Do songbirds attend to song categories when selecting breeding habitat? A case study with a wood warbler

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Abstract
Breeding habitat selection strongly affects reproduction and individual fitness. Among birds, using social cues from conspecifics to select habitat is widespread, but how different types of conspecific social cues influence breeding habitat selection remains less understood. We conducted a playback experiment evaluating if the yellow warbler (Setophaga petechia), a species with two song categories linked to pairing status, uses categories differently when selecting breeding habitat. We hypothesized that yellow warblers use second-category singing mode, which is mostly sung by paired males, over first-category singing mode for habitat selection, as successfully paired males should indicate higher-quality habitat. We broadcast yellow warbler first-category singing mode, second-category singing mode, and silent controls at sites in Illinois. Yellow warblers were more abundant at sites treated with second-category singing mode compared other sites. Our results demonstrate that yellow warblers use social cues informing successful pairing over other types of social cues to select breeding habitat.

Keywords
habitat selection, social information, conspecific attraction, social cue, song category, yellow warblers.

1. Introduction
Breeding habitat selection is a critical decision-making process because of its direct effects on fitness (Holmes et al., 1996; Arlt & Pärt, 2007). To maximize reproductive success, individuals can collect information on habitat quality and choose the highest-quality habitat available (Koops, 2004; Stamps & Krishnan, 2005). Often times, individuals base their decisions on reproductive experience in a habitat (e.g., win-stay lose-switch:
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Schmidt, 2004; Chalfoun & Martin, 2010), directly assessing predation risk (e.g., predator presence/absence: Emmering & Schmidt, 2010; Buxton et al., 2017), or by sampling environmental cues linked to successful reproduction (e.g., vegetation cues: Rosenzweig, 1973; Cody, 1981; Martin, 2001; food abundance: Murkin et al., 1997). Although these cues provide information for decision-making, collecting this information can be time consuming and costly (Valone, 2007). Alternatively, individuals can use social information to assess habitat quality by sampling cues from other individuals settled in the environment (Seppänen et al., 2007). Social information use can remove the cost of search time typically incurred when acquiring personal information or directly sampling the environment (Valone & Templeton, 2002). Moreover, social cues can enhance fitness by steering individuals toward higher-quality habitat where reproductive success is high (Fletcher, 2006).

Using intraspecific social cues for habitat selection, termed conspecific attraction (Stamps, 1988; Reed & Dobson, 1993; Ahlering et al., 2010), is particularly beneficial due to similar breeding habitat requirements among conspecifics (Holt, 2009). Indeed, conspecific attraction is a common phenomenon observed across taxa (arthropods: Fletcher & Miller, 2008; amphibians: Buxton et al., 2015; molluscs: Lecchini, 2011; reptiles: Scott et al., 2013; birds: Ahlering et al., 2010; mammals: Matthysen, 2005).

It is clear that many species use conspecific attraction to select breeding habitat, but what remains less understood is whether the type of social cue present affects settlement decisions (Betts et al., 2008; Szymkowiak et al., 2016). Location-based social cues, such as the position of other individuals or visual presence, contain information about conspecific presence in a prospective habitat (Betts et al., 2008). These social cues, however, do not provide much information on reproductive performance and success of those settled in the habitat (Betts et al., 2008; Rushing et al., 2015). In contrast, performance-based social cues, such as offspring presence, directly inform habitat quality because the reproductive consequences of settlement decisions are made apparent by presence of the cue (Danchin et al., 2004; Valone, 2007; Betts et al., 2008). Females of some insect species, for example, select oviposition sites using the presence of conspecific eggs and nymphs rather than the presence of adult conspecifics (Rudolf & Rödel, 2005; Fletcher & Miller, 2008; Raitanen et al., 2014). Many bird species, particularly among songbirds, use performance-based social cues to select breeding habitat (Brown et al., 2000; Ward, 2005; Betts et al., 2008; Pärt et al., 2011;
Rushing et al., 2015), with one study demonstrating that performance-based social cues elicit more individuals to settle than location-based social cues (fledgling vocalizations versus adult song; Betts et al., 2008). Similarly, theoretical models suggest that strategies using cues of conspecific reproductive success outperform other strategies for breeding site selection (e.g., conspecific presence: Doligez et al., 2003). With all else being equal, individuals should use performance-based social cues over location-based cues because of their high reliability for assessing breeding habitat quality (sensu Parejo et al., 2007).

Most studies consider signs of reproductive success as performance-based social cues (e.g., Brown et al., 2000; Betts et al., 2008; Kelly & Schmidt, 2017). These cues, however typically can only be sampled at the end of the breeding season and used after a one-year delay. Migratory songbirds could use the singing behaviour of territorial males as a performance-based social cue available directly upon spring arrival at the breeding habitat (e.g., Rushing et al., 2015). In some songbirds, males have two distinctive singing modes for specific contexts: one mode is mostly sung while unpaired for mate attraction (i.e., ‘first-category singing mode’; Catchpole, 1983; Spector, 1992; Titus, 1998), and the second is mostly sung after successfully pairing (i.e., ‘second-category singing mode’; Spector, 1991, 1992; Proppe & Ritchison, 2008). Depending on the species, first- and second-category singing modes are referred to as either ‘Type I and Type II’, where singing behaviour distinguishes the two categories (Spector et al., 1989; Spector, 1991; Staicer, 1996; Beebee, 2002; Jane & Ryker, 2011), or ‘accented and unaccented,’ where the aural/phonetic characteristics distinguish the categories (Morse, 1966; Weary et al., 1994a; Byers, 1996; Hof & Podos, 2013). In both naming systems, first- and second-category singing modes may contain different information about reproductive opportunities within the habitat. First-category singing mode would inform prospectors of where territorial males are located, while second-category singing mode informs prospectors of which sites contain successfully paired males.

For socially monogamous songbird species, individuals could expect more extra-pair copulation opportunities in habitat where many males are paired (e.g., Mayer & Pasinelli, 2013 and references therein). Thus, songbirds may treat first- and second-category singing modes as location-based and performance-based social cues to select habitat with, and choose sites where second-category singing mode is more prevalent because knowing
pairing status is a step closer towards reproductive success. To date, most research addresses distinction between singing mode categories in the context of sexual selection or territoriality (reviewed in Byers & Kroodsma, 2009; Reichard & Anderson, 2015), but rarely do studies consider singing mode categories in terms of different social cues useful for habitat selection (e.g., Szymkowiak et al., 2016).

We used experimental playbacks to test if the yellow warbler (Setophaga petechia), a wood warbler with well-studied singing mode categories (Morse, 1966; Fickens & Fickens, 1970; Spector, 1991; Weary et al., 1994b; Beebee, 2002), select breeding habitat based on how much first- and second-category singing mode is present at the breeding site. In yellow warblers, singing mode functions as a sex-specific signal: males engage in more in first-category singing mode when interacting with females before pairing, and typically sing more in second-category singing mode when interacting with males after successfully pairing (Spector, 1991; Weary et al., 1994b; but see Beebee, 2004). Thus, second-category singing mode contains useful information about potential mating opportunities that individuals can usurp when making settlement decisions. We expected that because the second-category singing mode indicates pairing success, yellow warblers would treat second-category singing mode as a performance-based social cue and select habitat with more second-category singing mode present than first-category. We further discuss the costs and benefits of settling near conspecifics singing second-category song from the perspective of both males prospecting for habitat and settled males singing second-category song.

2. Material and methods

2.1. Study species

The yellow warbler is a long-distance migratory songbird that arrives at most breeding grounds between early to mid-May (Lowther et al., 1999). Males arrive a week earlier than females in our system (J.K.K., personal observation), and up to ten days earlier in other systems (Lowther et al., 1999). Yellow warblers breed in a wide variety of shrublands, such as overgrown fields (Lowther et al., 1999), shrubby wetlands and uplands (Hemple & Burnett, 2010), as well as in developed areas such as along roadsides or in suburban parks (Rousseau et al., 2015). Yellow warblers have moderate site fidelity with return rates around 0.30 (Yezerinac et al., 1996; but see Cilimburg et
al., 2002 for return rates up to 0.42) such that immigration/emigration between breeding sites is likely in this species (Anders & Marshall, 2005). Thus, we expect that adults make settlement decisions based on social cues (specifically song categories) sampled upon arrival, as these cues should be more accessible than environmental cues (Valone, 2007).

2.2. Study sites

We established 44 study sites at shrublands throughout central and northern Illinois on both state and private land (see Figure A1 in the Appendix for locations by county). Sites were selected opportunistically. We used satellite imagery on Google Earth PRO 7.1 (Google Inc. 2013) to locate and measure the area of shrublands, and ground-truthed locations to verify that each shrubland contained habitat suitable for yellow warblers. Honeysuckle (Lonicera spp.), multi-flora rose (Rosa multiflora), autumn olive (Elaeagnus umbellate), young dogwood (Cornus spp.) and young willows (Salix spp.) were the dominant shrubs at each site. A mix of forest, agricultural fields, and suburban landscapes surrounded shrublands. All shrublands were >1 km apart to ensure independence. We measured site area by visually delineating shrublands in Google Earth PRO 7.1 using the Polygon option within the Ruler tool (Google Inc. 2013). Sites ranged considerably in size (1.16–41.76 ha, mean: 8.87 ha), but the variation was comparable among sites for each treatment (in ha; first-category sites: max 33.74; min 1.56; mean 8.09; second-category sites: max 47.96; min 1.95; mean 11.18; silent control sites: max 32.88; min 1.16; mean 7.49).

2.3. Playback experiment

During the 2014 breeding season, we conducted a playback experiment and randomly assigned study sites one of three treatments: (1) first-category singing mode (location-based social cue, \(n = 15\)), (2) second-category singing mode (performance-based social cue, \(n = 14\)), or (3) silent controls with no playback equipment or stimulus (\(n = 15\)). We did not broadcast procedural sounds (e.g., white noise) at silent control sites because similar experiments found no difference in response between procedural controls and control sites without any playback equipment (e.g., Emmering & Schmidt, 2011; Hua et al., 2013). At sites with song treatments, we established stations comprised of one FOXPRO model NX3 or NX4 game caller (FOXPRO, Lewiston, PA, USA) powered by a 12 V deep-cycle car battery.
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and operated by a Diehl 12V DC digital timer (Diehl Stiftung, Nuremberg, Germany). Equipment was housed in a plastic bin with mesh-covered openings for sound transmission and camouflaged with spray-paint. Playback stations were placed directly on the ground. Broadcast started mid-April before males arrived at sites (the first male at any site was detected on 30 April). Broadcast ran daily until early-July for approx. 10 weeks total, and encompassed both the earliest and peak portions of the breeding season (late May to early June; J.K.K., personal observation). Playback was broadcast in the morning (0500–0800 h) and late in the afternoon (1700–1900 h) to mimic natural vocal activity of yellow warblers (Lowther et al., 1999), as well as two periods at night (2200–0000 and 0200–0300 h) to simulate the vocal activity of migrants known to attract conspecifics (Alessi et al., 2010).

We used recordings of yellow warblers provided by the Borror Laboratory of Bioacoustics from the Midwestern United States (specifically Illinois, Indiana and Ohio) to avoid confounding effects of song dialect. Yellow warblers singing modes are described as both Type I versus Type II (characterized, respectively, by high and low repetition of songs throughout the male’s repertoire; Spector, 1991; Weary et al., 1994b; Beebee, 2002), as well as accented versus unaccented (characterized aurally by the downward or upward-sloping structure of a song’s last syllable; Morse, 1966; Fickens & Fickens, 1970; Bankwitz & Thompson, 1979). Thus we incorporated both characterization systems (Type I/Type II and accented/unaccented) to construct first-/second-category singing mode playlists for our treatments (Figure 1). As per Spector’s distinction between singing mode categories (1991), we selected songs for our first-category singing mode playlist that had higher-frequency first syllables with less variation among first syllable frequencies across songs compared to the second-category singing mode playlist (mean frequency for first-category playlist ± SD: 6562.50 ± 290.47 Hz; second-category: 5625.00 ± 660.26 Hz). We also made our first-category singing mode playlist more repetitive than our second-category singing mode playlist (0.50 vs. 0.23, where repetition is the proportion of songs on the playlist followed by the same song; Spector, 1991).

Considering how we constructed playlists for our treatments, we recognize the alternative way to refer to treatments are: (1) accented songs with less immediate variation (location-based cue) and (2) unaccented songs with more immediate variation (performance-based cue). Nonetheless, we think the playlists deliver two types of social cues with information
Figure 1. Example of two songs from the first-category (top) and second-category (bottom) singing mode playlists. The first-category playlist was comprised solely of accented songs easily distinguished by upward-sloping terminal syllables (dashed underline), whereas the second-category playlist contained only unaccented songs with distinctive downward-sloping terminal syllables (dashed underline). Note the repetitive phrases (A) in the first-category playlist to simulate Type-I singing, and low repetition of phrases (B versus C) in the second-category playlist to simulate Type-II singing.

about pairing status, and can be used as location-based and performance-based cues for habitat selection. For brevity, we refer to treatments as: (1) first-category singing mode and (2) second-category singing mode treatments.

We used RavenPro 1.4 (Bioacoustics Research Program 2011) to remove extraneous noise (e.g., anthropogenic sounds or heterospecific song), and then constructed a one-hour playlist for each treatment. To avoid possible confounding effects of song type sharing in second-category singing mode (e.g., Beebee, 2002; Gordinho et al., 2015), we included six songs from six different males for each playlist (i.e., exemplars) such that song type variation was equal in first- and second-category treatments. We randomly assigned the order of exemplars to avoid habituation to playback, but in the first-category playlist included duplicates of exemplars in a series to simulate the repetitive nature of first-category singing (Spector, 1991; Beebee, 2002, 2004; Figure 1). Playlists consisted of 2–3 min of song interspersed with 2–3 min of silence to avoid habituation to playbacks and to mimic nat-
ural singing behaviour of territorial males (e.g., Ward & Schlossberg, 2004; Andrews et al., 2015). Playlists were adjusted to peak amplitude in order to standardize amplitude across exemplars so that all broadcast at similar volumes; we did not use filters on either playlist.

We quantified yellow warbler abundance at each site by conducting weekly 10-min point counts after playbacks started (5 May through 1 July 2014, \( n = 8 \) surveys per site) to correspond with breeding activity of yellow warblers at our sites. At each site, we conducted two point counts, one at the playback station and one >300 m away in a random direction to ensure independence. Sites were surveyed simultaneously by four people, with one person per site conducting both counts. To improve detection, we turned playbacks off during counts. Detection likely did not differ between treatments, as yellow warblers do not seem to change vocal behaviour in response to different singing mode categories (such as song rate or song type sung; Beebee, 2004). We conducted counts from sunrise until 1000 h and recorded all yellow warblers seen or heard within 100 m of each sampling point. During counts, we also recorded whether individuals within earshot used accented (location-based social cue) or unaccented singing (performance-based social cue) to quantify the amount of natural second-category singing. Of the 613 detections where males sang, 20% used both accented and unaccented singing. For these cases, we categorized the song as a performance-based social cue because mixed accents likely indicates successful pairing (Fickens & Fickens, 1965; Morse, 1966; Bankwitz & Thompson, 1979). We added the total number of individuals singing accented and unaccented songs during the two counts at each site, and then calculated the ratio of unaccented to accented singing per site visit to represent relative amounts of unaccented singing at sites in analyses (herein referred to as ‘males using unaccented song’). Sampling order was rotated each week to ensure all sites were sampled early in the morning at least once. We did not conduct point counts during high winds or heavy rain. For statistical analyses, we used average number of yellow warblers observed per site visit as the metric for abundance.

2.4. Statistical analyses

Count data were not normally distributed and variance was unequal across treatments. Thus, we built a generalized linear mixed model fitted with a Poisson distribution with site treated as a random factor. We used individual
counts at sites as the response variable and treatment, site area, males using unaccented song, and all 2-way interactions (treatment × unaccented song, treatment × area, area × unaccented song) as main effects. Initially, we also included sampling week in the model to assess if responses to treatments changed over time, but removed the term and all interactions as none were significant ($F_{1,2,669} = 0.01–1.38$, $p = 0.24–0.98$). To determine if our three treatments significantly differed from one another in yellow warbler abundance, we contrasted least squares mean estimates for each treatment, while centring area and unaccented song (Schielzeth, 2010). We built all models in SAS 9.3 (SAS Institute, Cary, NC, USA).

3. Results

Yellow warbler abundance was greater at sites where second-category song was played (Figure 2), as well as where a higher proportion of males were singing unaccented song (Figure 3, Table 1). There was a significant difference in yellow warbler abundance between the treatments (least-squares mean estimate ± SE; silent: $−1.35 ± 0.20$, $p < 0.001$; first-category: $−0.64 ± 0.11$, $p < 0.001$; second-category: $−0.59 ± 0.11$, $p < 0.001$; Figure 2). There were twice as many yellow warblers at second-category

![Figure 2](image-url). Mean yellow warbler abundances, measured via weekly point counts at 44 playback treatment sites in 2014. The bar graph is of actual mean estimates from the data. Bars represent standard error.
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Figure 3. Regression of mean yellow warbler counts, measured via weekly point counts at 44 playback treatment sites in 2014, on the proportion of males at sites using unaccented song (with regression lines, $R^2$ coefficients), where x-marks indicate silent controls sites with no playback (dashed–dotted line), circles first-category song treatment sites (dashed line) and triangles second-category song treatments sites (solid line). Points are actual mean estimates from the data. Bars represent standard error.

Singing mode treatment sites than silent control sites; warblers were $\sim$20\% more abundant at second-category song treatment sites than first-category singing mode sites (Figure 2). There were also significant interactive effects between treatment and males using unaccented song on yellow warbler abundance. Specifically, yellow warblers abundance was highest at second-category singing mode treatment sites where more males sang unaccented song (i.e., natural second-category singing) compared to other treatments (Figure 3). Yellow warbler abundance was not correlated with the area of a site ($R = 0.16$, $p = 0.28$; Table 1). However, interactions between area and treatment, as well as between area and males using unaccented song did influence yellow warbler abundance (Table 1). Yellow warblers were most abundant at sites where more unaccented songs are present (Figure 3), and of these sites, the largest second-category song treatment areas had the most yellow warblers (Figure 4).
Table 1.
Generalized linear mixed model results regressing counts of yellow warblers at sites on playback treatment (first-category song, second-category song or silent controls), relative proportion of males singing unaccented song at sites (unaccented song) and site area (ha).

<table>
<thead>
<tr>
<th>Effect</th>
<th>Estimate</th>
<th>SE</th>
<th>df_{num, denom}</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.25</td>
<td>0.16</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Treatment</td>
<td>–</td>
<td>–</td>
<td>671, 2</td>
<td>7.96</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Silent</td>
<td>−0.84</td>
<td>0.21</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>First-category</td>
<td>−0.48</td>
<td>0.21</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Unaccented song</td>
<td>−2.28</td>
<td>0.22</td>
<td>671, 1</td>
<td>222.17</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Area</td>
<td>−0.05</td>
<td>0.01</td>
<td>671, 1</td>
<td>0.22</td>
<td>0.64</td>
</tr>
<tr>
<td>Area × Treatment</td>
<td>–</td>
<td>–</td>
<td>671, 2</td>
<td>20.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Silent</td>
<td>0.13</td>
<td>0.02</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>First-category</td>
<td>0.04</td>
<td>0.01</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Unaccented song × Area</td>
<td>0.05</td>
<td>0.01</td>
<td>671, 1</td>
<td>18.77</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Unaccented song × Treatment</td>
<td>0.05</td>
<td>0.01</td>
<td>671, 2</td>
<td>4.92</td>
<td>0.01</td>
</tr>
<tr>
<td>Silent</td>
<td>0.78</td>
<td>0.26</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>First-category</td>
<td>0.25</td>
<td>0.24</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Regression estimates, standard error (SE) and degrees of freedom (df: numerator, denominator) are given for each model. Second-category song treatments served as the reference level for regression estimates.

Figure 4. Modelled estimates from regression of mean yellow warbler counts on the area of the site (ha), where x-marks indicate silent controls sites with no playback (dashed–dotted line), circles first-category song treatment sites (dashed line) and triangles second-category song treatments sites (solid line). Points are mean estimates from the regression model. Bars represent standard error.
4. Discussion

Yellow warblers appear to distinguish singing mode categories as different sources of social information and select breeding habitat based on the category present. Sites with high numbers of males using unaccented song had more yellow warblers, providing further support for the hypothesis that yellow warblers select habitat based on the type of social cue present, specifically by choosing habitat with performance-based social cues, rather than location-based social cues.

Many studies demonstrate that songbirds use both location-based and performance-based social cues to select breeding habitat with (reviewed in Szymkowiak, 2013). Moreover, both theoretical models (Doligez et al., 2003) and other playback experiments (e.g., Betts et al., 2008) demonstrate that songbirds rely more on performance-based social cues than location-based social cues for habitat selection. Often times, however, performance-based social information is only available during the post-breeding season and is inaccessible to most individuals (Nocera et al., 2006; Betts et al., 2008; Rushing et al., 2015). Male yellow warblers arrived at our sites in late-April, and some males paired with females as soon as they arrived the first week of May. Males continue to arrive/pair throughout May, with peak-nesting/territory defence occurring late May through early June. Nesting slows throughout June, and the breeding season ends with territories breaking down in early July (J.K.K., personal observation). Thus, our results suggest that performance-based social cues are as available during the pre-breeding season as location-based social cues are for habitat selection (late April through early May in our system), specifically in the form of second-category singing mode.

Second-category singing mode may not be available to first-arriving males, and performance-based social cues will become more prevalent later in the season. As the breeding season progresses, individuals may switch to using other social cues more readily available later in the season, such as fledgling activity (Betts et al., 2008; Kelly & Schmidt, 2017) or post-breeding singing activity (Nocera et al., 2006; Betts et al., 2008; Farrell et al., 2012). These other social cues would be particularly useful to individuals prospecting for future breeding locations during the post-breeding season (e.g., Betts et al., 2008; Pärt et al., 2011). With our results, we cannot determine if yellow warblers prioritized pre-breeding performance-based social cues (second-category singing mode, in this case) over other social
cues available throughout the entire breeding season. In several instances, however, we detected males at our treatment site before any nestlings or fledgling were present (J.K.K., personal observation). Future studies could test if second-category singing mode ‘trumps’ other sources of social information indicative of habitat quality (sensu Betts et al., 2008), or if songbirds prioritize pre- over post-breeding performance-based social cues for habitat selection.

We only altered one song characterization, singing mode category, to serve as location-based and performance-based social cues, but male song contains even greater variation that songbirds undoubtedly recognize and respond to. Many male songbirds attract mates by changing acoustic characteristics (e.g., frequency modulation, song length, song matching; Beecher et al., 2000; Searcy & Beecher, 2009; Searcy et al., 2014), and switch between song types to signal aggression towards territorial intruders (Byers, 1996; Hof & Podos, 2013). For example, a similar experiment found that songbirds treat male song quality as a social cue for habitat selection and preferentially settle where poor-quality song is broadcast (Szymkowiak et al., 2016). In effort to control for all other song characteristics that could affect settlement decisions (e.g., Szymkowiak et al., 2016), we used the same playlist at all sites within a treatment. By using the same playlists, there could have been qualities other than singing mode category specific to the songs we chose that we were unaware of. A more robust approach could be to play a variety of exclusive second-category and first-category singing mode playlists at sites (see Kroodsma et al., 2001). This design, however, inevitably introduces greater variation due to the many different acoustic characteristics, and makes it challenging to associate social information with particular song features. Future studies might work to resolve this issue by using species with two simple song categories whose song has been intensively studied. Similarly, with our design we cannot tease apart whether individuals settled used unaccented singing or the Type-II singing mode as the performance-based social cue in our second-category song treatment. Although more research is needed to address the specific acoustic characteristics songbirds use for habitat selection, our experiment takes the first step towards understanding how song variation may be distinguished as location-based and performance-based social cues during the habitat selection process.

Another area of study worth investigating is sex-specific habitat selection in response to songs. This study focused solely on adult breeding males, as
only 7% of the 712 yellow warbler detections were female. Females eventually settle in the same location as males, but may show different settlement responses to song categories due to sex-specific audiences commonly linked to each singing mode category (e.g., first-category for females, and second-category for males; Kroodsma et al., 1989; Spector, 1991; Byers, 1996). For example, if females prioritize their own pairing success with a social mate, then habitat with more first-category singing mode prevalent could be more attractive to females looking for unpaired males. Similarly, age-specific differences in habitat selection could also occur. Second-category singing mode, for example, may be more readily available to second-years individuals (i.e., individuals experiencing their first breeding season), which often arrive 1–2 weeks later than adults (e.g., Lozano et al., 1996; Stewart et al., 2002), presumably when adults have paired and switched to second-category singing mode. It also possible that some individuals do not attend to singing mode categories at all when selecting breeding habitat, but instead use site-fidelity and return to the same breeding sites regardless of social cues present. Site-fidelity likely influenced settlement decisions at our sites given that up to 40% of the bird may be returning individuals (Yezerinac et al., 1996; Cilimburb et al., 2002). Determining how sex, age and personal experience (particularly site-fidelity) influence the types of social cues used for habitat selection would be a fruitful direction in this field.

From the perspective of a male prospecting for a breeding location, there are potential costs and benefits to using second-category singing mode as a performance-based cue for settlement decisions. For benefits, if a male is present and successfully attracted a female, then the habitat is leastwise high enough quality for a female to settle and support a nesting attempt. In addition, the presence of other females could provide extra-pair mating opportunities that often increase with increasing female densities (e.g., Westneat & Sherman, 1997). Extra-pair mating is common among yellow warblers (Hobson & Sealy, 1989; Yezerinac & Weatherhead, 1997; Grunst & Grunst, 2014), as well as other species with two singing mode categories (e.g., wood warblers: reviewed in Spector, 1992; sparrows: Groschupf, 1985; Lohr et al., 2013) that exhibit some level of extra-pair paternity (reviewed in Westneat & Stewart, 2003). In terms of costs, established males could also cuckold the male settling nearby (e.g., Balsby & Dabelsteen, 2005). Likewise, competition for space, food, and mates (e.g., Rodenhouse & Holmes, 1992; Richmond et al., 2011) could be greater at sites with more performance-based
social cues such that later arriving males may be at a competitive disadvantage (sensu the ‘mate opportunity’ and ‘rank advantage’ hypotheses on male arrival times; reviewed in Kokko et al., 2006).

The male broadcasting second-category song also faces potential costs and benefits of males settling near them. The cost of attracting more males in the vicinity that in turn use second-category singing mode is likely lower than cost of not using second-category singing mode while the male’s female is nesting. In larger patches of habitat, second-category singing mode should not be costly due to fewer crowding effects (Fretwell & Lucas, 1970; Holmes et al., 1996). That is, with ample space for territories, males could afford to compete with males settling in response to second-category singing. Indeed, we found significant interactions between area and song category treatment, and between area and amount of unaccented singing by males (Table 1). These interactions could indicate that second-category singing mode, either produced by singing males or used by males assessing social cues for settlement decisions, mostly occurs when there enough space to avoid negative density-dependent effects (Fretwell & Lucas, 1970; Holmes et al., 1996).

We found a positive correlation between yellow warbler abundance and the amount of unaccented singing by males (i.e., natural second-category singing), with highest abundances and amounts of unaccented song occurring at second-category treatment sites (Figure 3). With our data, we cannot determine if increased abundances at second-category singing mode treatment sites caused males to use unaccented singing, or if our second-category singing mode treatment caused males to sing more unaccented song, which turn attracted more conspecifics. Other studies on wood warblers, however, could shed light on a mechanistic explanation for this correlation as well as the settlement responses our experiment induced. In other wood warblers, males use second-category singing during male-male aggressive interactions (Byers, 1996; Hof & Podos, 2013). Thus, either crowding effects or ‘perceived male-male aggression’ from the playback could have caused males to sing more unaccented song. There may be a positive feedback loop to second-category singing mode: more individuals result in more second-category singing due to male-male territorial interactions, and more second-category singing attracts more males and lead to more second-category singing. This feedback could ultimately lead to clustered distributions of yellow warblers, a pattern that has been observed in this species (Clark &
Robertson, 1979). In conclusion, we believe this study is the first step in understanding how specific song variants, in this case different singing mode categories, influence habitat selection.

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References


Song categories are social cues for habitat selection


Figure A1. Map of study sites located throughout central and northern Illinois during 2014 (lines indicate county boundaries), where circles indicate first-category song treatments, triangles second-category song treatments, and x-marks silent controls with no playback. Site sample sizes by county were as follows: Champaign \((n = 4)\), DeKalb \((n = 2)\), DeWitt \((n = 1)\), DuPage \((n = 9)\), Fulton \((n = 1)\), Iroquois \((n = 1)\), Kane \((n = 4)\), Kankakee \((n = 3)\), LaSalle \((n = 1)\), Lee \((n = 1)\), Ogle \((n = 1)\), Macon \((n = 1)\), McHenry \((n = 2)\), McLean \((n = 1)\), Vermilion \((n = 3)\), Will \((n = 3)\) and Winnebago \((n = 6)\). The map was created using ArcGIS version 10.4 (ESRI, Redlands, CA, USA). Map source: Illinois Natural Resources Geospatial Data Clearinghouse, Illinois State Geological Survey, https://clearinghouse.isgs.illinois.edu/data/reference/illinois-county-boundaries-polygons-and-lines (accessed 14 April 2017).