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Fledgling calls are a source of social information for conspecific, but not heterospecific, songbird territory selection

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Abstract. The choice of breeding territory can strongly affect an individual's fitness. Individuals can use information obtained from social cues emitted by other organisms to assess territory quality when making settlement decisions. Social information sourced from cues indicating the current inhabitants' reproductive success (i.e., performance-based cues) can be especially valuable as such cues may directly reveal territory quality. We tested social information use in a songbird system using experimental playbacks of Veery (*Catharus fuscescens*) fledgling calls (evidence of prior nest success) during the postbreeding season. We demonstrated that with year effects considered, Veeries used performance-based social information available during the postbreeding season to select sites for territory establishment in the following year. During the first year of the study, Veeries occupied a greater proportion of plots with experimental broadcast of fledgling calls relative to control plots, whereas Ovenbirds (*Seiurus aurocapilla*), a coexisting heterospecific ground-nesting species, did not. Fledgling call treatments did not have carryover effects that influenced Veery settlement decisions during the second year of the study. Ovenbird abundance varied with treatment combinations between years, but evidence indicating a carryover effect was limited. Our results indicate that postbreeding social information may vary among years for both conspecifics and heterospecifics, therefore highlighting the importance of considering year effects in studies on social information use.

Key words: breeding territory selection; conspecifics; heterospecifics; postbreeding season; social cues; social information; songbird; year effects.

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INTRODUCTION

The decision of where to establish a breeding territory is critical to reproductive success and is therefore under strong selective pressure (Holmes et al. 1996). Territory establishment can be challenging to decision-makers as individuals likely have imperfect information about local habitat quality (e.g., predation risk, resource availability; Koops 2004). To reduce uncertainty, individuals can collect information on the quality of prospective sites to bias their choice when

selecting locations for territory establishment. Thus, individuals can benefit by collecting information on territory quality that can directly influence their breeding success (Valone 2007).

There is growing evidence that individuals collect information on territory quality by observing the outcome of other individuals' choices (i.e., social information, SI; reviewed in Seppänen et al. 2007). Past research demonstrates that SI use for assessing territory quality is widespread across taxa, with individuals using cues sourced from both conspecifics (e.g., arthropods:

Fletcher and Miller 2008, Teng et al. 2012, birds: Danchin et al. 1998, reviewed in Ahlering et al. 2010, herptiles: Stamps 1988, Buxton et al. 2015) as well as heterospecifics (e.g., arthropods: Miller et al. 2013, birds: reviewed in Seppänen et al. 2007, Jaakkonen et al. 2015, herptiles: Pupin et al. 2007, reviewed in Goodale et al. 2010). The early literature on SI suggested that social indicators of reproductive success might be important cues used for territory establishment (e.g., Beletsky and Orions 1987). Among these indicators, performance-based cues (e.g., offspring presence; Wagner and Danchin 2010) may provide more accurate estimates of territory quality compared to non-performance-based social cues (e.g., conspecific presence only). As such, using performance-based cues to select a breeding site may bias settlement within high-quality habitat better than non-performance-based SI cues (Valone 2007).

The postbreeding period is rich with SI sourced from performance-based cues because higher quality territories are more likely to produce offspring (Danchin et al. 2004). Indeed, several studies have demonstrated that birds collect SI for territory establishment by prospecting conspecific as well as heterospecific territories during the postbreeding season for evidence of reproductive success or failure (Danchin et al. 2004). Although there is a growing number of passerine examples of postbreeding SI use (e.g., Arlt and Pärt 2008, Betts et al. 2008), few have manipulated potential sources of postbreeding SI used for territory selection (but see Nocera et al. 2006, Betts et al. 2008, Farrell et al. 2012), and studies rarely extend beyond a single year (see Ward and Schlossberg 2004, Andrews et al. 2015). Hence, it remains unclear how widespread SI use is, especially among songbirds, and to what extent it shapes avian ecology at both the population and community levels.

We designed a playback experiment to manipulate the availability of SI, specifically Veery fledgling calls, across experimental plots to test whether Veeries and Ovenbirds (*Seiurus aurocapilla*), a coexisting heterospecific ground-nesting passerine, use postbreeding SI to assess territory quality for territory selection in the subsequent breeding season. Ovenbirds are subject to the same suite of nest predators as Veeries (Schmidt and Ostfeld 2003a). Thus, Veery fledgling calls

should indicate, on average, a high-quality (i.e., successful) territory option for either species. We therefore hypothesized that Ovenbirds would also use Veery fledgling vocalizations as a source of postbreeding SI for territory selection (e.g., Parejo et al. 2005).

MATERIALS AND METHODS

Study site and species

We conducted our study at the Cary Institute of Ecosystem Studies in Dutchess County, New York, United States. The property contains ~ 325 ha of continuous eastern forest dominated by oaks (*Quercus rubra* and *Q. prinus*) with an understory of oak, sugar maple (*Acer saccharum*), smaller trees (*Ostrya virginiana*, *Carpinus caroliniana*), and multistemmed shrubs (e.g., *Berberis*, *Hamamelis*, *Lonicera*, *Viburnum*). Veeries are low-shrub or ground-nesting migratory thrushes that breed in deciduous forests and riparian habitats across North America (Moskoff 1995). Ovenbirds are obligate ground-nesting warblers that breed in mature mixed deciduous–coniferous forests (Van Horn and Donovan 1994). Both species are common breeding birds throughout the property and initiate breeding in early- to mid-May (J. K. Kelly and K. A. Schmidt, *personal observation*).

Social information playback experiment

Prior to the 2009 breeding season, we randomly assigned one of two postbreeding season treatments (SI and silent control, see below) to 52 experimental plots. We defined the postbreeding season as the time period following both the average peak of breeding activity and first observed fledging date (15 June; J. K. Kelly and K. A. Schmidt, *personal observation*). In 2009 (28 June to 30 July) and 2010 (22 June to 15 July), half of the plots were treated with Veery fledgling vocalizations (SI treatment). We designated the remaining plots silent controls with no playback equipment or sound stimulus during the postbreeding season. Lack of stimulus/equipment in controls was justified based on a previous experiment that demonstrated Veery and Ovenbird responses were not artifacts of equipment or field procedures (Emmering and Schmidt 2011). Playback plots contained two speakers placed 180 degrees apart at a 25 m distance from the plot

center. Plot centers were spaced ~200 m apart (linear distances not accounting for terrain topography, mean: 200.9, max: 228.5, min: 174.1). Treatments were interspersed among plots with minimal clustering (five or fewer speakers ≤ 200 m from one another) such that spatial arrangement likely did not bias results.

Quality recordings of Veery fledglings are difficult to obtain and require close human presence, which may introduce unwanted distress or alarm signaling. Therefore, in 2009 and 2010 we placed a shotgun microphone ~1 m from nests to record nestling begging vocalizations >15 min after the observer had vacated the area. Fledglings from recorded nests were then located within 24 h of fledging to record additional begging calls. We used these recordings as well as fledgling calls provide by the Cornell Lab of Ornithology Macaulay Library to create six unique exemplars used as the postbreeding SI cue in our experiment. Recordings were edited in RavenPro 1.3 (Bioacoustics Research Program 2008) to remove extraneous noise and non-target species vocalizations. Each exemplar consisted of recordings from one of six separate nests containing nestlings near the mean date of fledging (ages between 10 and 14 d, with Veeries typically fledging by day 11; J. K. Kelly and K. A. Schmidt, *personal observation*). Given the source of calls, our recordings may be better considered as cues of fledglings and/or nests surviving to “imminent fledgling” (between 2011 and 2013, only two of 126, or 1.6% nest predation events, occurred on nestlings older than 10 d; J. K. Kelly, *personal observation*). For simplicity, we refer to this treatment as “fledgling” in our study. Playbacks were broadcast daily (barring 1–2 inclement weather days per season) between 07:00 and ~14:00 hours with MP3 players set to loop continuously through a playlist. Playlists contained two 8- to 10-min bouts of fledgling begging and contact calls followed by 20–30 min of silence. Vocal bouts consisted of ~75% vocalizations interspersed with 1–5 s of silence. The pair of playback stations within a plot broadcast identical exemplars, but staggered in time to simulate activity of multiple fledglings at a plot.

Carryover effects

In year two of our experiment, we rotated playback treatments among plots to test for a

carryover effect of SI by creating four combinations of postbreeding season treatments across two years ($n = 13$ per combination): (1) plots treated with SI in year one but not year two, (2) plots treated with SI both years, (3) plots treated with silent controls in year one and SI in year two, and (4) plots treated with silent control both years. We tested for carryover effects by comparing settlement responses in year two across the four treatment combinations. Our response variables (explained below) were collected the year following experimental manipulations, and plots were reassigned treatments. No stimuli were used in 2011 when collecting responses to 2010 treatments.

Cue conflict

Initially, our experiment included prebreeding season playback of Eastern chipmunk (*Tamias striatus*) vocalizations at half the postbreeding SI plots in each year. This playback experiment was designed similar to Emmering and Schmidt (2011), but using the two-speaker setup described in the SI playback experiment rather than using three speakers as in Emmering and Schmidt (2011). The objective was to test whether plots with higher apparent nest predator abundance would be rejected as prospecting sites later in the breeding season (i.e., within-year cue conflict). Based on a randomization test in MATLAB ver. 8.0 (The Mathworks 2012), where we randomized occupancy with respect to treatment (chipmunk treatment vs. silent control) and compared these results with a binomial distribution, we failed to find statistical evidence for a direct effect of the chipmunk treatment on plot occupancy for either Veeries (38.5% vs. 39.7%, chipmunk and control, respectively, $P = 0.734$) or Ovenbirds (57.7% vs. 56.4%, $P = 0.52$; see *Settlement by veeries and ovenbirds* for a description and definition of plot occupancy). Because there was no direct effect of the chipmunk treatment, we did not consider this treatment further and focused instead on the postbreeding season SI manipulation. Empirical evidence strongly suggests predator cues would have a negative effect, if any, on breeding site selection (e.g., Emmering and Schmidt 2011). Therefore, combining data from all SI plots without regard to the chipmunk cue should be neutral to, or weaken, our ability to detect a positive effect of SI on plot occupancy.

Settlement by veeries and ovenbirds

Plot occupancy.—We quantified plot occupancy using nest data to evaluate settlement responses to experimental treatments in years following playbacks (2010 and 2011). For nest data collection, we systematically searched for and monitored Veery and Ovenbird nests within a 100 m radius of all plots from May through July each year. Plots without nests were further targeted for more extensive nest searching independent of treatment. We monitored nests every two to three days to confirm hatch date and nest fate. Only nests active before 15 June (earliest observed fledging date for both species; J. K. Kelly and K. A. Schmidt, *personal observation*) were used in analyses to eliminate possible confounding effects of the current year's fledgling activity (i.e., movement to plots based on within season information). Plots were considered occupied by a species if we located or backdated an active nest within a 100 m radius of plot centers prior to our cutoff date. Suspected renests (e.g., nests located in the same plot, and not overlapping in their activity dates) were excluded from the analyses.

Natural background fledgling activity could vary across plots and influence settlement responses, but this influence was unlikely in our study. During playback years, Veery nest success, and hence fledgling activity, was low throughout the entire study site. The numbers of successful nests, based on all nests with known fates, were 12 of 65 (2009) and 18 of 76 (2010). This corresponds to one successfully fledged nest per 11.8–17.5 ha. As our playback experiment was conducted at a smaller scale than the entire study site, the experiment itself represents a 116% (2009) and 174% (2010) increase in perceived fledgling activity relative to natural conditions over the two-year period (J. K. Kelly and K. A. Schmidt, *personal observation*).

Last, we used a t-test to confirm that long-term occupancy, a surrogate for site quality, did not differ between the two treatments. From 2008 to 2015, exclusive of the experimental response years, the mean number of occupied years was 2.81 ± 0.40 for SI plots and 2.65 ± 0.46 for silent plots; $t_{50} = 0.86$, $P > 0.70$.

Adult songbird abundance.—We quantified the abundance of adult Veeries and Ovenbirds on site by conducting two 15-min point counts at all

plots each year (between 26 May 2010 to 9 June 2010, and 6 June 2011 to 18 June 2011). We assumed singing males at the plots represent breeding individuals because count data and territory counts are frequently positively correlated at similar scales in forest systems (e.g., Toms et al. 2006). Additionally, point count data can account for non-breeding adults that may not be nesting in plots (e.g., Pagen et al. 2002). Each year, point counts occurred from 05:00 to 09:00 hours and were separated by 5–10 d. We recorded all individuals seen or heard within 50 m of plot centers, placing them into two distance categories (<25 and 25–50 m). For the second round of counts, we reversed the point count order of plots to ensure each plot was surveyed shortly after sunrise. For analyses, we used total annual count for each plot.

Statistical analyses

We tested for differences in plot occupancy by building separate generalized linear mixed models for Veeries and Ovenbirds in SAS ver. 9.3 (SAS Institute 2012, Cary, North Carolina, USA). For both species, we first tested for post-breeding SI treatment effects in Year 1, with nest presence at fledgling plots in 2010 as a binary response variable and Year 1 treatment as the main effect. To test for carryover effects, we used nest presence at plots in 2011 as a binary response variable and Year 1 treatment, Year 2 treatment, and their interaction as main effects to test for different responses among the four between-year treatment combinations. We used a dichotomous variable rather than raw nest counts to represent which plots were occupied by breeding adults. For each test, we treated plot as a random effect to account for non-independence, but considered nests as independent of one another. Treating plot as the unit of replication produced the same qualitative results as treating nest as the unit of replication.

To evaluate changes in Veery and Ovenbird abundances in response to treatments, we built separate general linear models for Veeries and Ovenbirds in SAS ver. 9.3 (SAS Institute 2012, Cary, North Carolina, USA) to first test for responses to postbreeding treatments in Year 1, and to then test for carryover effects from Year 1 and Year 2 treatments. For Veeries and

Ovenbirds, we built generalized linear models with individual counts at plots in 2010 as the response variable and Year 1 treatment as the main effect. To test for carryover effects, we used Veery or Ovenbird counts at plots in 2011 as the response variable with Year 1 treatment, Year 2 treatment and their interaction as main effects.

RESULTS

General occupancy patterns

At the plot level, Veeries occupied (i.e., nests ≤ 100 m from plot center) 21 and 22 plots in 2010 and 2011, respectively. Plot occupancy by Veeries in 2011 was significantly associated with occupancy status in 2010 (Pearson's $\chi^2 = 12.24$, $df = 1$, $P < 0.005$); Veeries occupied 15 plots in both years, whereas 24 plots were never occupied. Ovenbirds occupied 28 and 31 plots in 2010 and 2011, respectively. Sixteen plots were occupied in both years, and nine plots were never occupied (Pearson's $\chi^2 = 0.57$, $df = 1$, $P = 0.45$). Based on plot co-occupation, Veeries and Ovenbirds did not appear to influence each other's settlement behavior. Both species co-occurred on 10 plots in 2010 and 14 in 2011. The expected number of dually occupied plots in 2010 and 2011 was 11.3 and 13.1, respectively.

Social information use (2010 plot occupancy and abundances)

Year 1 SI treatments (i.e., the postbreeding season treatments of 2009) strongly influenced the likelihood of Veeries nesting in 2010 (Table 1a). Twenty-five Veery nests were located in SI plots compared to only six nests in control plots (Fig. 1). Ovenbird nests showed no significant response to treatments (Table 1a) and were randomly distributed with respect to SI cues (Fig. 1). Based on abundance analyses, neither Veeries nor Ovenbirds showed significant responses to Year 1 treatments (Table 2a).

Social information use and carryover effects (2011 plot occupancy and abundances)

Veery and Ovenbird 2011 plot occupancy was not related to Year 2 treatments (i.e., SI effect; Table 1b). Veery plot occupancy in 2011 in relation to Year 1 treatments (i.e., carryover effects) was marginally non-significant, but was not significantly related to Year 1/Year 2 treatment

Table 1. Generalized linear mixed model results regressing (a) the presence of Veery and Ovenbird nests at plots in 2010 on Year 1 treatments (fledgling or silent) and (b) nest presence at plots in 2011 on year 1 treatments, Year 2 treatments, and their combinations (four total) to test for carryover effects.

Effect	Num df	Denom df	F ratio	P
(a) Postbreeding SI (year 1)				
Veery model	1	50	8.640	0.005
Ovenbird model	1	50	0.690	0.410
(b) Carryover effects (year 2)				
Veery model				
Year 1 treatment	1	48	3.650	0.062
Year 2 treatment	1	48	0.020	0.902
Year 1 \times year 2 treatments	1	48	0.840	0.364
Ovenbird model				
Year 1 treatment	1	48	1.830	0.183
Year 2 treatment	1	48	0.000	0.967
Year 1 \times year 2 treatments	1	48	0.050	0.825

Notes: Separate models were built for each species in each test. Numerator (num), denominator (denom), and degrees of freedom (df) are given for each model.

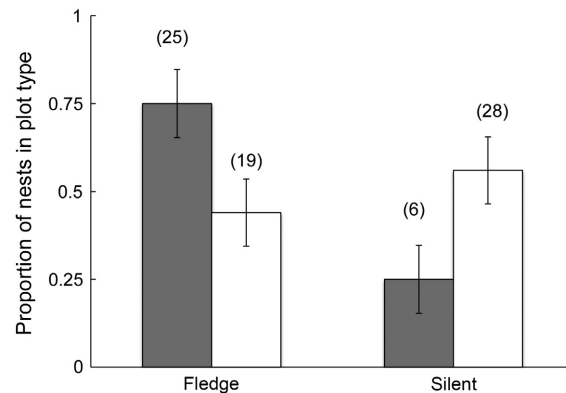


Fig. 1. Proportion of Veery (gray) and Ovenbird (white) nests at fledgling plots and silent controls in 2010, based on nest presence/absence. Error bars represent standard error. Numbers in parentheses represent nest numbers at each treatment.

combinations (Table 1b, Fig. 2). Ovenbirds showed no relationship between 2011 plot occupancy and Year 1 treatments or Year 1/Year 2 treatment combinations and 2011 plot occupancy (Table 1b, Fig. 2).

Based on the abundance analysis, there was no significant difference in 2011 Veery abundance related to Year 1, Year 2, or Year 1/Year 2 treatment

Table 2. Generalized linear model results regressing (a) counts of Veeries and Ovenbirds at plots in 2010 on Year 1 treatments (fledgling or silent) and (b) Veery/Ovenbird counts in 2011 on Year 1 treatments, Year 2 treatments, and their combinations (four total) to test for carryover effects.

Effect	df	Estimate	SE	X ²	P
(a) Postbreeding SI (year 1)					
Veery model					
Intercept	1	0.342	0.194	3.110	0.078
Treatment	1	0.050	0.276	0.030	0.855
Ovenbird model					
Intercept	1	0.693	0.159	19.110	<0.0001
Treatment	1	0.293	0.213	1.890	0.170
(b) Carryover effects					
Veery model					
Intercept	1	-0.167	0.322	0.270	0.604
Year 1 treatment	1	0.435	0.413	1.110	0.292
Year 2 treatment	1	0.013	0.446	0.000	0.977
Year 1 × year 2 treatments	1	0.067	0.577	0.010	0.907
Ovenbird model					
Intercept	1	1.149	0.158	52.820	<0.0001
Year 1 treatment	1	-0.669	0.272	6.070	0.014
Year 2 treatment	1	-0.354	0.241	2.160	0.142
Year 1 × year 2 treatments	1	0.886	0.371	5.690	0.017

combinations (Table 2b). For Ovenbirds, however, there was a difference in 2011 abundance related to Year 1/Year 2 treatment combinations (Table 2b): There were more Ovenbirds present at fledgling/fledgling and silent control/silent control treatment combinations than at plots treated with fledgling/silent control combinations (Fig. 3).

DISCUSSION

Our experimental results support the hypothesis that Veeries use postbreeding SI from Veery fledgling calls when establishing breeding territories in the subsequent year. Specifically, Veeries were more likely to occupy plots treated with fledgling calls than those with silent controls. We only found statistical support for SI use in the first of a two-year study. The lack of an effect of SI in Year 2 may have several causes, including differences in plot quality and carryover effects. In

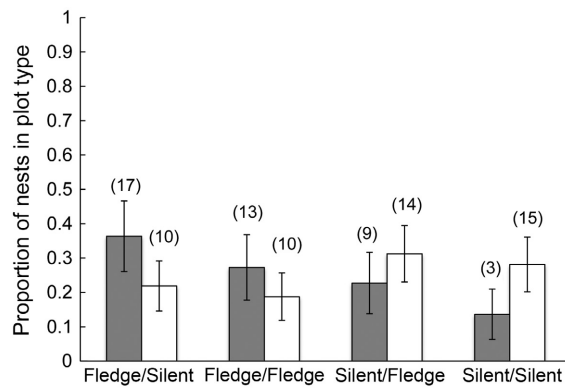


Fig. 2. Proportion of Veery (gray) and Ovenbird (white) nests at plots in 2011 based on Year 1/Year 2 treatment combinations across plots. Error bars represent standard error. Numbers in parentheses represent nest numbers in each treatment.

similar studies, individuals have been shown to favor SI over environmental measures of habitat quality (e.g., vegetation cues; see Arlt and Pärt 2007, Betts et al. 2008). Point count data showed no significant difference in the mean number of recorded individuals across treatments. It is possible that not accounting for imperfect detection in our analysis could have skewed results (e.g., MacKenzie et al. 2002). We consider occupancy based on nests, however, to be more accurate indicators of territory establishment, and reflects decision-making by females. Unmated males without territories can be scored during point counts (e.g., Pagen et al. 2002), which could inflate detections, independent of treatments.

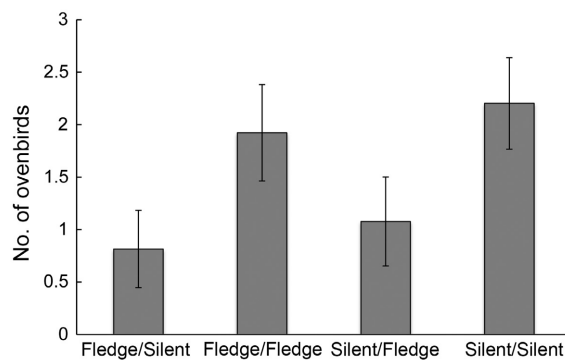


Fig. 3. Counts of Ovenbirds in 2011 at Year 1/Year 2 treatment plot combinations. Error bars represent standard error.

Based on plot occupancy data, support for carryover effects in response to Year 1 treatments was marginally non-significant ($P = 0.062$, Table 1b). In addition to this direct test, we found that site status in 2011 was not independent of its status in 2010. Only 13 of 52 plots changed status between years; specifically, 15 of 21 plots occupied in 2010 were occupied in 2011. This pattern could result from site fidelity by individuals that used SI in 2010 and returned to the same site in 2011 independently of treatment. Such a response is plausible as site fidelity is common in songbirds (e.g., Hoover 2003, Schlossberg 2009, Piper 2011). Additionally, individuals may have used conspecific presence in 2010 (habitat copying, Parejo et al. 2005, or conspecific attraction, reviewed in Ahlering et al. 2010) as a cue for selecting sites in 2011, which would have the effect of dampening the carryover effects SI treatments had on settlement decisions. Unfortunately, we had too few nests with known parents to evaluate either of these hypotheses.

Based on plot occupancy from nesting data, we did not find evidence that Ovenbirds established territories using SI from Veery fledgling vocalizations. Point count data, however, indicated that Ovenbird abundance in 2011 was negatively related to Year 1 and Year 2 treatment combinations. Specifically, Ovenbirds were less abundant at plots treated with fledgling and silent controls across years compared to plots treated with just fledgling or silent controls throughout the study, suggesting carryover effects from SI in previous years negatively influenced Ovenbird settlement decisions (Fig. 3). Adults, however, were equally abundant at plots treated with silent controls each year as at those treated each year with fledgling calls (Fig. 3). We do not have a biological rationale for this response. It is possible this result is spurious and driven by unmeasured factors, such as environmental cues associated with high-quality habitat or social cues from conspecifics. Indeed, since finishing this project, there has been growing evidence that Ovenbirds select habitat using conspecific presence (Thériault et al. 2012, DeJong et al. 2015). Nonetheless, we cannot rule out the possibility that our treatments may have had carryover effects on Ovenbird abundances at plots. Similar experimental studies on songbird communities found both repulsion and attraction

by heterospecific social cues (e.g., Fletcher 2007, Forsman et al. 2008).

For Veeries, our statistical evidence for a sequential response to an SI cue (Year 1) is stronger than for a carryover effect (Year 2). We were not able to replicate the positive effect of postbreeding SI use in the second year, possibly because of a carryover effect. Social information use experiments in birds are dominated by single-year studies (e.g., Betts et al. 2008). Szymkowiak's (2013) review of the literature of SI use among songbirds found that of the 12 studies documenting a short-term (within season) attraction to experimental conspecific cues, only one tested for, and confirmed, a long-term effect (Ward and Schlossberg 2004, but see Andrews et al. 2015). The remaining 11 studies lacked relevant data to examine long-term effects. Postbreeding season SI manipulations are even less common than within season. With the exception of the present study, we are not aware of any postbreeding SI manipulation studies that have been conducted or monitored beyond a single breeding season. This is an important omission, especially because mechanisms of habitat use, such as habitat familiarity (e.g., Piper 2011), predict that carryover effects may arise. That is, dispersing individuals and first-time breeders that initially choose a breeding territory based on habitat and social cues may exhibit long-term tenure. If so, carryover effects may obscure multiyear SI manipulations. We thus recommend that not only should researchers replicate SI experiments over time, but should also design experiments to test for carryover effects, ideally with a large population and individually marked individuals.

In conclusion, our results demonstrate between-season conspecific SI use in Veeries and strongly suggest carryover effect to the following year. Significant year effects noted in our study highlight the importance of conducting multi-year studies in playback experiments. Most previous studies demonstrating SI use for territory selection in songbirds have consisted of only one year for playback experiments (e.g., Betts et al. 2008, Parejo et al. 2012) or do not consider year effects on responses to treatments (e.g., Nocera et al. 2006, Arlt and Pärt 2008). The postbreeding season remains a relatively neglected part of the avian life cycle, and we hope our experiment

will motivate others to explore this period in the avian life cycle.

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