

## EFFECTIVENESS OF ARTIFICIAL SONG PLAYBACK ON INFLUENCING THE SETTLEMENT DECISIONS OF AN ENDANGERED RESIDENT GRASSLAND PASSERINE

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**Abstract.** Social information in the form of songs, calls, or other overt behaviors may assist birds in assessing the quality of potential breeding habitat by providing direct public information about a site's quality or by providing indirect cues (e.g., the presence of conspecifics) that may be used to infer its quality. Broadcast of song has been used to demonstrate the influence of conspecific cues on the decisions of migratory passerines to settle; however, there is currently a dearth of information regarding resident species. We tested the influence of conspecific attraction and the effectiveness of song playback on an endangered resident of grassland, the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*). We broadcast recorded song over large areas of suitable breeding habitat in the Florida Everglades in an attempt to influence the settlement of male sparrows during territory establishment. Our analyses included the creation of a qualitative sound map that formed a basis for measuring the species' response to playback. Our results suggested that territory establishment by Cape Sable Seaside Sparrows was influenced by these artificial conspecific cues. Our findings have important conservation implications for the species in light of continuing large-scale efforts at habitat restoration in the Everglades ecosystem.

**Key words:** Cape Sable Seaside Sparrow, conspecific attraction, grassland birds, habitat selection, resident species, song playback.

### Efectividad de la Reproducción Artificial de Cantos para Influir las Decisiones de Asentamiento de un Paserino en Peligro Residente de las Praderas

**Resumen.** La información social provista por cantos, llamadas y otras manifestaciones de comportamiento pueden ayudar a las aves a evaluar la calidad de los potenciales hábitat reproductivos, al proveer información pública directa sobre la calidad del sitio o brindando señales indirectas (e.g., la presencia de individuos coespecíficos) que pueden ser usadas para inferir su calidad. La reproducción del canto ha sido usada para demostrar la influencia de señales de individuos coespecíficos en las decisiones de asentamiento de paserinos migratorios; sin embargo, existe actualmente una escasez de información sobre las especies residentes. Evaluamos la influencia de la atracción de individuos coespecíficos y la efectividad de la reproducción de cantos en una especie en peligro residente de las praderas, *Ammodramus maritimus mirabilis*. Reprodujimos cantos grabados a lo largo de grandes áreas de hábitat reproductivo adecuado en los Everglades de Florida, en un intento por influenciar el asentamiento de los machos durante el establecimiento del territorio. Nuestros análisis incluyeron la creación de un mapa de sonido cualitativo que constituyó la base para medir la respuesta de la especie a la reproducción de los cantos. Nuestros resultados sugieren que el establecimiento del territorio por parte de *A. m. mirabilis* estuvo influenciado por estas señales artificiales de individuos coespecíficos. Nuestros hallazgos tienen implicancias importantes para la conservación de la especie frente a los esfuerzos continuados a gran escala de restauración de hábitat en el ecosistema de los Everglades.

## INTRODUCTION

The selection of suitable breeding habitat is a critical choice for birds because it directly affects reproduction and survival and thus influences population dynamics. Social information in the form of songs, calls, or other overt behaviors may assist birds in assessing the quality of potential breeding habitat.

Social cues provide direct public information about a site's quality and indirect cues (e.g., the presence of conspecifics) that may be used to infer the site's quality (Stamps 1988, Danchin et al. 2004). In the context of bird conservation, failure by managers to recognize the importance of social cues in habitat selection can lead to large inefficiencies in

Manuscript received 12 October 2010; accepted 10 March 2012.

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the use of scarce political and monetary resources. Managers may restore or protect habitat highly suitable for a threatened species, but the benefits of this action in terms of population increases may never materialize if the target species does not settle in these areas because of the lack of social cues (Ahlering and Faaborg 2006). One possible solution to this issue is to erect systems of audio playback within unused but suitable habitat and broadcast calls and songs of the target species during appropriate times of the year (e.g., early in the breeding season). These artificial song-playback systems then provide the social cues necessary to attract individuals to settle and breed in the restored or protected habitat (Ahlering et al. 2010). Here we test the effectiveness of an artificial song-playback system, and thus the role of social cues in making settlement decisions, in the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), a highly threatened passerine resident year round and endemic to the Florida Everglades.

Understanding the way species use social information in habitat selection decisions is critically important for the conservation of endangered species (Podolsky and Kress 1992, Jeffries and Brunton 2001, Ward and Schlossberg 2004). A primary conservation goal is to increase population size, and creating or improving habitat for breeding often accomplishes this. However, it may not be as simple as “if you build it they will come” if the use of social cues strongly influences the habitat-selection process (Ahlering and Faaborg 2006). In recognition of this issue, several researchers have successfully used artificial song playback as a way to encourage settlement of migratory passerines including the Black-capped Vireo (*Vireo atricapilla*), Baird’s Sparrow (*A. bairdii*), American Redstart (*Setophaga ruticilla*), and Black-throated Blue Warbler (*S. caerulescens*) into protected or restored habitat (Ward and Schlossberg 2004, Ahlering et al. 2006, Hahn and Silverman 2006, 2007). The use of song playback may be most beneficial for species that are philopatric, tend to occur at naturally low densities, and have fast life histories. Philopatry tends to slow a population’s response to habitat changes as it tends to “pin” the distribution of breeding individuals to sites occupied previously (Hahn and Silverman 2006, 2007). At low population densities, an individual’s chances for encounters with conspecifics are reduced, so providing artificial conspecific cues may encourage settlement in managed habitat that dispersers might otherwise ignore. The use of song playback to encourage settlement may be particularly beneficial for management of species with fast life histories since these species have fewer lifetime opportunities to reproduce. Grassland birds, as a group, tend to show many of these traits, and, accordingly, several grassland species have been shown to use social cues in selecting breeding territories (Ahlering et al. 2006, Nocera et al. 2006, 2009). Since North America’s grassland birds have seen precipitous population declines over recent decades (Brennan and Kulesky 2005), this group is a prime target for the use of artificial song playback as a conservation tool.

The Cape Sable Seaside Sparrow is restricted to short-hydroperiod marl prairies of the Florida Everglades. The density of most subpopulations is very low, and the birds are short-lived and strongly philopatric (Boulton et al. 2009a, Pimm et al. 2002). The subspecies has experienced recent population declines due in large part to degradation of the Everglades ecosystem (Pimm et al. 2002, Cassey et al. 2007). However, the sparrow may benefit from unprecedented large-scale habitat-restoration efforts currently underway. If Cape Sable Seaside Sparrows respond to artificial song playback, the process of colonization of newly restored habitats in the Everglades may be sped up. In restored habitat, these early settlers should initiate establishment of philopatric residents that will later serve as natural attractants to maintain a new, or expanded, subpopulation (Ahlering and Faaborg 2006). Increasing the number of subpopulations of the Cape Sable Seaside Sparrow, and increasing the number of individuals in existing subpopulations, would greatly increase the probability of the subspecies’ long-term persistence by spreading out stochastic risks of extinction across space.

## METHODS

### STUDY AREA

The Cape Sable Seaside Sparrow is currently distributed among four small (A, C, D, and F) and two large subpopulations (B and E; Fig. 1). In winter, adult sparrows stay within 2 km of breeding territories, and they are strongly philopatric. Our study site, which covered 900 ha, was located in the range of subpopulation C (25° 43’ N, 80° 61’ W) in the eastern portion of Everglades National Park. Since 2006 we have studied the subpopulation’s demography intensively (Virzi et al. 2009), which provided us with detailed knowledge about the distribution of sparrows prior to our experiment with artificial song playback. We selected this study site because we had these prior distributional data and because there was unoccupied habitat apparently suitable for sparrow breeding.

### PLAYBACK SYSTEM DESIGN

We designed a playback system to broadcast sparrow song over large areas (radius >1 km) of sparrow habitat. The playback units consisted of an Apple iPod Nano connected to a JBL marine amplifier (model MA-6002) wired with a programmable timer (Flexcharge 8 Event Timer) to turn the units on and off daily. All electronic components were housed in a waterproof Pelican Case (model 1520) modified for the electronics and necessary wiring. Each unit broadcasted song through two 16-inch unidirectional speakers (Dayton RPH16) powered by 75-watt speaker drivers (Dayton D1075T) mounted to tripods approximately 2 m above the ground, which was high enough to mimic the height at which sparrows perch to sing but low enough to be unobtrusive in the environment. The playback units were powered with 12-volt marine batteries (Battery Werker WKDC12-33J) charged with solar power generated by a single

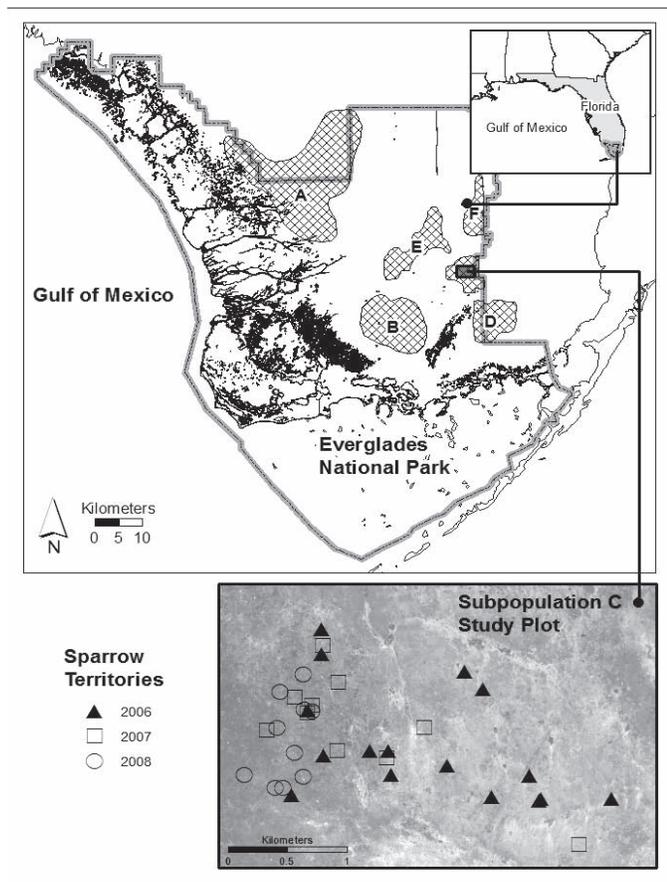


FIGURE 1. Approximate extent of Cape Sable Seaside Sparrow habitat (cross-hatched areas) in Everglades National Park, Florida; subpopulations are labeled A–F. Inset (lower right): study plot for experiment with playback of conspecific song in subpopulation C, showing location of sparrow territories observed over previous three years (2006–2008).

BP solar panel (model SX320M) mounted on the tripod next to the speakers. The design allowed song to be broadcast daily throughout the season without the need for us to visit the units regularly, which was necessary because of the difficulties in accessing remote areas of the Everglades where sparrows breed.

We deployed two playback units on 2 February 2009; male sparrows typically begin to establish territories in early February (Pimm et al. 2002). Both playback units were placed in the eastern portion of our study area where there was unoccupied suitable breeding habitat (Virzi et al. 2009). Units were placed 700 m apart to ensure adequate coverage of broadcast song across this area. Timers were initially set to begin broadcasting at sunrise for 3 hr, approximately the time of the sparrow's peak singing. The start time was adjusted earlier as the breeding season progressed to account for change in sunrise. The songs broadcast had been recorded from several individuals breeding within Everglades National Park in previous years. To reduce the risk of the playback interfering

with breeding, we turned the units off on 13 April 2009, when we first observed nesting behavior by sparrows in the subpopulation.

#### STATISTICAL ANALYSES

*Sound field.* Prior experiments testing the response of birds to broadcast song either never defined the reach of the sound through available habitat or made simplifying assumptions about where song could reasonably be heard (e.g., within a certain radius around the playback unit). However, sound does not diffuse through air uniformly but instead follows established and predictable physical laws. We modeled the sound field generated by our playback units according to these laws and tested for sound quality in the field.

Sound waves from a unidirectional source propagate through space in a conical shape by the inverse square law, with the decibel level decreasing as distance from the source increases, while at the same time the waves spread with distance at a scale dependent on the shape of the speakers (Celik and Guremen 2008). To create a qualitative map of sound generated from our playback units, we used data on sound quality recorded by observers in the field to seed a sound model based on these principles. Observers walked line transects at 45° angles away from each speaker, stopping every 50 m to record the level of sound being broadcast in one of four categories: (1) song heard faintly—sounds natural, (2) song heard well—sounds natural, (3) song loud—sounds unnatural, and (4) song very loud—sound quality degraded by distortion. We recognize that variability in observers' hearing and differences in environmental conditions could influence the scoring. To reduce bias in scoring, we trained all observers together and compared their scores, and all field data were recorded under consistent ambient conditions (e.g., low wind speed). We further recognize that our scoring system represents a crude estimate of the soundscape for birds since avian hearing is far superior to human (e.g., birds have more precise temporal resolution for complex sounds; Dooling et al. 2002). We entered these data into a geographic information system (GIS, ArcMap version 10.0, ESRI) and used the kriging function in ArcMap to interpolate a sound field in which broadcast song could be heard around each speaker. We categorized the mapped area of the sound field on the basis of the sound values indicated above, generating a map of sound "quality." Mapped areas with sound values <3 we considered to have the most natural sounding song broadcast by our playback units. Thus these areas were where we expected to observe settling male sparrows' strongest response to our song playback. From these maps, we estimate that 35% of our study area was regularly inundated with broadcast song, while the remaining 65% was not. We thus expected that if the sparrows used broadcast song to decide where to establish their breeding territories, they should be more likely to establish those territories within this sound field. We expected there to be no pattern of territory placement relative to the sound field

if sparrows effectively ignored the playback and territories to be preferentially placed outside the sound field if the birds responded negatively to the playback.

*Vegetation surveys.* A central assumption in our analysis is that all habitat within our study area was suitable for sparrow breeding and thus plays no appreciable role in determining territory placement. To test this assumption we analyzed vegetation data recorded by Florida International University in a separate study along eight 100-m line transects spaced 1 km apart within the boundary of our study site (Sah et al. 2009). Vegetation composition (percent cover) was estimated in 10 subplots (5 × 5 m) spaced at 6-m intervals along each of the eight transects. The vegetation data were recorded on a 3-year rotation, so data used in our analyses were from multiple years (2006–2009). Although vegetation structure may also play a role in the sparrow's habitat selection we did not include structure in our analyses because these data were not available.

Following La Puma et al. (2007), to examine the similarity of sampling sites across our entire study area, we analyzed species composition with the multivariate software Primer-E. We calculated the full Bray–Curtis species-similarity matrix for all samples, then used this matrix as the basis for analyzing compositional similarity by nonmetric multidimensional scaling (Clarke and Warwick 1994). We compared relative similarities of sampling sites across our study area by analysis of similarity (ANOSIM), which is similar to a standard univariate analysis of variance. ANOSIM calculates a test statistic ( $R$ ) that is used to compare compositional similarity. Values of  $R$  range between +1 and –1, taking the value of +1 when samples at one site are more similar to each other than to samples at other sites and –1 in the opposite situation. In the event of any observed dissimilarity between plots, we used the SIMPER routine in Primer-E to disaggregate the Bray–Curtis similarity matrix and computed the average dissimilarity between all pairs of intergroup samples to identify which species were driving the dissimilarity (Clarke and Warwick 1994). This allowed us to assess, on the basis of previous analyses of the sparrow's requirements for breeding habitat (Lockwood et al. 2003), whether vegetative dissimilarities were likely to influence the suitability for sparrows of the study area's habitats.

*Measuring sparrow response.* In an attempt to locate all sparrows occupying territories in 2009, we surveyed the entire study area on multiple occasions each week from 24 March to 29 July. Two to four researchers made systematic surveys at least once per week (usually twice) over the period, with equal effort in areas where playback was audible or not. We defined a territory as occupied if an adult male was observed singing on multiple occasions, aggressive toward neighbors, and/or paired with a female. Most male sparrows in the study area were color-marked, making the accurate identification of individuals possible. During surveys we recorded the location of all sparrows and nests encountered with a hand-held

global positioning system (GPS) device that allowed us to map territory boundaries for later GIS analysis.

We imported the GPS data collected during our sparrow surveys into ArcMap and used these point data to generate polygons of the territories of all adult male sparrows observed in our study area with the minimum-convex-polygon tool in Hawth's Analysis Tools for GIS version 3.27 (Beyer 2004). We then located the central position of each polygon and considered it to represent the center of each male sparrow's territory. Next, we buffered each observed territory point by 80 m in ArcMap to create a hypothetical 2-ha territory for each male sparrow, which is the approximate size of actual sparrow territories (Pimm et al. 2002).

To evaluate the influence of song playback on territory distribution in our study area, we compared the locations of "real" sparrow territories to a set of simulated territory distributions that we created on the basis of competing hypotheses (described below; Fig. 2). The first step in the simulation process was to create vector files to constrain the placement of random territory centroids within spatial bounds expected from each competing hypothesis (gray-shaded areas in Fig. 2). Once these vector files were created, we used ArcMap to generate randomized territory distributions under each competing hypothesis. In each simulation we generated 14 random points, matching the number of "real" sparrow territories found in our study area (see Results), to create a set of expected territory locations that we could overlay onto observed territory locations. We simulated territories by buffering the random points by 80 m to create 2-ha sparrow territories, as described above for observed data. For each hypothesis we ran 1000 simulations generating 14 points per simulation to obtain a frequency distribution of resultant territory locations.

Male sparrows' decisions to settle may be influenced by factors including habitat quality, philopatry, conspecific attraction, or a combination of these factors. Therefore, we developed six competing hypotheses (shown in Fig. 2) to explain these decisions. The first three hypotheses (A–C) assume no influence of our song playback, and the remaining three hypotheses (D–F) assume some influence, as described below.

Since Cape Sable Seaside Sparrows are known to cluster breeding territories (Pimm et al. 2002), for our first hypothesis (hypothesis A<sub>Clustered</sub>) we assumed that sparrows clustered during settlement whether because of the influence of natural conspecific cues or some other mechanism. This hypothesis assumed that there was no effect of artificially generated song cues created by our playback system. Thus, when we generated random points for this hypothesis, we allowed the first point in each simulation to fall anywhere in the study area but forced clustering of all remaining points on the basis of randomly selected nearest-neighbor distances within the range (160–1400 m) observed in subpopulation C in 2006, the year of maximum observed density in the plot.

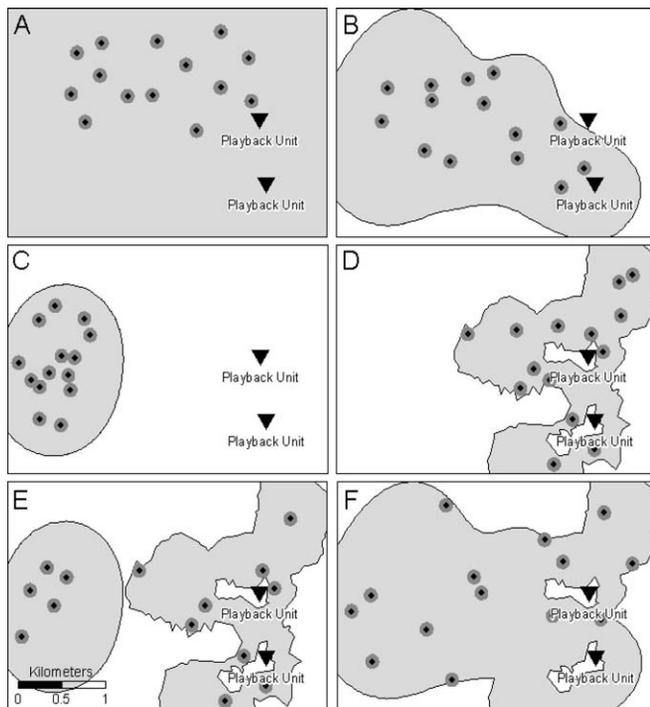


FIGURE 2. Competing hypotheses explaining the distribution of territories of Cape Sable Seaside Sparrow subpopulation C in 2009 relative to location of song-playback units (black triangles). Each panel of the figure shows one example of a simulation of 14 random points (black circles) generated under each hypothesis (A–F) and buffered to create 2-ha territories (gray circles). For each hypothesis, the placement of random points was constrained to areas in gray as follows. Hypothesis  $A_{\text{Clustered}}$ : points could occur anywhere in study area, but clustering of points was forced at a level observed naturally. Hypothesis  $B_{\text{Habitat}}$ : points constrained to area where the sparrows bred 2006–2008. Hypothesis  $C_{\text{Philopatry}}$ : points constrained to area where the sparrows bred in 2008 only. Hypothesis  $D_{\text{Playback}}$ : points constrained to area where broadcast song could be heard at natural-sounding levels according to the model. Hypothesis  $E_{\text{Playback/Philopatry}}$ : points allowed only in areas of both song playback and 2008 breeding. Hypothesis  $F_{\text{Playback/Habitat}}$ : points allowed in areas of either song playback or 2006–2008 breeding.

For hypothesis  $B_{\text{Habitat}}$  we assumed that sparrows based settlement decisions on habitat quality alone. Given the degree of uncertainty inherent in using analyses of vegetation data to infer habitat quality, we based our assessment of habitat quality on the prior distribution of sparrow territories with the study area rather than on habitat measures. For this hypothesis we therefore constrained random points to the area where sparrows were observed breeding 2006–2008, making the assumption that the presence of breeding sparrows in previous years indicates consistent habitat quality in this area. This constraint takes into consideration how characteristics of the site's microhabitat not measured in our vegetation analysis might have influenced settlement decisions.

Since adult Cape Sable Seaside Sparrows have strong fidelity to a breeding site in successive years (Pimm et al. 2002), we developed a hypothesis that takes philopatry into consideration. Thus, hypothesis  $C_{\text{Philopatry}}$  assumed that settlement decisions were influenced most strongly by the sparrows' fidelity to areas where they nested in the previous year. Therefore, we constrained the selection of random points to the area where sparrows were observed breeding in 2008, forcing a high level of philopatry.

The remaining three hypotheses take into consideration the effect on settlement decisions of the sound field generated by our playback. For hypothesis  $D_{\text{Playback}}$  we assumed that settlement decisions by male sparrows were influenced most strongly by the artificial song cues we provided. For this hypothesis we constrained the selection of random points to areas within the sound field generated by our playback units (see Results, Fig. 3) where the broadcast was expected to sound most natural. Thus we did not allow points to be generated close to the speakers where we thought, from our modeling, the sound was too loud to mimic natural cues.

The final two hypotheses consider that settlement decisions by male sparrows may be influenced by artificial song cues working in conjunction with other cues such as philopatry and habitat suitability. For hypothesis  $E_{\text{Playback/Philopatry}}$  we assumed that settlement decisions were influenced to some degree by both the playback and adults' philopatry. Thus for this hypothesis we combined the constraints placed on the generation of random points from hypotheses  $D_{\text{Playback}}$  and  $C_{\text{Philopatry}}$ , taking into consideration the potential effect of both artificial song cues and adults' philopatry. Finally, for hypothesis  $F_{\text{Playback/Habitat}}$  we assumed that settlement decisions were influenced by both the playback and habitat suitability. Thus for this hypothesis we combined the constraints placed on the generation of random points from hypotheses  $D_{\text{Playback}}$  and  $B_{\text{Habitat}}$  into a single model.

We analyzed differences in the location of simulated and real sparrow territories with a one-way ANOVA (program R version 2.11.1). The response variable in our ANOVA was the mean number of overlapping territories ( $\Omega_{\text{Overlap}}$ ) detected when we plotted simulated territory locations over observed territory locations. We used  $\Omega_{\text{Overlap}}$  as our response variable since we considered any overlap an indication that we could not differentiate between the location of the simulated and observed (real) territories. We also ran our ANOVA comparing  $\Omega_{\text{Overlap}}$  at larger territory sizes (3, 4, and 5 ha) to account for uncertainty in the size of sparrow territories, as Boulton et al. (2009b) found that in small subpopulations sparrow territories may be larger. We compared hypothesis  $A_{\text{Clustered}}$  to all other competing hypotheses, all of which we set as factors in the ANOVA, to determine if there were significant differences from a simple clustered distribution. To evaluate the significance of competing hypotheses, we used

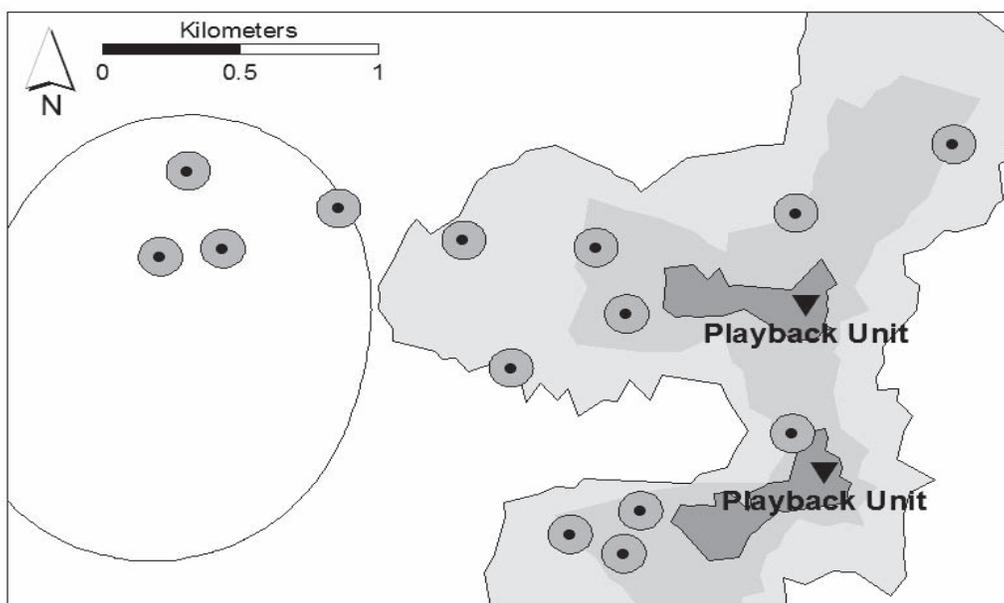


FIGURE 3. Distribution in 2009 of Cape Sable Seaside Sparrow territories observed in study plot in subpopulation C (gray circles, boundaries of 2-ha territories) relative to location of playback units (black triangles), sound field (shaded area), and location of breeding population in 2008 (solid line enclosing unshaded area). Each playback unit broadcast song from two speakers; north unit speakers faced NE and NW; south unit speakers faced N and SW. Sound field shows volume of perceived sound across space; lighter gray indicates areas where song sounded most natural (values  $<3$ ); darker gray surrounding playback units indicates area where high decibel levels degraded sound quality (values  $>3$ ).

the Tukey honestly significant difference (HSD) method for multiple comparisons. Values reported under Results are means  $\pm$  SE (or SD as indicated) and significant  $P$ -values are based on  $\alpha = 0.05$ .

## RESULTS

### VEGETATION COMPOSITION

The ANOSIM comparing vegetation composition across our study plot found some difference in species composition ( $R = 0.258$ ,  $P = 0.001$ ). The SIMPER results indicated that the relative abundances of two species, *Muhlenbergia capillaris* and *Cladium jamaicense*, were driving the dissimilarity between plots. Comparing the similarity within plots for all samples revealed that these were the most abundant species in all plots; however, their rank order differed by plot (Table 1). Thus across our entire study area the vegetation community may be classified as *Muhlenbergia-Cladium*, which is known to be suitable breeding habitat for the Cape Sable Seaside Sparrow (Lockwood et al. 2003).

### SPARROW RESPONSE

We observed 14 instances of settlement on a territory ( $n = 13$  individuals; one male sparrow changed its territory location after a failed nesting attempt) during our surveys and used these data to map territories (mean number of GPS points per bird = 13). Two adult males had been color-marked in previous

years on their breeding territories within our study plot. We captured and marked 10 of the remaining 11 adult male sparrows, bringing the total marked population of males in 2009 to 12. Since 9 out of the 10 male sparrows breeding in subpopulation C in 2008 had been color-marked, the unmarked individuals found during our study were likely individuals that either recruited into the population as first-year juveniles or dispersed into our study area in 2009.

Ten of the male sparrows that settled in our study plot in 2009 established territories within the sound field generated by our playback systems (Fig. 3). All were in areas of the sound field where sound values were  $<3$ , which is where we expected the song broadcast from our playback units to sound most natural. Furthermore, no sparrows established territories in areas where sound values were  $>3$  (one male's territory bordered this area). One of the four male sparrows that settled in the area outside the sound field had been previously marked as an adult and settled in close proximity to its territory in the previous year (distance = 128 m). A second male that established its territory outside the sound field had been previously marked as a nestling and settled relatively close to its natal site (distance = 984 m). Thus all sparrows that established territories in our study plot either settled in areas where artificial conspecific song cues could be heard or in areas where sparrows had nested in the previous year, despite the availability of suitable breeding habitat across the entire study plot.

TABLE 1. Average similarity (Sim, SD) of vegetation cover (Cover) within vegetation plots by contribution (%Con) from each species. Includes only species whose cumulative contributions account for 90% of similarity.

Plot and species	Cover	Sim	SD	%Con
C-01-03				
<i>Cladium jamaicense</i>	10.8	34.6	1.8	74.4
<i>Muhlenbergia capillaris</i>	6.6	10.4	0.7	22.5
C-02-02				
<i>Cladium jamaicense</i>	6.7	23.2	1.0	71.7
<i>Paspalum monostachyum</i>	1.5	3.7	0.5	11.4
<i>Rhynchospora tracyi</i>	0.9	2.6	0.4	8.0
C-02-03				
<i>Muhlenbergia capillaris</i>	20.8	36.5	1.4	93.8
C-02-04				
<i>Cladium jamaicense</i>	9.4	18.2	1.4	46.7
<i>Muhlenbergia capillaris</i>	6.8	8.7	0.7	22.3
<i>Centella asiatica</i>	3.2	5.7	0.8	14.6
<i>Panicum tenerum</i>	1.9	4.4	0.9	11.3
C-03-03				
<i>Muhlenbergia capillaris</i>	18.6	43.9	2.3	70.9
<i>Cladium jamaicense</i>	9.9	17.7	1.1	28.5
C-03-04				
<i>Muhlenbergia capillaris</i>	16.5	51.3	4.0	80.5
<i>Cladium jamaicense</i>	2.3	8.3	1.6	13.0
C-03-05				
<i>Muhlenbergia capillaris</i>	8.8	39.5	2.2	64.2
<i>Cladium jamaicense</i>	3.2	17.2	3.0	28.0
C-04-07				
<i>Cladium jamaicense</i>	4.8	13.9	1.0	40.1
<i>Muhlenbergia capillaris</i>	9.0	12.7	0.7	36.6
<i>Rhynchospora tracyi</i>	1.8	3.1	0.7	8.8
<i>Vernonia blodgettii</i>	0.7	2.1	0.7	6.0

The frequency distributions of overlap between simulated and observed (real) territories were normally distributed for all competing hypotheses (Fig. 4). We report only the results based on simulated territory sizes of 2 ha because the results were identical when we increased the size of territories to 3, 4, and 5 ha (except that  $\Omega_{\text{Overlap}}$  increased under all hypotheses). For the first three hypotheses ( $A_{\text{Clustered}}$ ,  $B_{\text{Habitat}}$ , and  $C_{\text{Philopatry}}$ ), our simulations resulted in little overlap between simulated and real territories. Two of the simulations that considered the effect of playback on territory location (hypotheses  $D_{\text{Playback}}$  and  $E_{\text{Playback/Philopatry}}$ ) showed more overlap between simulated and real territories. The  $\Omega_{\text{Overlap}}$  was highest for hypothesis  $D_{\text{Playback}}$  (mean =  $3.5 \pm 0.05$ ), suggesting that this hypothesis

may explain the observed distribution of sparrow territories best (Fig. 5). Hypothesis  $E_{\text{Playback/Philopatry}}$  also yielded a number of simulated territories overlapping real ones substantially higher than that from any of the first three competing hypotheses (mean =  $2.8 \pm 0.05$ ). The final hypothesis that considered the interactive effect of song playback and habitat suitability ( $F_{\text{Playback/Habitat}}$ ) generated less overlap between simulated and observed territories than did hypotheses D and E (mean =  $2.2 \pm 0.04$ ). Our ANOVA rejected the null hypothesis that  $\Omega_{\text{Overlap}}$  from competing hypotheses was the same as that under hypothesis  $A_{\text{Clustered}}$  ( $F_{5,5994} = 183.1, P < 0.001$ ). Tukey HSD pairwise comparisons of ANOVA results from the six competing hypotheses showed nonsignificant differences for hypotheses  $B_{\text{Habitat}}$ ,  $C_{\text{Philopatry}}$ , and  $F_{\text{Playback/Habitat}}$ , which thus formed one group indistinguishable from each other (Table 2). Results from hypotheses  $D_{\text{Playback}}$  and  $E_{\text{Playback/Philopatry}}$  were not significantly different from each other but were significantly different from results from all other hypotheses. Thus both the artificial cue and philopatry explained the distribution of sparrow territories to some degree.

## DISCUSSION

Our results suggest that Cape Sable Seaside Sparrows use social cues, in the form of song, produced by conspecific individuals as one criterion for selecting breeding habitat. Ours is one of the few studies to show that a resident bird uses social cues from conspecifics in making settlement decisions (see Parejo et al. 2007 for an example showing the use of public information by resident Blue Tits, *Cyanistes caeruleus*). Our results indicate that Cape Sable Seaside Sparrows use a mixed strategy, making settlement decisions on the basis of philopatry and conspecific cues, a strategy that is expected to be the theoretical stable solution for many settlement problems (Doligez et al. 2003). Sparrows responded to song broadcast over a large area of suitable breeding habitat, most strongly in areas where modeling predicted sound quality to be closest to that of natural song. Our findings have important conservation implications for the Cape Sable Seaside Sparrow in light of the large-scale habitat restoration underway in the Florida Everglades.

Our results suggest managers may successfully use song playback to increase the number of subpopulations or promote settlement of sparrows in newly restored habitats in the Everglades. While our results show that settlement decisions can be influenced on a local scale, the true benefit of this management tool would be its efficacy in influencing the settlement decisions of individuals that disperse long distances. Long-distance dispersal between sparrow subpopulations does occur, and, although rare, such dispersal is likely to influence population dynamics (Nathan et al. 2003, Van Houtan et al. 2010, Gilroy et al. 2012). Once restored habitat becomes suitable for breeding it may be possible to encourage faster

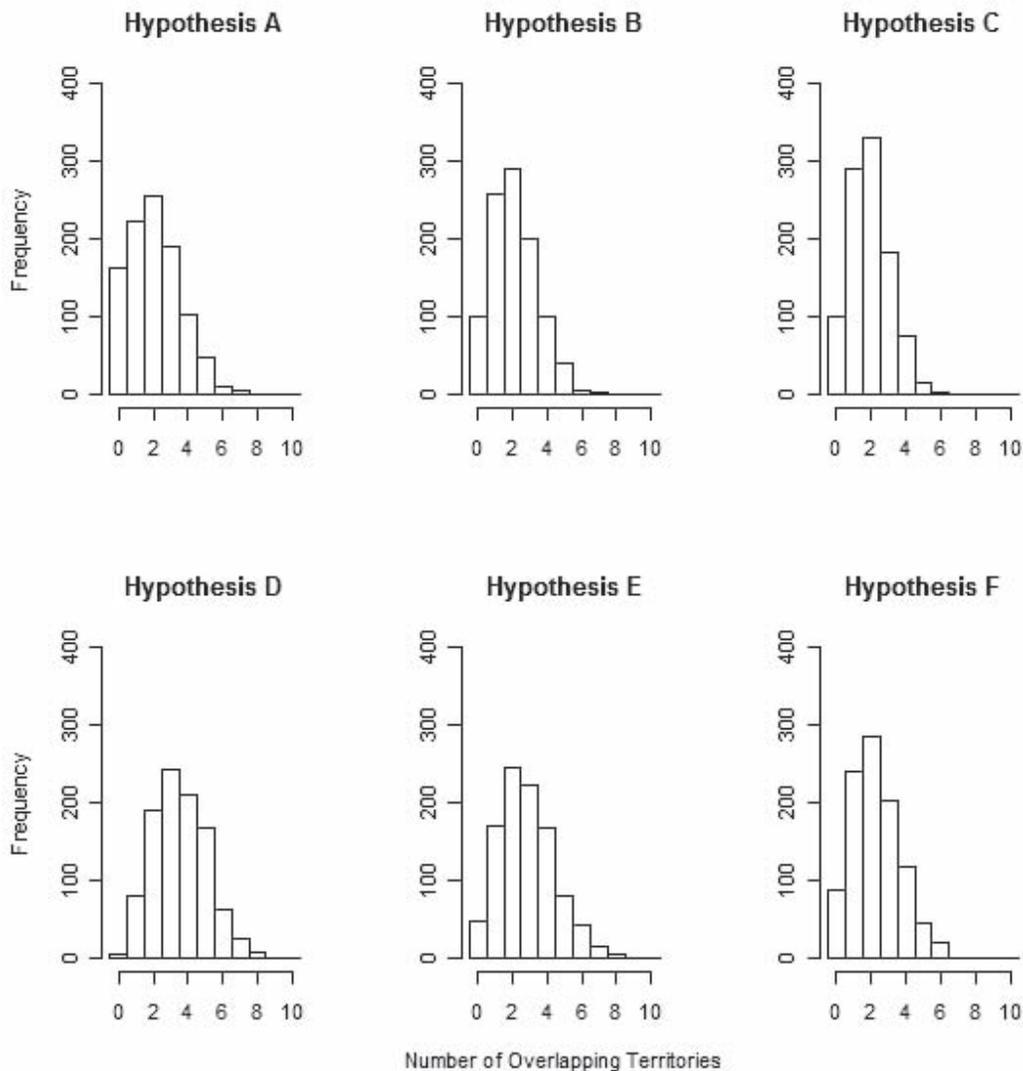


FIGURE 4. Frequency distributions of levels of overlap between observed locations of Cape Sable Seaside Sparrow territories in subpopulation C in 2009 ( $n = 14$ ) and simulated territory locations ( $n = 1000$ ) under six competing hypotheses:  $A_{\text{Clustered}}$ ,  $B_{\text{Habitat}}$ ,  $C_{\text{Philopatry}}$ ,  $D_{\text{Playback}}$ ,  $E_{\text{Playback/Philopatry}}$ , and  $F_{\text{Playback/Habitat}}$ . Results in this figure were based on territories of 2 ha.

recruitment and settlement of long-distance dispersers into restored areas by strategically placing several playback systems there. Since Cape Sable Seaside Sparrows winter near their breeding territories, are philopatric, and have a higher probability of dispersing short distances, placing song-playback systems near existing breeding populations may also encourage residents to expand into any neighboring newly restored habitat. The location of playback systems should take into consideration the properties of the artificial cues being broadcast to ensure that the best-quality sound is broadcast directly to the speakers themselves. The systems we designed can be used to create appropriate cues over a large area (250 ha) and are relatively inexpensive to build and implement, making them a viable conservation tool for this species.

In any attempts to redistribute Cape Sable Seaside Sparrows across the Everglades, care should be taken to avoid creating ecological traps, given that careless placement could encourage the birds' settlement of poor-quality habitats (Betts et al. 2008). Because of low sample sizes we did not test whether sparrows that nested within the sound field generated by the playback units had nesting success higher or lower than that of individuals that nested outside the field. This aspect of the use of playback in conservation of the Cape Sable Seaside Sparrow, or any other endangered species, is a critical question to be answered. At a minimum, managers should use the most accurate habitat models available to assess the quality of restored habitat for sparrows before encouraging recruitment into these areas. Additionally, effects on the avian community as a whole should be taken into consideration, as broadcasting

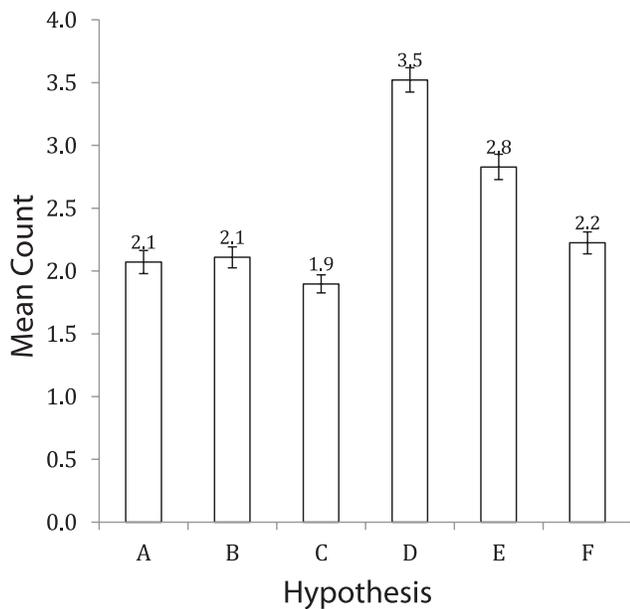


FIGURE 5. Mean number of overlapping observed and simulated Cape Sable Seaside Sparrow territories ( $\pm$  SE) under six competing hypotheses: A<sub>Clustered</sub>, B<sub>Habitat</sub>, C<sub>Philopatry</sub>, D<sub>Playback</sub>, E<sub>Playback/Philopatry</sub>, and F<sub>Playback/Habitat</sub>. Results in this figure were based on territories of 2 ha.

song of one species may cause other species to abandon suitable sites (Betts et al. 2008, 2010, Ahlring et al. 2010).

While our results suggest that the Cape Sable Seaside Sparrow uses early-season song as a cue for habitat selection at that time, the birds, particularly failed breeders and/or the year's fledglings, possibly also use late-season song as a cue for selecting a territory in the following year (Doligez et al. 2002, Danchin et al. 2004). Older, more experienced individuals tend to use previous experience to select high-quality breeding sites, while younger, less experienced birds settle near older birds (Nocera et al. 2009). It is these inexperienced settlers that are most likely to collect information on habitat quality by observing the settlement decisions of others (Serrano et al. 2004, Nocera et al. 2006, Nocera and Forbes 2010). Since the Cape Sable Seaside Sparrow is a resident with strong site fidelity, dispersers are likely using early-season song as an important cue for selecting habitat each year. However, we have observed adult and juvenile sparrows searching areas near our playback units after breeding (M. Davis pers. obs.), indicating that sparrows may indeed be using late-season song as a social cue. Future conspecific-attraction experiments for this species should measure the sparrows' response to both early- and late-season song playback to improve the efficiency of attempts to manipulate sparrows to settle in new areas.

Finally, we address an important aspect of playback studies that has received little attention in the literature: the effect of sound quality and amplitude on a species' response to social cues in making settlement decisions (Ahlring et al. 2010). If song amplitude is too low, it could provide stimulation too

TABLE 2. Pairwise comparisons by the Tukey HSD of mean number of overlapping territories observed and simulated under six competing hypotheses (A–F). All competing hypotheses are significantly different from A<sub>Clustered</sub>. Hypotheses D<sub>Playback</sub> and E<sub>Playback/Philopatry</sub> are significantly different from all other competing hypotheses.

Hypotheses	Difference	LCI	UCI	<i>P</i>
A–B	0.04	–0.15	0.22	0.99
A–C	–0.17	–0.36	0.01	0.08
A–D	1.45	1.27	1.63	0.00
A–E	0.76	0.57	0.94	0.00
A–F	0.17	–0.01	0.35	0.09
B–C	–0.21	–0.40	–0.03	0.01
B–D	1.41	1.23	1.60	0.00
B–E	0.72	0.54	0.90	0.00
B–F	0.13	–0.05	0.32	0.31
C–D	1.62	1.44	1.81	0.00
C–E	0.93	0.75	1.11	0.00
C–F	0.34	0.16	0.53	0.00
D–E	–0.69	–0.88	–0.51	0.00
D–F	–1.28	–1.46	–1.10	0.00
E–F	–0.59	–0.77	–0.40	0.00

weak to elicit a response. If song amplitude is too high, the intense stimulation or sound distortion could disrupt or deter settlement. Recognizing that the method of sound scoring we used may represent only a crude estimate of the actual soundscape for the sparrows, we were able to incorporate some measure of sound quality into our analyses. Deciding how to measure a species' response to playback is a difficult task, especially for rare species with small population sizes; therefore, understanding how sound quality affects the response can vastly improve such studies. In our study, sparrows did not establish territories near speakers where high amplitude resulted in sound degradation, according to our qualitative assessment. It is possible that the high amplitude deterred sparrows from settling near our speakers, but the birds may also have simply avoided these areas thinking that another territorial male had already settled there (territoriality hypothesis). While we cannot rule out the equally parsimonious territoriality hypothesis, our study does highlight the importance of taking into consideration the properties of artificial cues in song-playback studies. By modeling sound quality across our study area, our study provides a more realistic measure of the response to song playback than do studies that assume species will approach playback units directly.

#### ACKNOWLEDGMENTS

We thank Casey Kittle ([planetinnovation@yahoo.com](mailto:planetinnovation@yahoo.com)) for his help in designing and constructing the song-playback systems used in this study. We thank David La Puma for his sparrow recordings and valuable input into the early design of the playback systems. We thank Jay Sah and Mike Ross from Florida International University

for providing the vegetation data used in our analyses. We are very grateful to those in the Grant F. Walton Center for Remote Sensing and Spatial Analysis for GIS assistance, including John Bogner, Scott Haag and Jim Trimble. We thank everyone at Everglades National Park, Fire Cache and Dispatch, who have aided us over the years, especially Sonny Bass. This research was funded by grants from the United States Fish and Wildlife Service and Everglades National Park's Critical Ecosystem Studies Initiative. All monitoring and protocols complied with our U.S. Fish and Wildlife Service permit and the park's permit restrictions.

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