



RESEARCH ARTICLE

When to use social cues: Conspecific attraction at newly created grasslands

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ABSTRACT

Social cues are often used by birds when selecting breeding habitats, however, little is known about the timing and influence of social cues within or across seasons. The ontogeny of social information within newly available habitat is essentially unknown and potentially relevant to habitat management, as the primary approach of many conservation initiatives is to simply create habitat. We investigated the influence of conspecific attraction via social cues (conspecific playbacks) on newly created grasslands for Grasshopper Sparrows (*Ammodramus savannarum*) in Central Illinois over a 2-year period. We found that Grasshopper Sparrows quickly locate and settle at newly created grasslands without the need for social cues, however, social cues are used later in the season. At sites where social cues (i.e. conspecific vocalizations) were broadcast the densities of Grasshopper Sparrows were nearly double that of sites without the additional social cues, however, this difference occurred later in the breeding season. We suggest that social cues are more valuable for Grasshopper Sparrows later in the breeding season as a potential cue of the reproductive success of individuals currently at the site, and therefore future reproduction at the site. Grassland birds are experiencing large population declines and the primary conservation approach is to provide additional habitat. By understanding how grassland birds select breeding sites we can better develop and implement conservation plans.

Keywords: conservation reserve program, conspecific attraction, Grasshopper Sparrow, habitat selection, social cues

Cuándo usar señales sociales: atracción de individuos coespecíficos en pastizales recientemente creados

RESUMEN

Aunque las señales sociales frecuentemente son usadas por las aves al seleccionar los hábitats de reproducción, se sabe muy poco sobre la sincronización e influencia de las señales sociales dentro de o entre temporadas. La ontogenia de la información social dentro de hábitats recientemente creados es esencialmente desconocida y potencialmente relevante para el manejo del hábitat, dado que la aproximación primaria de muchas iniciativas de conservación es simplemente la creación de hábitat. Investigamos la influencia de la atracción de individuos coespecíficos por medio de señales sociales (reproducción de sonidos de coespecíficos previamente grabados) en pastizales recientemente creados para *Ammodramus savannarum* en el centro de Illinois por un periodo de dos años. Encontramos que *A. savannarum* rápidamente localiza y se establece en pastizales creados recientemente sin la necesidad de señales sociales, pero las señales sociales son usadas más tarde en la temporada. En los sitios donde las señales sociales (i.e. vocalizaciones coespecíficas) fueron transmitidas, la densidad de *A. savannarum* fue casi el doble de la de los sitios sin las señales sociales adicionales, aunque esta diferencia apareció tarde en la temporada reproductiva. Sugerimos que las señales sociales son más valiosas para *A. savannarum* tarde en la temporada reproductiva como una pista potencial del éxito reproductivo de los individuos que ocupan actualmente un sitio, y por ende, de la reproducción futura en ese sitio. Las aves de pastizal están experimentando grandes declives poblacionales y la aproximación primaria de conservación es proveer hábitat adicional. Entendiendo cómo las aves de pradera seleccionan los sitios para su reproducción podemos desarrollar e implementar mejores planes de conservación.

Palabras clave: *Ammodramus savannarum*, atracción coespecífica, programa de reservas de conservación, selección de hábitat, señales sociales

INTRODUCTION

Selection of breeding habitats has important consequences for the establishment and persistence of populations (McPeck et al. 2001). Animals can use social cues, such as the presence of conspecifics, to locate and select a breeding location (Stamps 1988, Danchin et al. 2004). For birds, vocalizations are the most obvious social cue allowing individuals to rapidly assess the presence of conspecifics (Seppänen et al. 2007, Ahlring et al. 2010). Social cues are also known to serve an important role in assessing the quality of habitat (Ward and Schlossberg 2004, Ahlring and Faaborg 2006, Nocera et al. 2006, Betts et al. 2008a, Ward et al. 2010). Experimental studies with birds commonly have found that seemingly appropriate, but unoccupied, habitat will be colonized when social cues are added (Ahlring and Faaborg 2006, Ahlring et al. 2006, Nocera et al. 2006, Betts et al. 2008a, Ward et al. 2011). Given that managers often create habitat for target species, understanding the role of social cues in locating these habitats and the key times (i.e. before, during, or after the breeding season) when social cues are assessed remains largely unknown (Ahlring et al. 2010). Given that the utilization of created habitat by select species is the benchmark for successful management, understanding the process underlying colonization of these sites is essential in evaluating many conservation programs.

Most bird species associated with grasslands in North America have declined over the last 30 years despite intensive efforts to create new habitats (Knopf 1994). In some situations, new habitats may not lead to increases in local populations because social cues are lacking and the sites are not colonized (Ahlring and Faaborg 2006). In the United States, over 14 million hectares are enrolled in conservation programs (e.g., Conservation Reserve Program, CRP). CRP converts rowcrop fields (e.g., corn and soybean) to grasslands, often with the goal of enhancing wildlife populations. Similar programs exist in Europe (e.g., agri-environmental programs) covering roughly 20% of farmlands (Herzog 2005). Since rowcrop fields are unsuitable for the majority of grassland birds, these programs provide an opportunity for conservation. If grassland birds, however, are using social information to locate grasslands, then these newly created sites may be colonized slowly, or not at all, and not achieve conservation goals without adding social information. Timely colonization of newly created grasslands is desirable since these sites undergo rapid succession with a short window of habitat suitability for a given species. Understanding how birds locate and select these newly created habitats after planting is critical in evaluating how effectively conservation programs such as CRP will benefit bird populations (Virzi et al. 2012).

The creation of new habitat also provides the opportunity to experiment with social cues and investigate how they are used over time. Birds can use information continually throughout a breeding season and across years when selecting breeding habitat (Hoover 2003, Pärt et al. 2011, Kearns and Rodewald 2013). Using new habitats allows us to eliminate the potential confound of older birds with experience using prior information to select habitat. Many bird species will also disperse to new nest sites mid-season, most often due to nest depredation and/or predation risk (Lima 2009, Kearns and Rodewald 2013). The strategy most often attributed to mid-season dispersal is a “win-stay, lose-switch” (WSLS) strategy in which birds will remain at a site if successful and switch to a new nest site or territory if their nest fails (Chalfoun and Martin 2010, Kearns and Rodewald 2013). If birds are shifting territories throughout the breeding season, then the availability and context of social cues will change over time conveying different information depending on the time of year (Nocera et al. 2006, Betts et al. 2008a, Alessi et al. 2010, Thomson et al. 2013). The perceived habitat quality can then change over time as a function of social cue density (Lima 2009, Chalfoun and Martin 2010, Kearns and Rodewald 2013). Birds can also use social information to influence site fidelity and habitat selection the following year (Hoover 2003, Danchin et al. 2004, Ward 2005, Nocera et al. 2006, Pärt et al. 2011).

We took advantage of the creation of new grasslands via a United States Department of Agriculture (USDA) conservation program to investigate how social cues influenced habitat selection of the Grasshopper Sparrow (*Ammodramus savannarum*) across the breeding season. We randomly assigned newly created grasslands to either an experimental treatment in which Grasshopper Sparrow vocalizations were broadcast, or a control with no vocalizations. We expected that the addition of social cues at newly created grasslands would result in the sites being more likely to be colonized and have an overall greater density than sites without added social cues. We also expected that the relative impact of the additional social cues on Grasshopper Sparrows may be greater later in the breeding season when reproductively unsuccessful individuals may move between sites and use vocalizations to indicate habitat quality.

METHODS

Study Species

Grasshopper Sparrows are migratory and multi-brooded, and nest in early successional grassland habitat with a mix of bare ground and litter cover for foraging substrate (Whitmore 1981). Similar to other grassland species, Grasshopper Sparrows have relatively low site fidelity (Ingold et al. 2010) and are known to move between

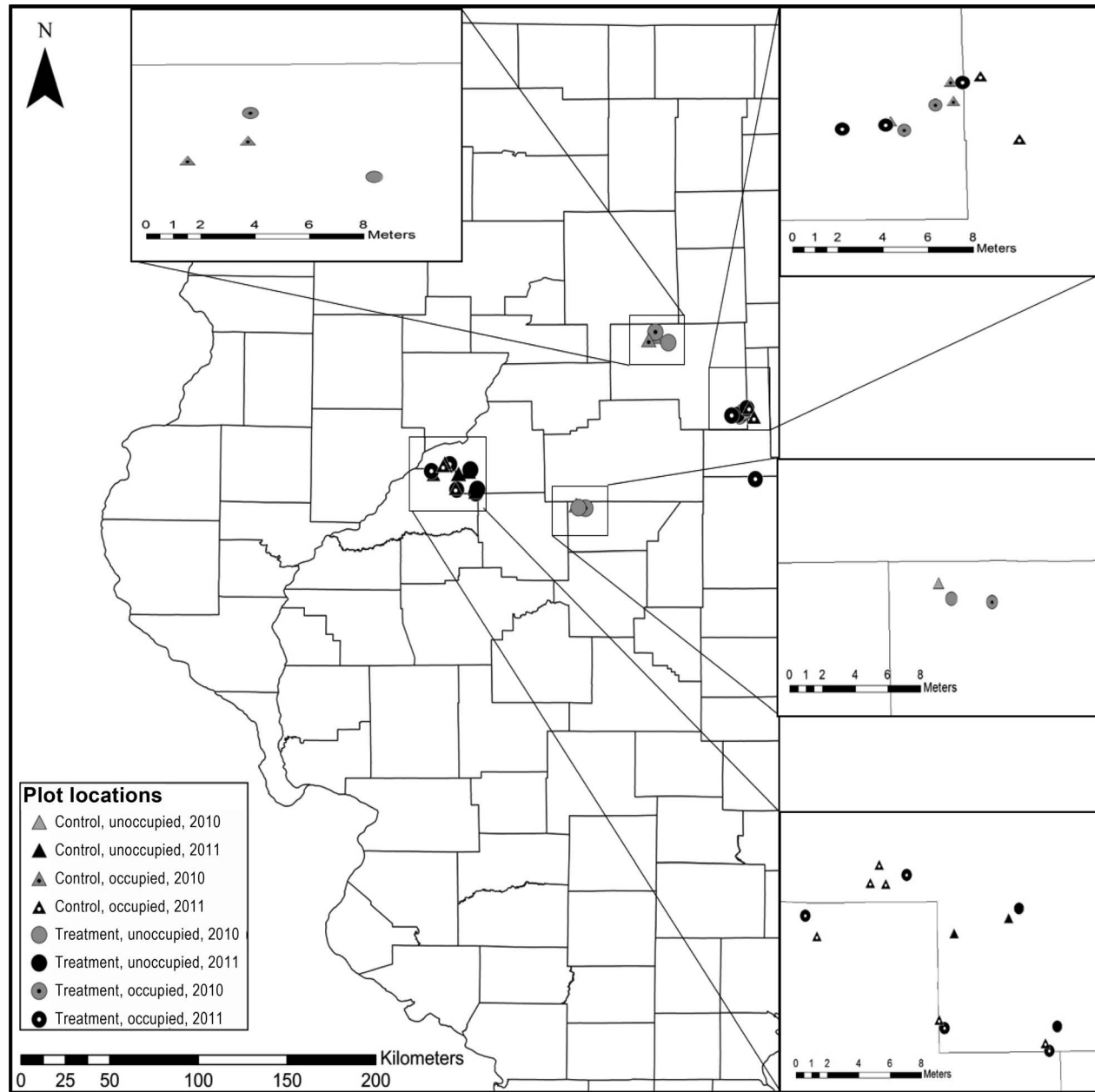


FIGURE 1. Map showing study sites throughout Central Illinois during 2010 (gray) and 2011 (black) breeding seasons. Triangles represent control sites with no vocalizations and circles represent playback treatments. Dots within symbols represent sites where Grasshopper Sparrows were detected while empty symbols represent sites where sparrows were never detected.

grasslands during the breeding season (Seigel 2009). Grasshopper Sparrows generally arrive in Illinois during the last week in April or first week in May (Vickery 1996). Fire every 2–3 years is used to maintain Grasshopper Sparrow habitat in the Midwestern U.S. (Herkert 1998). Grasshopper Sparrows are listed as a species of conservation concern in Illinois owing to a >60% decline in population since the 1960s (Herkert 1995), but remain a fairly common species in early successional CRP habitat (Best et al. 1997).

Study Areas

We established 32 study sites at 4 areas in Central Illinois within an intensive agricultural landscape (Figure 1). All sites consisted of newly planted grasslands enrolled in the State Acres for Wildlife Enhancement (SAFE) program, a version of USDA's CRP. Prior to our experiment, sites had either been in corn or soybeans (the region's dominant cover types) for 5 or more years. Sizes of fields ranged between 2.5 and 30.0 ha with cool-season grass mixes as the predominant cover. Sites were at least 1 km apart,

ensuring that vocalizations from one site could not be heard at another site. Dominant plant species observed include smooth brome (*Bromus inermis*), foxtail (*Hordeum murinum*), giant foxtail (*Setaria faberi*), Canada wild rye (*Elymus canadensis*), alfalfa (*Medicago sativa*), big bluestem (*Andropogon gerardii*), and partridge pea (*Chamaecrista fasciculata*).

Field Experiment

We conducted playback experiments during the 2010 and 2011 breeding seasons. In 2010, 12 newly created grassland sites were used; in 2011, we repeated our experiment with 20 more newly planted sites. Each year, we randomly assigned half of the sites to playback treatments (broadcast vocalizations) or controls (with no vocalizations added). To determine if the addition of social cues in the first year of planting new grassland influenced the density of sparrows in the second year, we revisited the 12 sites used in 2010 for a second breeding season in 2011, but did not broadcast vocalizations in the second year. It could be argued that a better control would have been the vocalizations of a non-grassland bird or a ubiquitous species such as the Red-winged Blackbird (*Agelaius phoeniceus*). We decided to go with no vocalizations as a control, primarily due to the additional cost and logistics of more game callers.

The design of the playback system followed methods established by Ward and Schlossberg (2004) with modifications similar those in Ahlring et al. (2006). Playback vocalizations consisted of commercially available male Grasshopper Sparrow vocalizations recorded in Indiana (Elliott et al. 2010). We used the audio editing software Audacity 1.2.2 (2004) to create tracks of primary and secondary songs and call notes randomly interspersed with quiet periods to avoid habituation and to mimic territorial behavior (Ward and Schlossberg 2004). The tracks were saved as wave files (.wav). Broadcast schedules included evening (~1600–1830 hrs), night (~2030–0500 hrs), and morning (~0700–0930 hrs) intervals to replicate natural vocal activity and to provide cues for nocturnal migrants. Over the course of the 2.5-hr periods, approximately equal parts of type 1 and type 2 songs were broadcast; the tracks also included chip notes, and approximately 30 min of silent periods. No songs were played for 30 min between sequential intervals of broadcasting. We began broadcasting vocalizations in late April and continued until late July with the same playback schedule.

FOXPRO game callers model NX4 (FOXPRO, Lewiston, PA, USA), powered by 12V deep-cycle batteries, were used to broadcast the vocalizations (audible at >500 m). While the vocalizations were broadcast at greater amplitude than Grasshopper Sparrows are able to sing, the fidelity of the game callers was much better than other mp3 players or the portable CD players the authors had used in other

studies. Given that Grasshopper Sparrows sing at high frequencies (i.e. 6–10 kHz) we paid particular attention to whether the game callers were broadcasting the songs at the appropriate frequency. Speakers were specially modified by FOXPRO to automatically turn on when power is added. The speakers, batteries, and Diehl digital timers (Diehl Stiftung, Nürnberg, Germany) were placed in a waterproof container with holes cut in both sides to allow for sound to be audible to birds. Mesh was then placed over the holes to prevent debris or wildlife from entering the systems. Lastly, the playback system was elevated on a cinder block to place speakers above or at an even level with surrounding grass for better broadcast and to simulate a more preferable perching height for singing Grasshopper Sparrows.

We visited all sites weekly conducting a 10-min, unlimited-radius point count in each field from May through the end of July (Bibby et al. 2000). Counts were conducted from sunrise until no later than 1000 hours and all birds heard and seen were recorded along with estimated distance from recorder. No counts were conducted in high winds, rain, or other inclement weather that would otherwise reduce detectability.

Characterization of Habitat Structure

Although treatment and controls were randomly selected, we assessed for possible confounds owing to differences in vegetation structure. We measured ground cover (bare ground, litter, grass and forb), litter depth, average height and density of vegetation in each site. Vegetation sampling was conducted during the last 2 weeks in June in both years. We conducted 5 line transects (25 m per transect) per site with measurements taken every 5 m along the line. Using a 50 × 50 cm quadrat frame and a modified 2-m Robel pole, we measured habitat variables (Daubenmire 1959, Robel et al. 1970).

Statistical Analysis

For the purposes of our experiment, we defined “occupancy” as the proportion of sites (treatment or controls) where at least one sparrow was detected during one or more census visits. A Fisher’s exact test was used to assess if occupancy differed between controls and treatments. Weekly and overall densities at each occupied site were estimated from point-count data and modeled using program Distance 6.0 v.2 (Thomas et al. 2010). The best fit model for these data was a half-normal distribution model with cosine series adjustments. To compare estimates of overall breeding densities between treatments and controls, we used a 2-way ANOVA with treatment and year as main effects. We originally included field size and habitat profiles derived from principal component scores (see below for details) as covariates, but these were not significant and were dropped from further analysis. We

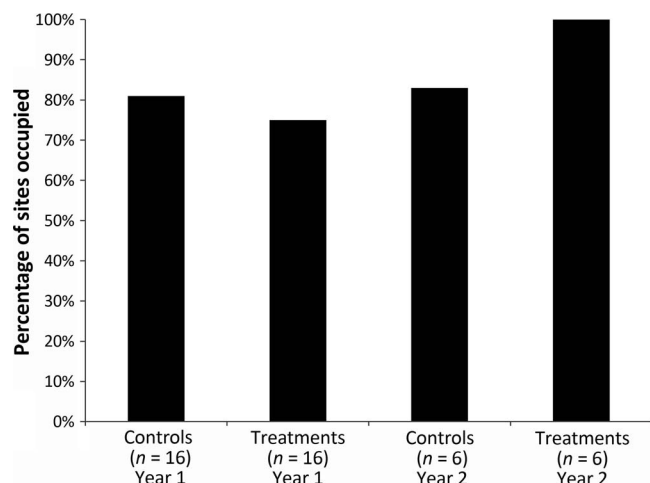


FIGURE 2. The proportion of sites with at least one Grasshopper Sparrow detected in year 1 and year 2 of monitoring. For the x-axis, year 1 refers to the first year of planting and includes sites used in 2010 and 2011 that were newly planted in those years. Year 2 refers to sites surveyed in their second year of planting ($n = 12$).

analyzed vegetation structure using principal component analysis (PCA) to reduce the dimensionality of the data. Six principle components were derived, but only 2 were retained (accounting for ~66% of the total sample variance) to compare overall habitat structure of the treatment and control sites.

To assess the effects of social cues and changes in weekly densities within a breeding season, we used a repeated measures ANOVA, with week as the within-subjects factor and the playback treatment as the between-subjects factor. Sparrow densities were not different by year (Treatment ($t_{2,23}$, $P > 0.05$) and control ($t_{2,11}$, $P > 0.05$)) and we therefore combined 2010 and 2011 data from newly planted sites when presenting the results. We used repeated measures ANOVA to determine if densities within treatment and control sites changed over the course of the 2 years.

RESULTS

Twenty-five of the 32 newly created grasslands became occupied, however Grasshopper Sparrows were not more likely to settle at treatment sites than control sites ($G_{adj} = 0.16$, $df = 1$, $P = 0.70$; Figure 2). Eight sites (25% of all sites) were settled in the first week of the experiment and by the third week 20 of the 32 sites (63%) were settled. The same pattern of occupation was observed on control and treatment sites, and time to initial occupancy did not differ between treatment and control sites ($G_{adj} = 0.51$, $df = 1$, $P = 0.48$; Figure 3).

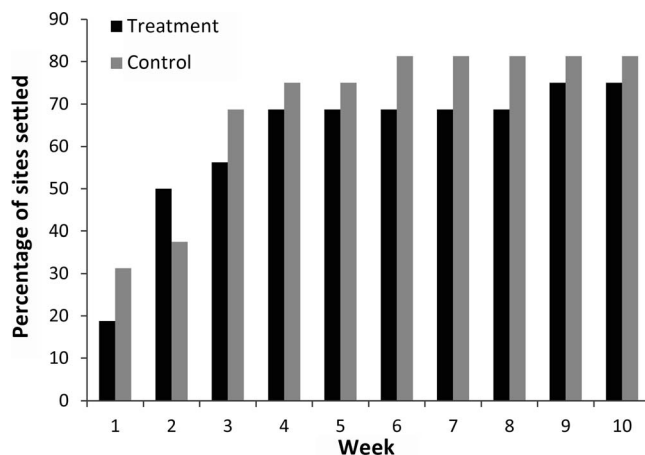


FIGURE 3. Percentage of sites settled (at least one sparrow detected) over the course of the 10-week study for sites in first year of planting (2010 and 2011 combined $n = 32$).

Though occupancy was not influenced by conspecific playbacks, breeding densities of birds on treatment sites (2.03 ± 0.64 birds ha^{-1}) were twice that of control sites (1.08 ± 0.26 birds ha^{-1} ; $F_{1,23} = 6.48$, $P = 0.02$). At treatment sites, densities increased sharply at the beginning of the season and remained high throughout the season (Figure 4). Conversely, control sites slowly increased in density throughout the season reaching a peak at the end of the July. During the first week, birds were observed in study sites, the density of sparrows was less than 0.5 birds ha^{-1} at treatments and controls. Starting the second week, densities doubled in treatment sites and continued to increase significantly ($F_{9,90} = 5.56$, $P < 0.01$).

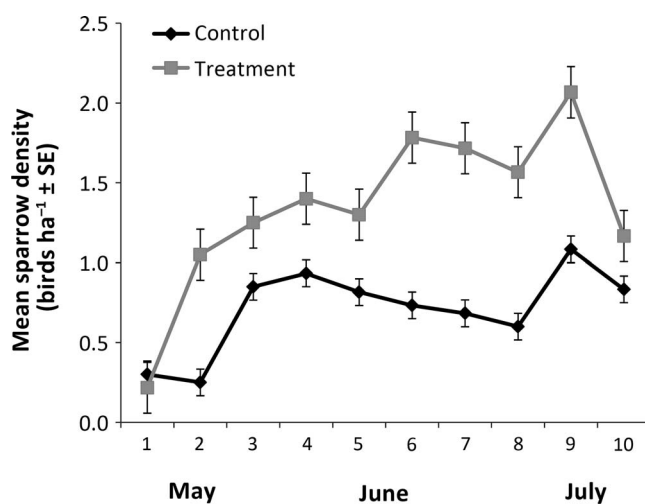


FIGURE 4. Mean density of Grasshopper Sparrows over time. Data represent newly planted sites in their first year of planting. Data from 2010 ($n = 12$) and 2011 ($n = 20$) and were pooled for analysis.

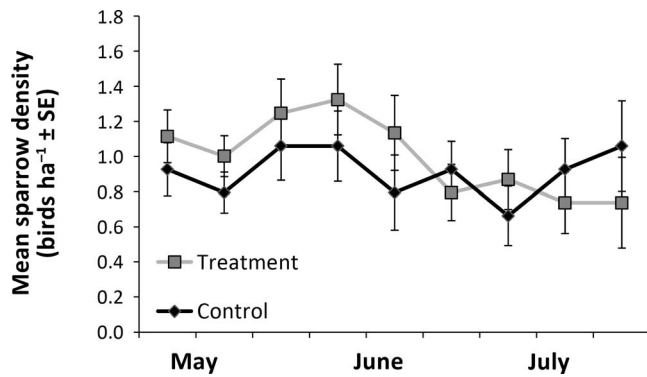


FIGURE 5. Mean density of Grasshopper Sparrows over time in year 2 of monitoring ($n = 12$). Data was collected from sites in their second growing season (Treatment = 6; Control = 6). Speakers with social information were only added in year 1; therefore, no sites in year 2 contained added social information.

while densities at control sites did not change significantly across the breeding season ($F_{9,108} = 1.71$, $P = 0.10$; Figure 4). Within treatment sites, we observed 2 peaks of density change in treatment sites within the first breeding season in new grasslands (e.g., week 2 and week 6; Figure 4).

Twelve sites were monitored for 2 consecutive years to investigate if the addition of social information in one year leads to increased settlement and density in the next year (with no playbacks added). In the second year, similar to the first, we found no significant differences in the proportion of treatment and control sites that were occupied ($G_{adj} = 0.05$, $df = 1$, $P = 0.83$). Unlike the first season, however, densities between treatment and control sites in year 2 were not different ($F_{1,10} = 0.06$, $P = 0.811$, $n = 12$; Figure 4). When comparing densities across years, treatment site densities in year 2 were not different from those in year 1 ($F_{8,32} = 0.73$, $P = 0.70$). At control sites, however, densities were significantly greater in year 2 ($F_{1,111} = 4.50$, $P = 0.04$; Figure 5).

DISCUSSION

Our results show that Grasshopper Sparrows do not rely on social cues upon their arrival on the breeding grounds, but use these cues to select breeding locations within the breeding season. Between years we did not observe that the addition of social cues increased density. We suggest that the habitat selection behavior of Grasshopper Sparrows is due to the habitat requirements of early successional species. Sparrows are quick to discover new habitats, likely via habitat cues, given that conspecific social cues would not be present at newly created sites. However, once social cues are present and provide valuable information these cues are used opportunistically.

Given the small window of opportunity (3 years) for Grasshopper Sparrows to utilize newly created habitat and

the relatively high rate of nest predation (Best et al. 1997), it is imperative that Grasshopper Sparrows actively search for high-quality sites. Birds have been shown to move to different breeding locations during the breeding season if nest sites fail or predation risk becomes too great, often employing a “win-stay, lose-switch” strategy (Howlett and Stutchbury 1997, Betts et al. 2008b, Chalfoun and Martin 2010, Kearns and Rodewald 2013). In the “lose-switch” scenario, birds may use social cues to select habitats mid-season (Kearns and Rodewald 2013), as they can indicate high reproductive success and/or low predation risk (Lima 2009) and, therefore, provide inference on habitat quality (Danchin et al. 2004, Ward 2005). The presence of a singing male Black-throated Blue Warbler (*Setophaga caerulescens*) later in the breeding season has been found to be associated with higher-quality habitats (Betts et al. 2008a). Also, post-fledgling males often sing late in the breeding season within appropriate habitat (Doligez et al. 2002, 2004), potentially providing cues that at least some conspecifics successfully reproduced at the site. Individuals may use both the presence of conspecific song and other cues with prospecting and assessing public information, such as the average reproductive success at a site (Ward 2005) or observe nest predation events (Seppänen et al. 2007) and the density of nest predators (Thomson et al. 2013) when visiting potential nesting locations. While there may be multiple cues that Grasshopper Sparrows are using to select breeding sites mid-season, the presence of conspecific song appears to be important for influencing habitat selection during the breeding season.

Not only can birds use social cues continually throughout a breeding season, they have been shown to use information from one season to influence habitat selection the following year (Reed et al. 1999, Pärt et al. 2011). Our playbacks broadcasted songs till the end of the season providing social cues during the post-breeding season. We predicted that there would be increased densities the year following playback experiments, likely due to prospectors from the previous year, but found no support for this in our study as densities in 2-year-old control and treatment sites were similar. Birds most likely to utilize social cues across seasons tend to use more stable habitats and have higher site fidelity (Switzer 1993, Hoover 2003). Grassland birds often have lower site fidelity (Jones et al. 2007) and may not benefit from previous information, as succession progresses and the value of this information degrades over time (Seppänen et al. 2007). Grasshopper Sparrows fit this mold with a moderately low return rate (10–20% depending on region; Ingold et al. 2010) and a reliance on early successional grasslands that can change quickly from year to year. Birds should use habitat selection strategies that incorporate information across seasons when it results in increased fitness (Pärt et al. 2011). No nest data were collected concerning reproductive success

in our experiment. Information on breeding success is crucial, however, to include with future studies of grassland birds to answer questions of how cues are used across seasons.

Applying Behavior to Management and Conservation

Traditionally, habitat management has focused on providing appropriate vegetation structure and composition (i.e. habitat; Cody 1981) with the assumption that simply creating suitable habitat will attract target species (Ahlering and Faaborg 2006). Our results, and those of other grassland bird studies (Ahlering et al. 2006, Nocera et al. 2006, Harrison et al. 2009, Vogel et al. 2011), show that social information can be an important part of the habitat selection process in grassland birds and knowledge of the hierarchical process through time can be important for management and conservation (Swaigood 2007). Despite this, social information is often omitted from habitat models (Campomizzi et al. 2008, Betts et al. 2008b). Including variables accounting for social information (i.e. clumped distribution) may improve the predictive power of models and refine conservation strategies (Campomizzi et al. 2008, Harrison et al. 2009). For example, Grasshopper Sparrows appear to be dispersing mid-season and using social cues to locate new breeding sites. Given this behavior, newly created habitats should be near one another to allow individuals to find and assess these sites more easily. Any habitat or social cue management can further be improved by accounting for temporal peaks in information use for habitat selection in this species. Presumably, the more sites they can assess the more information they have to use to make a decision regarding the highest-quality nesting site. Therefore, when developing programs such as CRP, locating sites near one another may increase the chances they are quickly colonized and potentially allow birds to select high-quality breeding sites, though more research is needed on the relationship between social cue use through time and reproductive success. Finally, if sites are found to be underutilized by a given species caution should be used, in order to avoid attracting individuals to a potentially low-quality site (i.e. artificially creating an ecological trap).

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