The Condor 111(4):722–729

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

Megan L. Harrison[1], David J. Green[1,3], and Pamela G. Krannitz[2]

[1]*Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada*
[2]*Canadian Wildlife Service, Environment Canada, 5421 Robertson Road, R.R. 1, Delta, British Columbia, V4K 3N2, Canada*

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.

Key words: Brewer's Sparrow, song playback, conspecific attraction, habitat selection, Spizella breweri breweri, *territory clustering.*

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 períodos, 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.

INTRODUCTION

Habitat models that identify the suitability of management units from the occupancy patterns of a species are a traditional approach to wildlife management (Jones 2001, Johnson 2007). However, there is increasing evidence that cues other than habitat may be equally or more important in directing settlement decisions, and scientists are advocating for the inclusion of these additional components in wildlife-management planning (Campomizzi et al. 2008). The nonhabitat cues that have most frequently been shown to influence individual settlement decisions include the locations or behavior of predators and

Manuscript received 3 July 2009; accepted 20 September 2009.
[3]E-mail: djgreen@sfu.ca

The Condor, Vol. 111, Number 4, pages 722–729. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2009.090126

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 playbacks in order to determine its viability for management.

Brewer's Sparrow (*Spizella breweri breweri*) is a shrub-steppe obligate, relying on shrub-steppe habitats during both breeding and wintering periods (Rotenberry et al. 1999). Breeding Bird Survey (BBS) data from 1966 to 2007 showed rangewide declines in Brewer's Sparrow of 2.1% per year (Sauer et al. 2008). Because of this decline and continued conversion of sagebrush habitats for agriculture and residential development, the species has now been identified as vulnerable or at risk in both the United States and Canada. However, while habitat loss is one of the factors implicated in Brewer's Sparrow's rangewide decline, implying that appropriate habitat is limiting, at the northern periphery of the species' range individuals cluster their territories into small areas within larger expanses of seemingly suitable habitat, leaving much apparently suitable habitat unoccupied (Cannings et al. 1987, Sarell and McGuinness 1996, Hobbs 2001). This clustering of territories and tendency to leave adjacent habitats unoccupied may be a consequence of social attraction.

We tested the conspecific-cueing hypothesis by investigating the response of Brewer's Sparrows to playback of conspecific song during settlement. We did not assess the response to playback after breeding because fledglings move to riparian areas (Yu 1999), suggesting that prospecting by juveniles is unlikely. Playbacks were conducted during two periods associated with the arrival of older, experienced breeders (after second year; ASY) and first-time breeders (second year; SY). We examined whether plots with playback both attracted and retained more territorial males than did untreated control sites, whether playback sites yielded more breeding pairs, and whether the response to playbacks varied with the period and hence age of the birds returning to the breeding grounds.

METHODS

STUDY AREA

This study was conducted in the South Okanagan region of British Columbia between 27 April and 9 June, 2008. Experimental plots were established at two sites: on land holdings managed by the Nature Trust of British Columbia (White Lake), and in the East Chopaka region of the Okanagan Grasslands Protected Area (International Grasslands). Plots were established over a set of point-count stations that had been used to survey grassland birds' abundance at the sites from 2003 to 2006. The dominant vegetation on all plots was big sagebrush (*Artemisia tridentata*) with a mixed understory of native and non-native grass species and a sparse forb layer dominated by lupine (*Lupinus sulphureus* and *L. sericeus*) and parsnip-flowered buckwheat (*Eriogonum heracloides*). All study plots were located within larger expanses of unconverted sagebrush.

EXPERIMENTAL DESIGN

As experimental plots for this study, we selected 22 point-count stations from each site that had not been occupied by Brewer's Sparrows during the previous two breeding seasons but that contained sagebrush of cover adequate to support breeding. Each plot was a circle with a 100-m radius, centered on the point-count station. Point counts had been conducted twice per season during the breeding period and consisted of 15 min of audio and visual observations where all birds within 100 m were noted. Plots were considered suitable for breeding if they had 10–30% cover of big sagebrush. Big sagebrush is the primary shrub for the species' nesting, foraging, and perching (Rotenberry et al. 1999), and we selected 10–30% cover as the suitable range on the basis of Harvey (1992) and Sarell and McGuiness (1996). Occupied habitats within the study area had a mean big sagebrush cover of 19.9 ± 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 recordings and six short songs (40–150 sec), plus four tracks of silence (60 sec), which were played at random. At each plot, three speaker systems were installed for each day of playback, emulating a group of three singing birds. The first speaker system was located at a random compass bearing 75 m from the center of the plot. The other two systems were also located 75 m from the plot's center, at 120° from the random bearing. Speaker systems were suspended from sagebrush shrubs to imitate perched singing males. Since treatments took place at two sites, which we could not visit simultaneously, each plot received a treatment every second day. This every-other-day design likely under-represented the singing patterns of real male Brewer's Sparrows, making our results conservative. We chose to use three speakers per plot and run playbacks for 6 hr per day following a small-scale pilot study in 2007. In the pilot study, we had only one speaker per plot and played recordings at each plot for only 1 hr per day (following the methods of Nocera et al. 2006) and found that plot-visitation rates were too low for us to conclude that birds had been able to detect the playbacks.

Each plot (treatment and control) was monitored for two 1-hr intervals during the playbacks to record visitation rates and then for 6 days immediately following the playback period to determine whether significantly more males established territories, attracted mates, and attempted to breed on plots where conspecific song was broadcast than on untreated controls. Any males attracted to treatment plots were captured with mist nets and color-banded. Birds were assigned to the ASY and SY age-classes at the time of banding on the basis of patterns of wear in their primary and tail feathers (M. Leu, pers. comm.; Pyle 1997). They were also sexed at the time of banding by the development of the cloacal protuberance. We succeeded in catching all of the males that established territories in the ASY settlement period and five of the seven males from the SY period, and the ages of all individuals corresponded correctly with the "peak settlement period" they responded in. We did not capture and age females. We revisited plots every 4 to 6 days in order to monitor banded birds and breeding pairs, locate nests, and determine breeding success.

VEGETATION SAMPLING

Once breeding was complete, we sampled vegetation at each plot to gather data on key vegetation characteristics that have predicted coarse-scale habitat occupancy in other studies of Brewer's Sparrow (Harvey 1992, Sarell and McGuinness 1996, Paczek 2002, Chalfoun and Martin 2007) and that could confound the response of birds to playbacks. We established two 50-m transects intersecting the center of each plot to assess shrub-level vegetation characteristics by the line-intercept method (Brower et al. 1989). The first transect was established at a random bearing, the second at 90° from the first. The intersection of the two 50-m transects created four 25-m transects at right angles from each other. We used the line-intercept method to measure percent linear cover of sagebrush and other shrubs. We also recorded the height of each shrub that crossed a transect.

STATISTICAL ANALYSES

We examined whether the experimental treatment in playback period 1 (ASY settlement) or 2 (SY settlement) influenced three response variables: whether or not males visited plots during 2 hr of observation, whether or not males established territories on plots, and whether or not breeding pairs colonized the plots. We also included the site, distance from the plot to the nearest cluster of breeding Brewer's Sparrows, the mean percent cover of big sagebrush, and shrub height as covariates in the analyses, to determine whether the likelihood of plots being settled was related to site, their distance to an existing cluster, or to the characteristics of their vegetation. Playbacks typically elicited either no response or attracted one male Brewer's Sparrow (very few plots attracted more than one male). Therefore, we analyzed the data with a yes/no response by using generalized linear models with a binomial distribution and a logit link. In all analyses we initially fitted a full model including treatment, period, site, distance to the nearest cluster, sagebrush cover, shrub height, and interactions between treatment and each of the other variables. We then removed nonsignificant terms sequentially, starting with the interactions and then the main effects until only significant terms remained. Significance was evaluated from the change in deviance (equivalent to χ^2) associated with dropping the term of interest from a fuller model. All statistical analyses were conducted in GenStat version 10 (VSN International, Hemel Hempstead, UK).

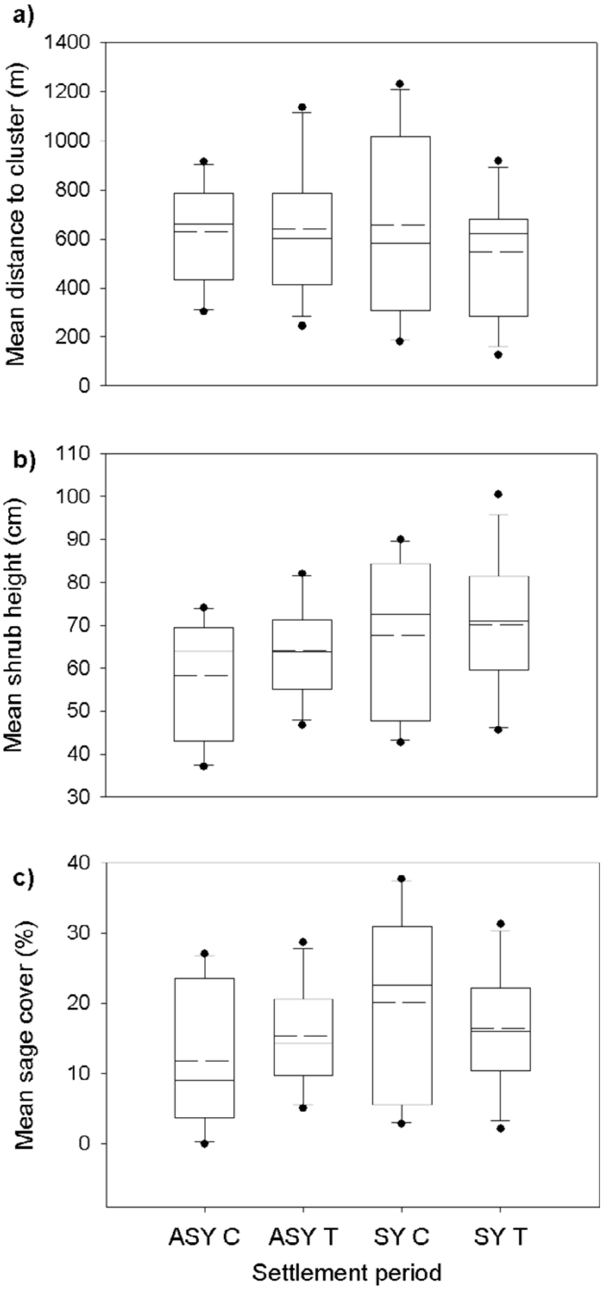

FIGURE 1. Means (center dashed lines), medians (center solid lines), upper and lower quartiles (boxes), 10th and 90th percentiles (whiskers), and outliers (dots) for the measures (a) distance to the nearest breeding cluster of Brewer's Sparrow, (b) shrub height, and (c) sagebrush cover within the 10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

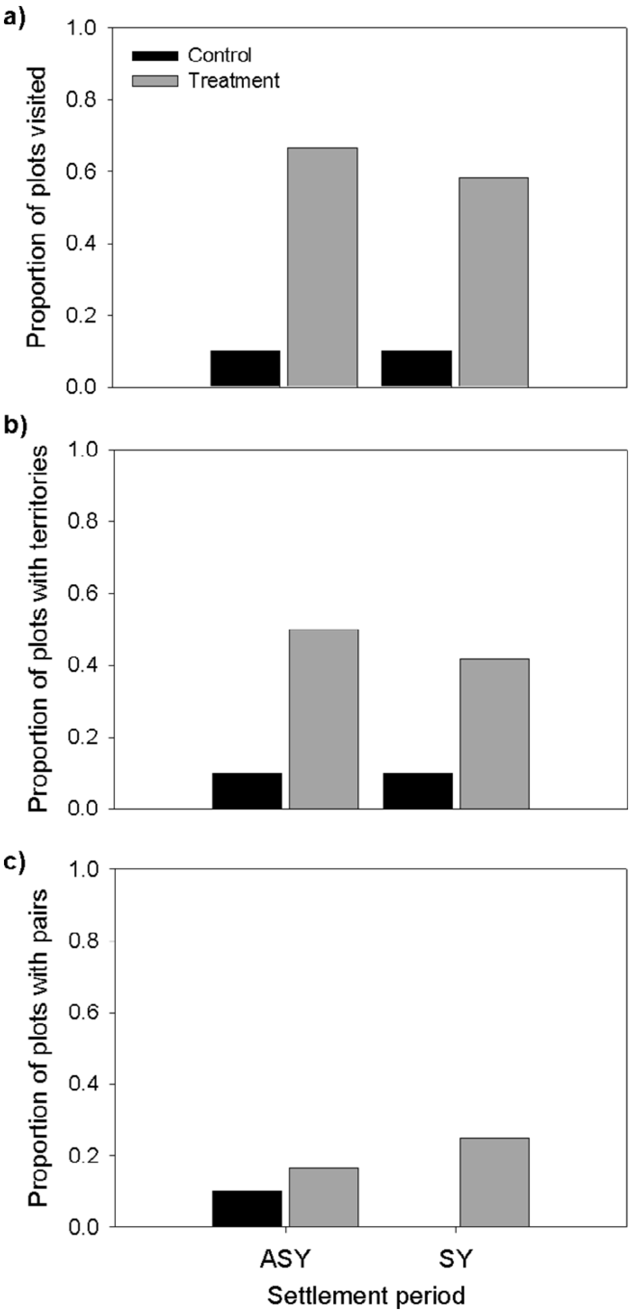

FIGURE 2. The proportion of treatment (playbacks performed) and control plots that were (a) visited by Brewer's Sparrows, (b) contained territories, and (c) contained pairs during the ASY and SY settlement periods. There were 12 treatment plots and 10 control plots in each period.

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).

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 by Brewer's Sparrows did not vary with the playback period (treatment × period: $\chi^2_1 = 0.10$, $P = 0.77$). Neither site nor the vegetation variables nor distance to the nearest cluster affected a plot's likelihood of being visited by Brewer's Sparrows (site: $\chi^2_1 = 1.23$, $P = 0.27$; sagebrush cover: $\chi^2_1 = 0.29$, $P = 0.59$; shrub height: $\chi^2_1 = 0.36$, $P = 0.55$; distance to cluster: $\chi^2_1 = 2.92$, $P = 0.087$). No interactions between treatment and any of the covariates were significant ($\chi^2_1 < 1.95$, $P > 0.163$).

In both periods, a greater proportion of the playback than of the control plots contained males that established and defended territories (Fig. 2b; treatment: $\chi^2_1 = 7.30$, $P = 0.007$; period: $\chi^2_1 = 0.30$, $P = 0.60$; treatment × period: $\chi^2_1 = 0.10$, $P = 0.79$). The rate of territory establishment was over four times greater on playback plots than on controls. Neither site nor the vegetation variables nor distance to the nearest cluster affected a plot's likelihood of containing territorial males (site: $\chi^2_1 = 1.17$, $P = 0.28$; sagebrush cover: $\chi^2_1 = 0.81$, $P = 0.37$; shrub height: $\chi^2_1 = 0.87$, $P = 0.35$; distance to cluster: $\chi^2_1 = 2.89$, $P = 0.089$). No interactions between treatment and any of the covariates were significant ($\chi^2_1 < 1.99$, $P > 0.158$).

Playback did not have a significant influence on the proportion of plots containing pairs of Brewer's Sparrows in either period (Fig. 2c; treatment: $\chi^2_1 = 2.60$, $P = 0.11$; period: $\chi^2_1 = 0.03$, $P = 0.87$; treatment × period: $\chi^2_1 = 1.60$, $P = 0.20$). Neither site nor the vegetation variables nor distance to the nearest cluster affected a plot's likelihood of containing pairs (site: $\chi^2_1 = 0.83$, $P = 0.35$; sagebrush cover: $\chi^2_1 = 0.22$, $P = 0.64$; shrub height: $\chi^2_1 = 0.24$, $P = 0.62$; distance to cluster: $\chi^2_1 = 1.86$, $P = 0.17$). No interactions between treatment and any of the covariates were significant ($\chi^2_1 < 0.86$, $P > 0.35$). We did not detect an effect of playback on whether pairs formed on experimental or control plots because not all males that established territories were able to attract a female. Four pairs attempted to breed, three from the ASY settlement period (one on a treatment plot, two on a control plot) and one from the SY period (treatment plot). All three pairs from the ASY period were successful in fledging young; the pair from the SY period was unsuccessful.

DISCUSSION

Conspecific attraction has been found to play a major role in the habitat-selection decisions of diverse species, including lizards (Stamps 1988), crabs (Donahue 2006), and birds (Danchin et al. 1998, Doligez et al. 2002, Nocera et al. 2006, Parejo et al. 2006). This study, which demonstrates that male Brewer's Sparrows use conspecific song as a cue before breeding when deciding to settle, adds to the mounting evidence that conspecific attraction can be an important habitat-selection cue in territorial songbirds. Eight songbird species have now been shown to use conspecific song in settlement (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). 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*), and Black-throated Blue Warbler (*Dendroica caerulescens*). However, Ward and Schlossberg (2004) suggested that this pattern reflects younger birds simply making up a greater proportion of the population settling in new sites and is not necessarily an indicator of greater use of conspecific cues by younger birds. Since the age ratios in the core populations at the two sites in this study are biased toward ASYs (approximately 3:1, ASY:SY), and nest failure in these populations is high enough to result in significant dispersal of failed breeders (Mahony et al. 2006), we would not expect significantly more SYs than ASYs at our treatment plots. Both Nocera et al. (2006) and Betts et al. (2008) found an SY-biased response to playbacks at plots that were unsuitable for breeding, suggesting that younger birds that have no previous breeding experience are more likely to be tricked into occupying poor-quality habitats than are experienced adults. Since all plots in our study were selected on the basis of consistent vegetation characteristics, we would not expect a difference between ASY and SY responses on the basis of previous experience with habitat. Since the criteria for plot selection was "suitable but unoccupied during the previous two seasons," we also know that the ASYs had not held territories in the playback plot locations in the previous years.

Although we found that song playbacks had an effect on the number of males that were attracted to and established territories in previously unoccupied plots, these treatments did not have a detectable influence on the number of pairs that subsequently formed. There are five possible explanations for this finding. First, these previously unoccupied plots may not have been as attractive to female Brewer's Sparrows as other sites where sparrows have settled before because they differed in terms of some characteristic not considered. Second, the number of females returning in 2008 may have been insufficient to allow all the males that responded to playbacks to attract mates. Third, the attracted males may have been of poor quality, so females chose to settle elsewhere. Fourth, female Brewer's Sparrows may require groups of males to exceed a threshold size before they will settle. Fifth, the site fidelity of female Brewer's Sparrows may be greater than that of males, so females are less likely to move into previously unoccupied habitats.

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 playbacks highlights one of the potential issues with the use of playbacks as a management tool. Only half of the studies so far published found evidence for preferential settlement of pairs (and not just males) in response to playback (Alatalo et al. 1982, Ward and Schlossberg 2004, Nocera et al. 2006, Fletcher 2007, Betts et al. 2008). Other issues with playback in management include the restricted capacity of playback to attract birds to habitats without existing populations nearby and the potential for playbacks to override other cues and draw birds into areas unsuitable for their breeding (Nocera et al. 2006, Betts et al. 2008).

While there is still uncertainty about the use of playback as a tool to manipulate the distributions of populations (Ahlering and Faaborg 2006), playback experiments are undoubtedly useful for testing the importance of social attraction in a population and can provide valuable insight into the reasons for territory clustering within larger areas of seemingly appropriate habitat (Campomizzi et al. 2008). Playbacks have provided evidence that Brewer's Sparrows use social cues in settlement, which indicates that for this species management decisions must incorporate components other than habitat (Campomizzi et al. 2008). Welstead et al. (2003) found that Brewer's Sparrow's choice of site is related to the distributions of avian predators, suggesting that predator distributions should be a component in future conservation planning for Brewer's Sparrow. This study suggests that the locations of existing populations are critical in predicting where newly immigrating Brewer's Sparrows will settle, so models that incorporate long-term occupancy data in conjunction with habitat data may identify target areas critical for conservation better than models that include habitat data alone. To improve the process for prioritizing areas for conservation, we suggest that intensive surveys for Brewer's Sparrow and its predators be included in conservation efforts for the species at the northern periphery of its range. Playback studies that test the influence of conspecific attraction in settlement are valuable precursors to the improvement of habitat-prioritization processes for species whose territories are clustered.

ACKNOWLEDGMENTS

We thank two anonymous reviewers, J. Reynolds, E. Elle, and the students and faculty within the Simon Fraser University Centre for Wildlife Ecology for their helpful comments on this manuscript, C. Rock, S. Moloney, and M. Huntley for their hard work in the field, and British Columbia Parks and the Nature Trust of British Columbia for granting permission for research on their properties. N. Mahony (Environment Canada) and J. Hobbs (British Columbia Ministry of Environment) also provided invaluable support in obtaining funding and hiring personnel. Funding for this project was provided by Environment Canada, the Centre for Wildlife Ecology, the Natural Sciences and Engineering Research Council, the Nature Trust of British Columbia (Brink McLean Grassland Conservation Fund), and the Forest Science Program (Graduate Student Pilot Project).

LITERATURE CITED

Ahlering, M. A., and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk 123:301–312.

Ahlering, M. A., D. G. Johnson, and J. Faaborg. 2006. Conspecific attraction in a grassland bird: the Baird's Sparrow. Journal of Field Ornithology 77: 365–371.

Alatalo, R. V., A. Lundberg, and M. Björklund. 1982. Can the song of male birds attract other males? An experiment with the Pied Flycatcher *Ficedula hypoleuca*. Bird Behavior 4:42–45.

Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008. Social information trumps vegetation site structure in breeding site-selection by a migrant songbird. Proceedings of the Royal Society B 275:2257–2263.

Brower, J. E., Zar, J. H., and C. N. von Ende. 1989. Field and laboratory methods for general ecology, 3rd edition. Wm. C. Brown, Dubuque, IA.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research 1:49–71.

Campomizzi, A. J., J. A. Butcher, S. L. Farrell, A. G. Snelgrove, B. A. Collier, K. J. Gutzwiller, M. L. Morrison, and R. N. Wilkins. 2008. Conspecific attraction is a missing component in wildlife habitat modeling. Journal of Wildlife Management 72:331–336.

Cannings, R. A., R. J. Cannings, and S. G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia, 1st edition. Royal British Columbia Museum, Victoria, BC.

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat quality and preference depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415–2428.

Dickman, C. R. 1992. Predation and habitat shift in the house mouse *Mus domesticus*. Ecology 73:313–322.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168–1170.

Donahue, M. J. 2006. Allee effects and conspecific cueing jointly lead to conspecific attraction. Oecologia 149:33–43.

Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology 11:624–632.

Fletcher, R. 2007. Species interactions and population density mediate the use of social cues for habitat selection. Journal of Animal Ecology 76:598–606.

Fontaine, J. J., and T. E. Martin. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. American Naturalist 168:811–818.

Forsman, J. T., M. B. Hjernquist, J. Taipale, and L. Gustafsson. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. Behavioral Ecology 19:539–544.

Grossman, G. D., R. E. Ratajczak, C. Crawford, and M. C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecies interactions. Ecological Monographs 68:395–420.

Hahn, B. A., and E. D. Silverman. 2006. Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. Biology Letters 2:337–340.

Hahn, B. A., and E. D. Silverman. 2007. Managing breeding forest songbirds with conspecific song playbacks. Animal Conservation 10:436–441.

Harvey, D. H. 1992. The distribution, density and habitat of Brewer's Sparrows (*Spizella breweri*) in the South Okanagan valley of British Columbia. Prepared for the British Columbia Ministry of Environment, Victoria, BC.

Hobbs, J. 2001. An inventory of Brewer's Sparrow in the grasslands of Southern and Central British Columbia. Ministry of Water, Land and Air Protection, Habitat Branch, Victoria, British Columbia.

Jeffries, D., and D. Brunton. 2001. Attracting endangered species to "safe" habitats: responses of Fairy Terns to decoys. Animal Conservation 4:301–305.

Johnson, M. D. 2007. Measuring habitat quality: a review. Condor 109:489–504.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

Kress, S. W. 1983. The use of decoys, sound recording, and gull control for reestablishing a tern colony in Maine. Journal of Field Ornithology 59:161–170.

Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology 72:2261–2273.

Mahony, N. A. 2003. Reproductive ecology and population viability of Brewer's Sparrows at the northern edge of the range. Ph.D thesis. University of British Columbia, Vancouver, BC.

Mahony, N. A., P. G. Krannitz, and K. Martin. 2006. Seasonal fecundity of Sagebrush Brewer's Sparrow (*Spizella breweri breweri*) at the northern edge of its breeding range. Auk 123:512–523.

Mills, A. M., J. D. Rising, and D. A. Jackson. 2006. Conspecific attraction during establishment of Least Flycatcher clusters. Journal of Field Ornithology 77:34–38.

Morton, E. S. 1990. Habitat segregation by sex in the Hooded Warbler: experiments on proximate causation and discussion of its evolution. American Naturalist 135: 319–333.

Nocera, J. J., G. J. Forbes, and L.-A. Giraldeau. 2006. Inadvertent social information in breeding habitat selection of natal dispersing birds. Proceedings of the Royal Society B 273:349–355.

Paczek, S. 2002. Effects of fine-scale and landscape-level habitat features on sagebrush breeding birds of the southern Okanagan and Similkameen valleys, British Columbia. M.Sc. thesis, University of British Columbia, Vancouver, BC.

Parejo, D., E. Danchin, and J. M. Aviles. 2004. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behavioral Ecology 16:96–105.

Parejo, D., D. Oro, and E. Danchin. 2006. Testing habitat copying in breeding habitat selection in a species adapted to variable environments. Ibis 148:146–154.

Parker, M. W., S. W. Kress, R. T. Golightly, H. R. Carter, E. B. Parsons, S. E. Schubel, J. A. Boyce, G. J. McChesney, and S. M. Wisely. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. Waterbirds 30:17–28.

Perry, E. F., and D. E. Anderson. 2003. Advantages of clustered nesting for Least Flycatchers in north-central Minnesota. Condor 105:756–770.

Pimm, S. L., and M. L. Rosenzweig. 1981. Competitors and habitat use. Oikos 37:1–6.

Pyle, P. 1997. Identification guide to North American birds, Part 1, Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

Rotenberry, J. T., M. A. Patten, and K. L. Preston. 1999. Brewer's Sparrow (*Spizella breweri*), no. 390. *In* A. Poole and F. Gill [eds.], The birds of North America. Birds of North America, Inc., Philadelphia.

Sarell, M. J., and K. P. McGuinness. 1996. Status of the Brewer's Sparrow in British Columbia. Wildlife Working Report WR-77. Ministry of Environment, Lands, and Parks, Wildlife Branch, Victoria, BC.

Sauer, R. J., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, Results and Analysis 1966–2007, version 2008.1. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD.

SEDGWICK, J. A., AND F. L. KNOPF. 1992. Decribing Willow Flycatcher habitats: scale perspectives and gender differences. Condor 94:720–733.

STAMPS, J. A. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist 131:329–347.

TAROF, S. A., AND L. M. RATCLIFFE. 2004. Habitat characteristics and nest predation do not explain clustered breeding in Least Flycatchers (*Empidonax minimus*). Auk 121:877–893.

THOMSON, R. L., J. T. FORSMAN, AND M. MÖNKKÖNEN. 2003. Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. Oecologia 134:431–438.

WARD, M. P., AND S. SCHLOSSBERG. 2004. Conspecific attraction and the conservation of territorial songbirds. Conservation Biology 18:519–525.

WELSTEAD, K., P. KRANNITZ, AND N. MAHONY. 2003. Using survival analysis of artificial and real Brewer's Sparrow (*Spizella breweri breweri*) nests to model site level and nest site factors associated with nest success in the South Okanagan region of Canada. USDA Forest Service General Technical Report PSW-GTR-191.

WERNER, E. E., AND B. R. ANHOLT. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77:157–169.

YU, J. H. Y. 1999. Postfledging habitat use and movements of Brewer's Sparrows (*Spizella breweri breweri*) in the South Okanagan region. M.Sc. thesis, University of British Columbia, Vancouver, BC.