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Original Article

Attracting songbirds with conspecific playback: a community approach

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The presence of conspecifics is an indicator of good habitat for a number of songbird species; a cue positively associated with territory selection. Thus, conspecific playback may be a cost-effective tool for attracting songbirds to particular, preselected sites of high-quality habitat. Previous studies have used conspecific playback to encourage the establishment of a single species; however, few have researched the potential for the simultaneous attraction of multiple species. Furthermore, empirical studies on the effect of song playback for nonfocal species are sparse. We investigated whether 6 migratory songbird species are more likely to establish nesting territories in response to multispecies playback. To evaluate the effect on the greater songbird community, we assessed the responses of 22 nonfocal species. Three of 6 focal species increased their use of areas near playback speakers, and none became less common. However, several nonfocal species were less likely to use playback sites. Phylogenetic comparison revealed that species closely related to playback species were those most likely to be affected. Our results suggest that conspecific attraction can be used to attract multiple songbird species simultaneously, but that its impact on nonfocal species should be considered before implementation.

Key words: community, conspecific attraction, conservation, forest, migration, niche, phylogeny, songbirds, song playback.

INTRODUCTION

Songbird numbers continue to decline across the globe (Hutto 1988; Finch 1991; Berthold et al. 1998). Although many factors are driving these trends, the single factor most often implicated is habitat loss (Kepler et al. 1996; Bender et al. 1998; Both et al. 2010). Human activities, such as clearing forests and extensive use of agricultural land, have drastically reduced available habitat for many species. As a result, ecologists place a high priority on habitat preservation and restoration (Fahrig 2003), especially for species with narrow habitat requirements (Kilgo et al. 1998; Rodewald and Vitz 2005). To date, much effort has been directed toward restoring vegetative conditions and reducing human intrusion (Miller et al. 2003). Unfortunately, many of these efforts have failed to restore target populations of the intended species, partially due to the organism’s inability to locate the intended habitats (Ahlering and Faaborg 2006). To address this, biologists continue to investigate a range of ecological and life-history traits associated with habitat selection.

Migratory songbirds use various cues to assess potential breeding and wintering habitats (Smith 1991; Jones 2001). These cues are often related to vegetation, patch size, and other microhabitat variations, with particular indicators varying across species (Lee and Rotenberry 2005, Fisher and Davis 2010). In general, an ideal breeding habitat will possess several intrinsic qualities, such as abundant food, water, and nesting material in addition to adequate protection from predators (Muller et al. 1997). Visual cues such as vegetative cover and structure can be used to quickly assess habitat suitability, but the use of acoustic signals, such as conspecific song, to determine habitat quality is quite common in songbirds as well (McCollin 1999). Songbirds’ ability to discriminate between less relevant sounds and salient biological signals is evident from both behavioral and neurobiological studies of bird song (Chew et al. 1996; Hoeschele et al. 2012). For example, female canaries will significantly increase copulatory solicitation behaviors in response to the presentation of conspecific song when compared with heterospecific song (Kreutzer and Vallet 1991). Further, the expression of ZENK, a gene associated with activity in the avian auditory neural pathway, is generally limited to playback of biologically salient songs (Mello and Clayson 1994; Mello et al. 2004). This suggests that processing acoustic information occurs differentially, and responses in songbirds are more likely to be associated with salient biological sounds, such as conspecific vocalizations. The process of using salient social information to inform behaviors such as habitat selection is widely known as conspecific attraction (Ward and Schlossberg 2004).

In birds, song primarily functions in territory defense and mate attraction (Catchpole 1989), but its use also appears to increase regional territory establishment in some migratory songbird species (Kiester and Slatkin 1974; Ward and Schlossberg 2004; Ahlering
et al. 2010). This positive relationship may stem from the direct assessment that conspecific presence indicates quality habitat, or from the perceived benefits of group living such as increased likelihood of extra pair mating or protection from predators (Kenward 1978; Wagner 1998; Hahn and Silverman 2006; Harrison et al. 2009). Previous studies have shown that playback of simulated conspecific song encourages conspecifics to establish territories in areas surrounding playback sites (Alatalo et al. 1982; Ward and Schlossberg 2004). For example, Ward and Schlossberg (2004) successfully attracted >70 endangered black-capped vireos into previously unoccupied areas of restored habitat. However, recent work in songbird communication suggests that many species are also responding to heterospecific vocalizations (reviewed in Valone 2007).

Although previous studies have used conspecific playback to encourage the establishment of individual species, the potential for simultaneous attraction of multiple species has not been examined. Additionally, it is possible that conspecific playback targeting particular species may have adverse effects on other nonfocal species within the community, causing them to emigrate away from healthy sites due to increased competition with the attracted target species and limited niche space (Fletcher 2008; Betts et al. 2010; Nocera and Betts 2010). Conversely, nonfocal species may be attracted to areas with high numbers of heterospecific residents when establishing breeding territories (Forsman et al. 2002; Thomson et al. 2003; Parejo et al. 2005). A handful of studies have examined the effect of conspecific attraction on a few closely related, nonfocal species (Morse 1971; Betts et al. 2010; Ward et al. 2010) and a single study has examined broader community effects (Fletcher 2008), but the effect of conspecific playback on the larger community of songbirds remains understudied (Nocera and Betts 2010).

To test the community-level effect of conspecific song playback, we investigated whether a community of forest and forest-edge songbird species would be more or less likely to utilize nearby habitat and establish territories in response to conspecific playback. To simulate a multispecies playback scenario, we simultaneously broadcasted songs of 6 locally common bird species. We predicted that the species chosen for playback would be found more regularly and establish territories in higher densities in habitats near playback speakers than at control sites. We expected nonfocal species to have differential responses based on heterospecific attraction and competition (Monkkonen et al. 1997). In significantly impacted nonfocal species, we examined the importance of niche overlap and phylogeny as potential mechanisms underlying repulsion or attraction.

**METHODS**

**Species selection**

Six focal songbird species were selected because they are locally common in the hardwood forests of Northern Michigan and are not regularly found in human altered areas: ovenbird (Seiurus aurocapillus), black-throated green warbler (Setophaga virens), rose-breasted grosbeak (Pheucticus ludovicianus), eastern wood-pewee (Contopus virens), great-crested flycatcher (Myiarchus crinitus), and hermit thrush (Catharus guttatus). Previous research has confirmed that all focal species respond antagonistically to acute conspecific playbacks (Wecden and Falls 1959; Smith 1988; Ficken and Ficken 1970; Kroodsma 1974; Smith and Smith 1966; Brown et al. 2000), but has not investigated whether continuous conspecific playback attracts males to establish territories. In addition to our 6 focal species, all other passerine species were surveyed at all locations. Any species with more than 10 observations was included in our analysis as a nonfocal species (Table 1). One nonpasserine species, the wild turkey (Meleagris gallopavo) was included for phylogenetic comparisons.

**Site selection**

We compared songbird use and territory establishment in 18 contiguous, mature hardwood forest sites which remain relatively unaffected by human development. Sites were located on state and private forests in northeastern Kalkaska County, Michigan, USA. Habitat types were initially determined via MiHUNT cover type databases (michigan.gov/mihunt) and ground truthed to confirm the presence of mature Northern hardwood forest. Nine experimental locations were exposed to playback of conspecific song, and 9 unmanipulated forest locations receiving no playback served as controls. Because previous studies show that songbirds are more likely to respond to conspecific and heterospecific acoustic signals than to less salient signals such as a tone (Mello and Clayton 1994; Mello et al. 2004), we did not establish acoustic controls where a

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**Table 1**

All bird species (>10 observations) included in the analysis of playback effects

<table>
<thead>
<tr>
<th>Bird species</th>
<th>Scientific name</th>
<th>Bird species</th>
<th>Scientific name</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Redstart</td>
<td>Setophaga ruticilla</td>
<td>Least Flycatcher</td>
<td>Empidonax minimus</td>
</tr>
<tr>
<td>American Robin</td>
<td>Turdus migratorius</td>
<td>Northern Flicker</td>
<td>Colopetes auratus</td>
</tr>
<tr>
<td>Black-billed Cuckoo</td>
<td>Coccothraulus erythropthalmus</td>
<td>Ovenbird</td>
<td>Seiurus aurocapillus</td>
</tr>
<tr>
<td>Black-capped Chickadee</td>
<td>Poecile atricapillus</td>
<td>Pleated Woodpecker</td>
<td>Dryocopus polianus</td>
</tr>
<tr>
<td>Blue Jay</td>
<td>Cyanocitta cristata</td>
<td>Red-bellied Woodpecker</td>
<td>Melanerpus carolinus</td>
</tr>
<tr>
<td>Black-throated Blue Warbler</td>
<td>Setophaga virens</td>
<td>Red-eyed Vireo</td>
<td>Vireo olivaceus</td>
</tr>
<tr>
<td>Black-throated Green Warbler</td>
<td>Bomyxilla edulis</td>
<td>Rose-breasted Grosbeak</td>
<td>Pheucticus ludovicianus</td>
</tr>
<tr>
<td>Cedar Waxwing</td>
<td>Setophaga carolinus</td>
<td>Scarlet Tanager</td>
<td>Piranga olivacea</td>
</tr>
<tr>
<td>Chestnut-sided Warbler</td>
<td>Contopus virens</td>
<td>Song Sparrow</td>
<td>Meloptes melodia</td>
</tr>
<tr>
<td>Eastern Wood-Pewee</td>
<td>Myiarchus crinitus</td>
<td>Vireo</td>
<td>Catharus fuscissens</td>
</tr>
<tr>
<td>Great Crested Flycatcher</td>
<td>Prionodura villosissima</td>
<td>White-breasted Nuthatch</td>
<td>Sitta carolinensis</td>
</tr>
<tr>
<td>Hairy Woodpecker</td>
<td>Catharus guttatus</td>
<td>Wild Turkey</td>
<td>Melaneeus gallopavo</td>
</tr>
<tr>
<td>Hermit Thrush</td>
<td>Passerina cyanea</td>
<td>Yellow-bellied Sapsucker</td>
<td>Sphyrapicus varius</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td></td>
<td>Yellow-billed Cuckoo</td>
<td>Coccothraulus americanus</td>
</tr>
</tbody>
</table>

Species whose songs were played back are in bold.
Although song playback is unlikely to be audible past 100 m, we selected an area 600 m in length for 2 reasons. First, if conspecifics are responding to playback they may establish territories in the immediate vicinity of the song source (<100 m), but they may also perceive the immediate area as occupied and establish territories nearby (e.g., 100–300 m). Second, because the spatial effects of conspecific playback experiments are not well delineated, extending our sampling to 600 m reduced the potential for missing longer range effects. Sites were separated by a minimum of 450 m, and sites were placed such that no survey point was closer than 700 m to the playback of a site other than its own. All transects began within mature forests located 30 m from a forest edge (necessary to provide solar power), and continued through contiguous forests of like habitat. Forest edges were comprised of small natural openings or abandoned oil wells surrounded by contiguous forests. To increase similarity between the control and experimental condition, sites were paired such that any unusual trait (e.g., ATV trail) in an experimental site was replicated in a control site.

**Songbird surveys**

Each site was visited 5 times between 0600 and 1000 h from 29 May 2014 to 11 July 2104, to assess habitat use and territorial establishment (Ralph et al. 1993). Surveys did not begin until 19 days after initiation of playback to provide time for territorial establishment, and to allow birds to habituate to song playback (Temeles 1994; Hyman 2005). Playbacks were discontinued immediately prior to and throughout the duration of point count surveys at experimental sites. At each site, intensive point counts (Bibby et al. 1992) were conducted at 4 points equally spaced along the length of the transect median (0, 166, 333, and 500 m; Gregory et al. 2004). At each point, 2 observers collaboratively recorded all passerine species seen or heard within a 100-m radius during a 5-min count period, and placed each observation on a map of the area using the distance and azimuth from the observer.

The 100 m radii between adjacent points overlapped by 33 m. This design was employed to reduce the amount of area not surveyed within each site (i.e., area outside of circular points but within our square plots; see Figure 1). Close proximity is not atypical for intensive point counts; however, resulting observations must not treated as observations of independent birds. This limitation was deemed acceptable because our objective was to establish territories through mapping procedures (Ralph et al. 1993). Sites were visited systematically such that no time bias existed between experimental and control conditions (Dolby and Grubb 1999). In addition, point order along each transect was alternated between forward (0–600 m) and reverse direction to reduce time bias between points.

**Analysis**

To test for proximity differences between the start point (playback speaker) at control and experimental sites, each transect was divided into 4 zones (Figure 1; see Harrison et al. 2009). Using these categories rather than raw distances was determined to be a more efficient method for detecting changes because we did not expect territorial establishment to change linearly as distance increased, and using nonlinear analyses with small sample sizes can quickly become difficult to interpret. Optimal zone size was determined to be ~100 m in radius because this encompassed the entirety of each point count. Because detectability varies by distance (Allredge et al. 2007a) within a point count area, incorporating the entire range of detectability within each zone increased comparability across treatments.

Due to the overlap between zones, we reduced the total width of zones 2–4 by 33 m. We chose to retain the full 100 m radius in zone 1 because these zones also included a portion of open and edge habitat (Figure 1). Zone 1 encompassed a 100 m radius in all directions from the playback station or flagged start point. Zones 2 through 4 were 166 m in width and included 101–266, 267–432, and 433–600 m from the start point, respectively. Due to size differences and the ecological effects of edge habitats, statistical comparisons were made between control and experiment conditions separately for each zone, rather than making comparisons across zones.

Using territory mapping procedures (Bibby et al. 1992; Gregory et al. 2004), we calculated the number of territories within each zone for all species by identifying clusters of observations. To
Figure 1  
Site layout with intensive point count locations buffered by 50 and 100 m radii. Zones 1–4 were used to quantify distance of territories and observations from playback speakers.

Visually delineate clusters, observations from all visits were overlaid in ArcGIS 10.2. In addition, average territory size for each species was determined from the Birds of North America database (bna.birds.cornell.edu), and overlaid as a buffer on each observation. Before visual assessment, all identifying characteristics were removed from each site so that observers were blind to whether each site was used as a control or experimental replicate. When territories overlapped multiple zones, they were assigned to the zone closest to the playback speaker or flagged start point. Territories were assessed independently by all 4 authors, and results were significantly correlated across individuals (Pearson’s r > 0.889, P < 0.001). In cases where disagreement occurred, the mean between observers was retained.

Although some error is inherent in any survey methodology (Granholm 1983; Allredge et al. 2007b), territory mapping produces results comparable to those provided by other survey methods, such as point counts and line transects (Greene and Pryde 2012; Newell et al. 2013), and may be ideal when surveying intensely within small areas (Gregory et al. 2004). These previous comparisons, combined with our high levels of between-observer agreement, suggest that territory mapping provides repeatable and accurate information about territorial distribution within a site.

Although we employed multiple methods for reducing subjectivity in territorial delineation, we also conducted a second analysis using raw data (termed observations) to evaluate the level of confidence in our results. Specifically, we calculated how often birds utilized habitat within each zone by summing total observations in each zone over all visits. If territorial delineation systematically skewed the distribution of our results, patterns in the raw data should be dissimilar. Alternatively, congruence in patterns of distribution would substantiate results from the territorial assessment. Second, there was some concern that our decision to assign territories spanning multiple zones to that closest to the speaker might alter results. Again, similar patterns from analysis of individual observations would suggest that prior to being clumped and amalgamated into a single territory, these observations spanned zones in a manner similar to our classification scheme. Thus, similar patterns would suggest assigning territories to the closest zone did not alter the observed patterns of distribution.

The number of territories between control and experimental sites were compared via a general linear model including treatment (control/experimental), species, and a species × treatment interaction. Each zone was compared in a separate model because edge effects prevented direct comparisons between zones 1 and 2, and so on. Post hoc comparisons were made for specific species when the treatment or interaction terms were significant. To test habitat utilization (observations), the same set of independent variables were incorporated into a generalized linear model with a Poisson log-linear distribution to account for the use of count data.

**Phylogenetic and ecological comparisons**

To examine potential mechanisms underlying attraction and repulsion of nonfocal species, we tested 2 competing hypotheses: nearest niche and phylogenetic relatedness. The nearest niche hypothesis suggests that species with high overlap in their ecological niche are subject to increased competition (MacArthur 1958). Thus, by increasing the presence (or simulated presence) of 1 species we are more likely to exclude heterospecifics with high levels niche overlap. Alternatively, the phylogenetic relatedness hypothesis suggests that species with more recent evolutionary divergence may be more sensitive to heterospecific vocal activity (e.g. de Kort and ten Cate 2001), often due to acoustic similarity (Fallow et al. 2011). Yet, acoustic sensitivity may also facilitate reproductive isolation in closely related species, because acoustic divergence appears to correlate with heterospecific identification and speciation events (Beckers et al. 2003; Bloomfield et al. 2003; Seddon 2005; Tobias et al. 2010). Under this hypothesis, we expect nonfocal species which are most closely related to our playback species to demonstrate the strongest responses to playback.

To test the nearest niche hypothesis, we collected data on 7 life-history traits from Birds of North America (bna.birds.cornell.edu, Cornell Lab of Ornithology) and All About Birds (allaboutbirds.org, Cornell Lab of Ornithology). Specifically, for each species we assessed preferred 1) vegetative density (1 = open, 2 = semiopen, 3 = closed), 2) habitat type (1 = forest woodland, 2 = open woodland), 3) diet (1 = herbivorous, 2 = omnivorous, 3 = carnivorous), 4) foraging location (1 = ground, 2 = bark, tree center, 3 = foli- age gleaner), 5) month of initiation of breeding (1 = March, 2 = April, 3 = May, 4 = June), 6) nest type (1 = cup, 2 = cavity), and 7) nest location (1 = ground, 2 = shrubs, 3 = trees). To calculate a single niche variable, data were organized so that each
column represented a unique species and each row represented a single habitat characteristic. Correlation was then assessed between each column such that every nonfocal species was compared with each of the 6 focal species. Perfect alignment among all habitat characteristics between a pair of species resulted in correlation of 1, whereas complete lack of alignment resulted in a correlation of 0. For each nonfocal species, we retained the highest measure of correlation between it and any of the 6 focal species.

Phylogenetic relatedness was determined by downloading 100 phylogenetic trees containing all species included in our study from birdtree.org (Jetz et al. 2012). We then developed a consensus tree in DensiTree 2.1.11, and displayed the consensus tree with associated node times (millions of years) in FigTree 1.4.2. To create a single measure of relatedness, we recorded the node time for the most recently shared ancestor between each nonfocal species and the closest focal species.

To assess overlap between these 2 hypotheses, we correlated the results from each analysis. Further, we determined whether each hypothesis significantly predicted the likelihood of response to playback by including both as independent variables in a binary logistic regression. Response to playback was categorized for each species as either nonsignificant (0) or significant (1, regardless of direction). All data were analyzed in SPSS (Version 18.0) and considered significant at $P < 0.05$. Results are reported as mean ± standard error unless otherwise noted.

**RESULTS**

**Focal species**

Comparisons between treatments revealed a significantly higher number of territories in zone 1 at playback sites (7.2 ± 0.70) than within the same zone at control sites (5.2 ± 0.56; $F_1 = 6.28$, $P = 0.012$; Figure 2a), but no significant species interaction with treatment ($F_2 = 4.90$, $P = 0.428$). Significant differences were not observed for zones 2, 3, or 4 in treatment ($F_1 < 1.04$, $P > 0.308$) or the interaction term ($F_2 < 4.93$, $P > 0.425$). When analyzed as observations, overall utilization of experimental sites was significantly higher than control sites in zone 1 (Wald $X^2_1 = 12.68$, $P < 0.001$; Figure 2b), but nonsignificant for zones 2, 3, and 4 (Wald $X^2_1 < 0.38$, $P > 0.533$). The interaction term was significant for zone 2 (Wald $X^2_1 = 11.79$, $P = 0.019$), but not for any other zone (Wald $X^2_1 < 9.13$, $P > 0.058$).

Post hoc examination of individual species revealed that territories were more common for all 6 species within zone 1 in playback sites than within the same zone for control sites (Figure 3, Supplementary Table S1). These patterns were the most pronounced for the hermit thrush ($Δ0.778$ individuals, 267% increase; Supplementary Table S1) and black-throated green warbler ($Δ0.694$ individuals, 139% increase). However, neither these species (BTNW: $F_1 = 2.33$, $P = 0.126$; HETH: $F_1 = 3.29$, $P = 0.070$), nor any others differed significantly by treatment ($F_1 < 1.13$, $P > 0.289$). When treated as observations, comparisons revealed similar patterns with significantly greater use of zone 1 in experimental sites for the hermit thrush (Wald $X^2_1 = 8.32$, $P = 0.004$), black-throated green warbler (Wald $X^2_1 = 6.62$, $P = 0.010$), and ovenbird (Wald $X^2_1 = 4.74$, $P = 0.029$; Figure 3). Species-specific comparisons for zone 2 revealed a significant increase in site use for black-throated green warbler (Wald $X^2_1 = 9.59$, $P = 0.002$), but no other species (Wald $X^2_1 < 1.03$, $P > 0.311$).

**Nonfocal species**

Territories and observations were compared for 22 nonfocal species, each with > 10 observations. Territory establishment did not differ significantly between experimental and control sites for any zone ($F_1 < 1.74$, $P > 0.188$; Figure 4a), although the species × treatment interaction term was significant for zone 2 ($F_1 = 2.08$, $P < 0.003$). The interaction was nonsignificant for other zones ($F_2 < 1.16$, $P > 0.274$). When analyzed as observations, higher numbers were reported in all control zones, although only zone 2 comparisons were significant (Wald $X^2_1 = 4.96$, $P = 0.026$; other zones, Wald $X^2_1 < 0.25$, $P > 0.614$; Figure 4b). The interaction term was not significant for any zone (Wald $X^2_1 < 24.28$, $P > 0.146$).

Species-specific analysis for zone 2 revealed significant overall declines in the number of territories in experimental sites for black-throated blue warblers ($F_1 = 11.53$, $P = 0.004$) and chestnut-sided warblers ($F_1 = 10.40$, $P = 0.005$; Figure 5), and increased numbers for American robins ($F_1 = 8.11$, $P = 0.012$). When treated as observations, reductions were observed in zone 2 for black-throated blue warblers (Wald $X^2_1 = 7.58$, $P = 0.006$), chestnut-sided warblers (Wald $X^2_1 = 13.27$, $P = 0.001$), and veerys (Wald $X^2_1 = 5.10$, $P = 0.024$). Increases were detected in American robins (Wald $X^2_1 = 10.04$, $P = 0.002$).

**Phylogenetic and ecological comparisons**

Phylogenetic relatedness and nearest niche results were not significantly correlated ($r = -0.153$, $P = 0.497$). Logistic regression revealed a significant relationship between phylogenetic relatedness and response to playback (Wald $X^2_1 = 6.10$, $P = 0.014$; Figure 6). Nonfocal species whose presence was affected by playback were separated on average by 9.01 ± 6.81 (SD) million years from the closest playback species, whereas unaffected species averaged 55.70 ± 32.95 (SD) million years of separation. The
The relationship between response and nearest niche was not significant (Wald $1.024$, $P = 0.878$).

**DISCUSSION**

Focal species were significantly more likely to establish territories near playback speakers (zone 1) than within similar areas without playback. This pattern of significance was also found when data were treated as observations, suggesting that territorial assessment did not artificially alter results. Zone 1 increases in experimental sites were evident in all 6 focal species, and significant for observational analysis in the hermit thrush, black-throated green warbler, and ovenbird. In nonfocal species, overall territory establishment did not differ significantly by treatment, but a zone 2 interaction revealed that chestnut sided and black-throated blue warblers were less common in experimental sites. Treating data as
observations also revealed significantly lower overall numbers for zone 2 in experimental sites, and added the veery to the list of nonfocal species negatively affected by playback. In turn, 1 species, the American robin, was more likely to establish territories in zone 2 of playback sites. Phylogenetic relationships, but not ecological traits, were a significant predictor of which nonfocal species were affected by playback.

Our results suggest that multiple species can be attracted simultaneously through playback, and that the larger community may be impacted both positively and negatively; however, the mechanisms underlying this phenomenon are complex and require verification before general patterns can be established. For example, 3 of our focal species did not significantly increase territorial establishment (although none decreased establishment). At face value, this might suggest that these species are insensitive to conspecific playback. However, at least 2 alternative mechanisms may underlie this phenomenon. First, it is possible that interspecific interactions between focal species prohibited increased establishment in some focal species. To test for this, it would be necessary to also establish a series of experiments for each individual species; playing only 1 set of species-specific songs in multiple sites. Although beyond the scope of this study, we suggest this type of experiment should be employed before any conclusions are made regarding response to playback for any single focal or nonfocal species.

Second, avoidance of edge habitats could prevent a species from utilizing near-speaker habitats in our experimental sites. To minimize the edge effect, we utilized abandoned well pads and small natural openings which were otherwise surrounded by contiguous, mature hardwood forests. However, logistical constraints required that each transect began near a forest edge. A post hoc zonal comparison for focal species revealed that 1 species, the eastern wood-pewee, was significantly less likely to utilize habitats closer to edges under both treatment conditions (Wald $\chi^2 = 11.6, P = 0.009$; Supplementary Table S1). This may be explained by their propensity to establish large, forest interior territories (Bond 1957) and is fitting with previous research documenting low densities at wooded edges (Stauffer and Best 1980).

The edge effect may also be important an important consideration for species which did respond to playback. Although nonsignificant (Wald $\chi^2 = 6.00, P = 0.109$), a pattern of edge aversion was also observed in 1 other focal species; the black-throated green warbler (Figure 3, Supplementary Table S1). Yet, conspecific playback significantly increased its use of near edge habitats. Although somewhat less constrained than some specialists (Smith and Dallman 1996), black-throated green warblers prefer interior
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In forest habitats (Parrish 1995, Cooper et al. 1997). In cases such as this, one must consider the possibility that playback is luring birds into suboptimal habitats which may function as sinks (Stamps 2001). Exploration of survivorship and reproductive success should be assessed before large scale attempts to lure songbirds into potentially suboptimal habitats.

Although multispecies playback did not induce trends of repulsion within targeted species, it did reduce territorial establishment in several nonfocal species. This pattern suggests that a broader ecological understanding of avian communities and interspecific interactions must be considered when conspecific playback is implemented. In this study, phylogenetic relationships were likely to predict which species would be affected by playback. However, we suggest that several interspecific interactions need to be examined before these results are more broadly generalized. First, heterospecific interactions may operate at distances other than those tested. For example, statistical inference suggested we determine species-specific differences in only zone 2 for nonfocal species. Yet, examination of the data (Figure 5) suggests that effects may have operated well beyond 100 m. It is possible that the scale of our analysis may preclude observance of some interspecific interactions. Second, dominance interactions could exclude some species regardless of phylogeny or niche overlap. For example, black-throated blue warblers and chestnut sided warblers were less common near playback speakers. Both species are closely related to the black-throated green warbler (Figure 6). Black-throated green warblers often dominate interspecific interactions (Parrish 1995, Holmes et al. 2005), which may largely explain the relationship between these species.

Less is known about the effect of the hermit thrush on the veery and American robin, but similar interactions may also exist (see Morse 1971).

Nevertheless, the phylogenetic relatedness and nearest niche hypotheses warrant further examination. Closely related kin often share many physical characteristics (Losos 2008); however, niche separation is a common mechanism used to reduce competition and hybridization between closely related species (Chesson 2000). When a niche is filled, the process of competitive exclusion would be expected to repel other species that use the most similar niches (Armstrong and Mcgehee 1980). Song playback should heighten this dynamic through the perception that associated niches are already utilized. However, this pattern was not observed in our study. Perhaps, distantly related heterospecifics do not rely on song

Figure 6
Phylogenetic consensus tree for 28 songbird species used in the study. Focal species are highlighted in gray. Nonfocal species which were affected by playback are displayed in black font. Unaffected nonfocal species are in gray font. Length of lines demonstrates relative evolutionary time.
as an indicator of niche fulfillment. Alternatively, song may be used as an indicator in a myriad of cues, such as visual presence (Piper 2011). The lack of other cues may reduce the effectiveness of exclusion in distant relatives. Further, a lower need to protect reproductive isolation may allow distantly related species to exist in closer proximity while sharing relatively similar niches (Butlin 1987; Zhou and Fuller 2014). The species in our study represent only a portion of the potential ranges in phylogeny and niche overlap, but provide fodder for further examination of these mechanisms.

In summary, the primary objectives of this study were to test whether multispecies playback could be used to increase territory establishment in a particular area for more than a single species, and to assess playback effects on a larger community of nonfocal species. Positive results for all 6 playback species, including a significant increase in 3 of those species, suggest that this approach should be considered when attempting to increase songbird establishment rates in particular areas. Adding playback of ecologically important secondary species may be valuable for maintaining such populations within targeted, single species management plans. However, our community analysis revealed that some nonfocal species may be less likely to establish near playback areas. Examining phylogenetic relationships, but not ecological niche, predicted which nonfocal species were most likely to be affected by song playback. This, and other mechanisms, should continue to be investigated as a potential tool for predicting the effects of playback on the larger community. Ultimately, we suggest that successful implementation of conspecific playback as a conservation tool should be preceded by weighing the benefits for target species with the unintended consequences on the greater songbird community. When implemented properly, conspecific attraction via song playback remains an attractive method for increasing songbird use of previously underutilized habitats, and can be used beyond the scope of a single species.

SUPPLEMENTARY MATERIAL
Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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