nest and territory scale, we did not assess initial male habitat selection at a broader landscape scale. Grasshopper Sparrow males may make initial habitat selection at a larger, landscape scale based on different criteria.

Current management practices on both of our study sites appear to provide suitable habitat for Grasshopper Sparrow territories and nest placement. Our study highlights the importance of vegetation structure (visual obstruction and vertical vegetation density) for territories, native grass species for placement of nests, and the complex relationship of territory and nest site selection in relation to shrub density. We emphasize that our scope of inference is limited to the range of values documented within our study. For example, our study documented a threshold above which grass structure was too high for Grasshopper Sparrows, where males selected territories amongst sparser vegetation structure. However, we propose that there is also a lower threshold in vegetation structure, not documented during the years of this study or on these study sites, below which Grasshopper Sparrows would not find sufficient grass structure to provide cover for foraging or nest building. This caveat is important in an arid ecosystem driven by drought/precipitation managed with fire and grazing.

Similar caveats should be applied when interpreting our results regarding shrub density and proportions of native grasses. At low shrub densities, male Grasshopper Sparrows selected territories with slightly higher shrub densities, while at higher shrub densities, there was no evidence of selection. However, we also propose that there is a point along the shrub density continuum above which Grasshopper Sparrows, as an open grassland species, would not find suitable grassland habitat for territories or nests. For example, the Buenos Aires National Wildlife Refuge (NWR) has significantly higher shrub density than any of the other 6 winter grassland study sites in southeastern Arizona (Ruth et al. 2014). Roadside breeding surveys of Grasshopper Sparrow indicate that only a small low-density population remains on Buenos Aires NWR compared with the Sonoita Valley (location of Audubon

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and Davis) (Ruth 2008). Although we did not find any indication of selection of native grasses for territories or nest sites, we did document the importance of native grasses for nest placement. This suggests some threats to Grasshopper Sparrows from loss of native grass species; there may be a threshold in proportion of native grass species below which females may not find sufficient native grasses under which to place their nests.

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