

CONSPECIFICS INFLUENCE THE SETTLEMENT DECISIONS OF MALE BREWER'S SPARROWS AT THE NORTHERN EDGE OF THEIR RANGE

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Abstract. At the northern periphery of its range Brewer's Sparrow (*Spizella breweri breweri*) is in decline and breeds in small clusters within larger areas of suitable habitat. Clustered breeding that is unrelated to the distribution of resources may be explained by social attraction (conspecific cueing). We used a song-playback experiment to test the conspecific-cueing hypothesis in this species. The experiment was conducted during the spring settlement period in habitat that appeared physically suitable for breeding but had not been occupied during the previous two breeding seasons. Treatments were split between two periods that reflected peak settlement of experienced and first-time breeders. In both periods, more Brewer's Sparrows visited and established territories in treatment plots than in untreated control plots. There were not, however, more treatment than control plots containing breeding pairs. This difference could mean that males attracted to playbacks are of lower quality than males in established breeding clusters and thus less attractive to females, that females settle only in groups of males larger than some threshold, or that females' site fidelity is higher than that of males. These results lend support to the conspecific-cueing hypothesis in this species, indicating that social attraction may play a role in Brewer's Sparrow's habitat selection. They also suggest that traditional habitat models, which consider only resource distributions and not social factors, may be inadequate tools for the conservation of this and other species.

Individuos Coespecíficos Influencian la Decisión de Establecimiento de Machos de *Spizella breweri breweri* en el Extremo Norte de su Distribución

Resumen. *Spizella breweri breweri* es una especie en disminución que en el extremo norte de su distribución se reproduce en pequeñas agrupaciones dentro de áreas de hábitat adecuado más extensas. La reproducción en grupo que no se relaciona con la distribución de los recursos, puede estar explicada por procesos de atracción social (señales coespecíficas). Realizamos un experimento utilizando reproducción de grabaciones de llamadas para probar la hipótesis de señales coespecíficas en esta especie. El experimento fue realizado durante el periodo de establecimiento en primavera en hábitats que parecían físicamente adecuados para la reproducción pero que no habían sido ocupados durante las dos épocas reproductivas anteriores. Los tratamientos fueron divididos en dos periodos que reflejaban los picos de establecimiento de reproductores con experiencia e inexpertos. En ambos periodos, un mayor número de individuos de *S. b. breweri* visitaron y establecieron territorios en las parcelas tratamiento que en las parcelas control. Sin embargo, no hubo más parcelas tratamiento con parejas reproductivas que parcelas control. Esta diferencia puede significar que los machos que son atraídos por las grabaciones son de menor calidad que los machos establecidos en agrupaciones reproductivas y por eso menos atractivos para las hembras; que las hembras se establecen en grupos de machos que sobrepasan un umbral de tamaño; o que la fidelidad de sitio es mayor para las hembras que para los machos. Estos resultados apoyan la hipótesis de señales coespecíficas, indicando que la atracción social puede tener un papel importante en el proceso de selección de hábitat en *S. b. breweri*. También sugieren que los modelos de hábitat tradicionales, que sólo consideran la distribución de recursos y no factores sociales, podrían ser herramientas inadecuadas para la conservación de esta y otras especies.

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competitors. Predator distributions have been recognized as an important factor in the habitat use of numerous species of prey (Longland and Price 1991, Dickman 1992, Werner and Anholt 1996, Brown 1999, Fontaine and Martin 2006). Similarly, the distributions of heterospecific competitors have been shown to alter habitat selection across a broad range of taxa (Pimm and Rosenzweig 1981, Grossman et al. 1998, Durant 2000). Both predators and competitors alter a species' distribution by causing it to avoid certain areas. However, recent research has shown that nonhabitat cues can also work in the opposite direction. Social attraction (both conspecific and heterospecific) has been identified as a primary habitat-selection cue in a number of species (conspecifics: Stamps 1988, Danchin et al. 1998, Doligez et al. 2002, Nocera et al. 2006, Donahue 2006, Parejo et al. 2006; heterospecifics: Thomson et al. 2003, Parejo et al. 2004, Fletcher 2007, Forsman et al. 2008). Individuals may choose to settle near conspecifics or heterospecifics because they reflect habitat quality or because benefits of joining a group (e.g., increased likelihood of mate attraction, extra-pair mating, or predator detection) exceed the potential costs (e.g., competition) of settling close to others.

The importance of conspecific attraction in the settlement of territorial songbirds has typically been demonstrated through the use of playback experiments that show individuals are attracted to and establish territories in areas where conspecific song is broadcast (Alatalo et al. 1982, Ward and Schlossberg 2004, Ahlering et al. 2006, Hahn and Silverman 2006, 2007, Mills et al. 2006, Nocera et al. 2006, Fletcher 2007, Betts et al. 2008). In some cases, individuals even settle in areas where habitat is unsuitable for breeding, demonstrating the strength of social attraction relative to other potential cues (Nocera et al. 2006, Betts et al. 2008). These results have led some scientists to suggest that song playbacks could be used as a management tool, allowing managers to establish populations in habitats where a target species was previously absent (Ahlering and Faaborg 2006, Hahn and Silverman 2007). This method of population re-establishment has already had some success in colonial species (Kress 1983, Jeffries and Brunton 2001, Parker et al. 2007). For species of conservation concern, it may be useful to test the potential for attraction to song play-

sagebrush cover of $19.9 \pm 2.8\%$ (95% CI), and the mean height of shrubs within the core of Brewer's Sparrow breeding clusters was 75.1 ± 2.9 cm (Harrison, unpubl. data). All plots were between 200 and 350 m from their nearest neighbor and between 200 and 1190 m from the core of a cluster. In the study area Brewer's Sparrow territories averaged 25 m in radius (Harrison, unpubl. data), so the >200 m between plots precluded repeated detections of the same birds on multiple plots. We randomly assigned the 44 plots as either controls or treatments (playbacks) in one of two periods, so that each period had 10 control and 12 playback plots. The two periods reflected peak settlement for experienced (ASY) birds and inexperienced (SY) birds. Peak settlement for the two age groups was determined from observations during a related study in 2007 (Harrison, unpubl. data).

Treatments consisted of playing songs of local males for 6 hr per day once every 2 days for 18 days. The first period, reflecting peak settlement for ASY birds, was between 27 April and 14 May, and the second period, reflecting peak settlement of SY birds, was between 15 May and 1 June. Each playback system included two Nexxtech portable speakers, powered by four C batteries, and one Centrios 2-GB mp3 player. These systems projected sound with volume sufficient for song to be heard by human observers standing 75 m from the source. Each mp3 player was loaded with 10 song tracks, four long song re-

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FIGURE 1. Means (center dashed lines), medians (center solid lines), upper and lower quartiles (boxes), 10th and 90th percentiles (whiskers), and outliers (dots) for the measures (a) distance to the nearest breeding cluster of Brewer's Sparrow, (b) shrub height, and (c) sagebrush cover within the 10 control (C) and 12 treatment (T) plots monitored during the ASY and SY settlement periods.

RESULTS

There was little variation between controls and treatments or between the ASY and SY settlement periods in sagebrush cover, shrub height, and distance to the nearest cluster of breeding Brewer's Sparrows (Fig. 1a-c).

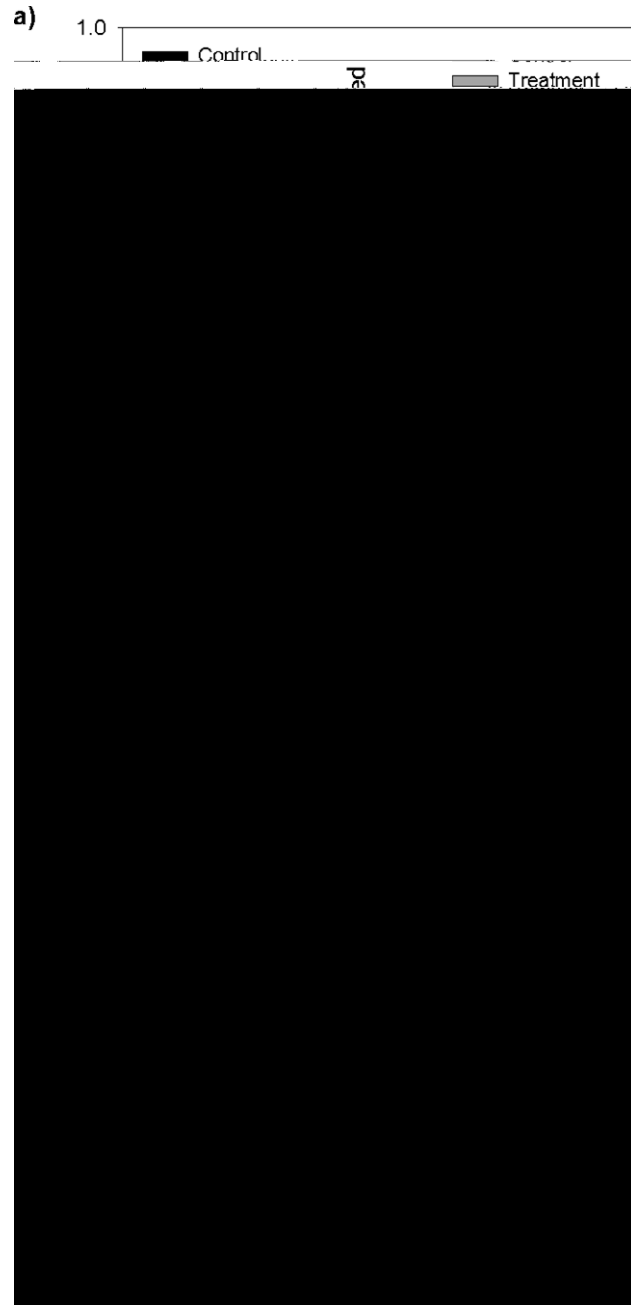


FIGURE 2. The proportion of treatment (playbacks performed) and control plots that were (a) visited by Brewer's Sparrows, (b) contained territories, and (c) contained pairs during the ASY and SY settlement periods. There were 12 treatment plots and 10 control plots in each period.

During both treatment periods, a greater proportion of playback than control plots was visited by males during two 1-hr observation periods (Fig. 2a; treatment: $\chi^2_1 = 14.00$, $P < 0.001$; period: $\chi^2_1 = 0.30$, $P = 0.58$). Males visited playback plots over six times more frequently than control plots. The proportion of playback versus control plots being visited

2006, Fletcher 2007, Betts et al. 2008). Conspecific attraction may therefore play a role in the clustering of territories observed in this (Cannings et al. 1987, Sarell and McGuiness 1996) and other species (Perry and Anderson 2003, Tarof and Ratcliffe 2004, Mills et al. 2006).

In our study song-playback treatments were effective in attracting male Brewer's Sparrows during the peak settlement periods of both ASY and SY birds. This finding contrasts with the results of Ward and Schlossberg (2004), Nocera et al. (2006), and Betts et al. (2008), who found greater use of such cues use by first time breeders than by adults in their studies of conspecific attraction in the Black-capped Vireo (*Vireo atricapilla*), Bobolink (*Dolichonyx oryzivorus*

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When selecting a site females may be more reliant on habitat cues, and the characteristics of the playback plots and the areas with established breeding clusters could have differed. Sexual differences in habitat selection has been found in the Hooded Warbler (*Wilsonia citrina*; Morton 1990) and Willow Flycatcher (*Empidonax traillii*; Sedgwick and Knopf 1992). Morton (1990) found that male and female Hooded Warblers selected for different habitat features in winter and suggested that successful breeding territories combine features preferred by males and those preferred by females. Sedgwick and Knopf (1992) found that female Willow Flycatchers are more discriminating in their choices of nest locations than males are in their choices of song perches. However, in a study of nest-site and nest-patch selection, Mahony (2003) demonstrated that female Brewer's Sparrows select habitats primarily on the basis of shrub-level characteristics, which is consistent with what has been found from studies focusing on territory selection by males (Chalfoun and Martin 2007; Harrison, unpubl. data). Since there has been little evidence for fine- or coarse-scale selection for habitat features beyond those used in the selection of plots for this study and males arrive first at breeding sites, establish territories, and sing to attract females (Rotenberry et al. 1999), it is unlikely that females are relying on alternative cues. This inference is also supported by Betts et al. (2008), who found that female Black-throated Blue Warblers responded directly to males' presence rather than to habitat or signs of previous success in a territory.

The second explanation, that pair formation at playback plots was limited by the number of returning females, can be tested by comparing the pairing rates of playback responders to those of birds within established breeding clusters (Harrison, unpubl. data). Eighty percent of males within established clusters were successful in attracting mates, as compared with 40% at playback plots, indicating that males' lack of success in attracting females to playback plots was not due to a population-level absence of females. The lower pairing rates at playback plots could indicate that the males that settle in response to playbacks are of lower quality and thus less desirable to females. However, it could also mean that females require male groups of a threshold size in order to settle and that the group sizes within playback plots were simply inadequate to elicit female settlement. Finally, it could also mean that females' site fidelity is higher than that of males, so females are less likely to disperse to new sites. If this were the case, we would expect the majority of the females pairing with males at playback plots to be first-time breeders. However, because we did not capture and age females, we could not evaluate that hypothesis.

The limited response of female Brewer's Sparrows to

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