

RESEARCH ARTICLE

Conspecific attraction for conservation and management of terrestrial breeding birds: Current knowledge and future research directions**Jonathon J. Valente^{1,2,*}, Christa L. LeGrande-Rolls³, James W. Rivers¹, Anna M. Tucker⁴,
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ABSTRACT

Conspecific presence can indicate the location or quality of resources, and animals settling near conspecifics often gain fitness benefits. This can result in adaptive conspecific attraction during breeding habitat selection as demonstrated in numerous terrestrial, territorial birds. There is growing interest in using simulated conspecific social cues (e.g., decoys, broadcasted vocalizations) to manage bird distributions, yet it remains unclear when this approach is likely to succeed. We reviewed published studies to evaluate whether the strength of conspecific attraction in terrestrial birds is mediated by characteristics of species (life history traits), simulated cues (e.g., timing and duration), sites (e.g., quality), and how conspecific attraction was measured. We identified 31 experiments that simulated social cues and compared conspecific settlement between treatment and control sites. We then used phylogenetically controlled meta-regression to assess the impacts of 19 moderators on settlement. Nearly all species included in these experiments were migratory passerines, and social cues generally had a strong, positive influence on their settlement decisions, as the odds of site occupancy were 3.12× (95% CI: 0.81–11.69) greater in treatment sites relative to control sites. Within this group, conspecific attraction was evolutionarily conserved with $\geq 25.5\%$ (95% CI: 5.1%–65.4%) of the variance in treatment effects explained by phylogenetic relatedness. However, we found no evidence that any covariates influenced the response to social cues, and we posit this stems from limited research specifically designed to identify the mechanisms mediating conspecific attraction. We therefore developed a research agenda that provides a framework for testing mechanistic hypotheses regarding how cue characteristics, species traits, and spatial contexts may mediate attraction to conspecifics. Evaluating these hypotheses will greatly advance the field by helping managers understand when, where, and why simulating social cues can be used to enhance populations of species that are of conservation concern.

Keywords: breeding birds, conspecific attraction, experimental manipulation, habitat selection, meta-analysis, performance information, social information

LAY SUMMARY

- Simulating the presence of terrestrial birds often attracts breeders of the same species, though how this varies among species, simulated cues, or locations remains unknown.
- We reviewed 31 experiments that examined conspecific attraction to simulated social cues in terrestrial breeding birds and tested the effects of 19 variables on attraction.
- These experiments, which focused primarily on migratory songbirds, revealed strong effects of simulated presence on settlement rates, but no strong evidence that any other variables affected settlement rate.
- Simulating social cues such as vocalizations could be useful for managers interested in attracting migratory songbirds, although whether this extends to other terrestrial species remains unknown.
- A greater understanding of how and where to use this technique will improve its utility as a tool for enhancing populations of species of conservation concern.

Atracción conespecífica para conservación y manejo de aves reproductivas terrestres: Conocimiento actual y futuras direcciones de investigación

RESUMEN

La presencia de individuos conespecíficos puede indicar la localización o la calidad de los recursos, y los animales que se instalan cerca de conespecíficos usualmente obtienen beneficios en su adecuación biológica. Esto puede resultar en una atracción conespecífica adaptativa durante la selección de hábitat reproductivo, como se ha demostrado en numerosas aves territoriales terrestres. Hay un interés creciente en usar señales sociales conespecíficas simuladas (e.g., señuelos, transmisión de vocalizaciones) para manejar las distribuciones de las aves, aunque no está claro cuándo es probable que este enfoque tenga éxito. Revisamos estudios publicados para evaluar si la fuerza de la atracción conespecífica en las aves terrestres está mediada por características de las especies (rasgos de la historia de vida), por señales simuladas (e.g., tiempo y duración), o por los sitios (e.g., calidad), y cómo la atracción de los conespecíficos fue medida. Identificamos 31 experimentos que simularon señales sociales y comparamos el establecimiento de conespecíficos entre sitios de tratamiento y control. Luego usamos una meta-regresión filogenéticamente controlada para evaluar los impactos de 19 moderadores de asentamiento. Casi todas las especies incluidas en estos experimentos fueron paserinos migratorios, y las señales sociales generalmente tuvieron una fuerte influencia positiva en sus decisiones de asentamiento, ya que las probabilidades de ocupación del sitio fueron $3.12\times$ (95% IC: 0.81, 11.69) mayores en los sitios de tratamiento que en los de control. Dentro de este grupo, la atracción de conespecíficos fue conservada evolutivamente con $\geq 25.5\%$ (IC: 5.1%, 65.4%) de la varianza en los efectos del tratamiento explicada por la relación filogenética. Sin embargo, no encontramos evidencia de que alguna covariable influenció la respuesta a las señales sociales, y postulamos que esto se deriva de una investigación limitada diseñada específicamente para identificar los mecanismos que median la atracción conespecífica. Por ende, desarrollamos una agenda de investigación que brinda un marco para evaluar hipótesis mecanicistas sobre cómo las características de las señales, los rasgos de las especies y el contexto espacial pueden mediar la atracción hacia los conespecíficos. Evaluar estas hipótesis ayudará a los gestores a entender cuándo, donde y por qué las señales simuladas pueden ser usadas para mejorar las poblaciones de las especies que son de preocupación para la conservación.

Palabras clave: atracción conespecífica, aves reproductivas, información de desempeño, información social, manipulación experimental, meta-análisis, selección de hábitat

INTRODUCTION

Effective management of avian species requires not only creating and restoring the habitat upon which they rely, but also ensuring that such areas are used (Ahlering and Faaborg 2006). Understanding how birds select habitat is thus critical for conserving and managing avian populations. Several decades ago, researchers first used simulated social cues (e.g., vocalizations and decoys) to demonstrate that conspecific attraction influences breeding habitat selection for colonial waterbirds (Kress 1983, Kotliar and Burger 1984, Burger 1988). These methods are now frequently incorporated into contemporary seabird restoration projects and are often considered essential (Jones and Kress 2012). More recent experiments show many terrestrial, territorial species—even those thought to be antagonistic to conspecifics during breeding—are also attracted to conspecific social cues when selecting habitat (Ahlering et al. 2010, Szymkowiak 2013, Buxton et al. 2020). In some cases, this attraction can be so strong that it trumps the importance of habitat structure (Nocera et al. 2006, Fletcher 2007, 2009, Betts et al. 2008, Farrell et al. 2012). As such, there is substantial interest in using social cues to attract non-colonial terrestrial birds to high-quality breeding sites (Ahlering et al. 2010, Schofield et al. 2018, Lewis et al. 2020).

There are numerous potential advantages that stem from being able to attract breeding birds to specific locations; these include making a population less vulnerable to

catastrophic events (e.g., fires or hurricanes), encouraging the use of protected areas, and facilitating range shifts necessitated by changes in climate and land use (Anich and Ward 2017). Indeed, researchers have already used simulated social cues to promote settlement in a habitat that is underutilized because it is on the edge of the species' range (Anich and Ward 2017), contained in small patches (Fletcher 2009), or was recently restored (Schofield et al. 2018). Simulating conspecific presence also tends to be relatively easy and inexpensive (Ahlering et al. 2010) and thus can be implemented across broad spatial scales. As noted in multiple recent reviews, however, there is a need to develop a more mechanistic understanding of the ultimate factors that impact fitness, as well as the characteristics of proximate cues that mediate conspecific attraction in terrestrial breeding birds (Ahlering et al. 2010, Szymkowiak 2013, Buxton et al. 2020, Lewis et al. 2020). This will streamline management by identifying the cases in which simulated social cues are unlikely to attract conspecifics (Bayard and Elphick 2012) and prevent adverse effects such as repulsion of the targeted species (Quilodrán et al. 2014).

Conspecific attraction occurs, in part, because birds require information about the distribution and quality of potential resources when selecting habitat; social information—acquired through interactions with, or observations of, other organisms—can likely be collected more efficiently than nonsocial information, obtained through direct observation of environmental elements (Danchin et al. 2004,

Wagner and Danchin 2010). Although heterospecifics can transmit social information (Seppänen et al. 2007), conspecific social cues indicate the presence of individuals with nearly identical resource requirements (location information) and can even reveal information about their reproductive performance (performance information; Danchin et al. 2004, Wagner and Danchin 2010). In addition, positive relationships between per-capita fitness and conspecific density, known as Allee effects, are relatively common and can arise through mechanisms that include increased mate access, heightened predator vigilance, and augmented genetic diversity (Courchamp et al. 1999, Stephens et al. 1999, Kramer et al. 2009). In fact, Allee effects can be driven specifically by the positive feedback stemming from the distribution of social information (Schmidt et al. 2015). Selecting habitat near conspecifics can thus result in numerous fitness benefits.

Attraction to conspecifics will not always be advantageous, however. Relying on social information alone can decrease individual fitness if social cues are decoupled from habitat quality (Giraldeau et al. 2002, Rieucou and Giraldeau 2011, Schmidt et al. 2015), or if settlement near conspecifics results in increased resource competition (Seppänen et al. 2007, Szymkowiak et al. 2016). Moreover, the reliability of both social and nonsocial information about the distribution and quality of habitat can degrade over space and time (Doligez et al. 2003, Seppänen et al. 2007). Thus, the inclination to settle near conspecifics is likely a function of complex tradeoffs between fitness costs and benefits, personal experience, and environmental heterogeneity (Giraldeau et al. 2002, Doligez et al. 2003, Fletcher and Sieving 2010, Pärt et al. 2011, Rieucou and Giraldeau 2011).

This complexity has led to researchers proposing numerous mechanistic hypotheses regarding how characteristics of species, sites, and treatments might mediate conspecific attraction in terrestrial breeding birds. At the species level, there are multiple life history characteristics that could make conspecific attraction more adaptive and evolutionarily conserved (Table 1, topical area 1). Social information may be more valuable to species that have less time to gather nonsocial information such as those with relatively “faster” life histories (e.g., shorter life spans, larger clutches; Sæther 1988) or migrants that select habitat shortly after arriving on their breeding grounds (Ahlering et al. 2010, Virzi et al. 2012). Social information may be more critical for species that use ephemeral breeding sites (e.g., wetlands, early successional uplands) than those that use habitat more constant in space and time (Ahlering et al. 2010). Indeed, conspecific presence itself may be an important habitat element for species prone to polygamy or breeding aggregations (Mills et al. 2006, Nocera et al. 2006).

Such interspecific differences in life history traits are insufficient, however, to explain all observed heterogeneity in avian responses to simulated social cues. For example,

song broadcast treatments induced settlement of the Black-throated Blue Warbler (*Setophaga caerulescens*) in Michigan (Hahn and Silverman 2007) but not in Vermont (Cornell and Donovan 2010). Intraspecific differences in conspecific attraction may instead be driven by heterogeneity in the biotic and abiotic factors to which local populations are exposed (Table 1, topical area 2). At a broad scale, social information may be more important for identifying habitat in areas with low conspecific densities (e.g., the edge of geographic ranges) or further from the equator where breeding seasons are shorter (Ahlering et al. 2010). At more local scales, attraction to conspecifics can trade off against competition for resources, and responses to simulated social cues may be mediated by patch size and whether patches are actually used by wild conspecifics (Ahlering and Faaborg 2006, Fletcher 2009). Habitat selection is also unlikely to occur without some personal assessment of resources, and social information may be trumped by nonsocial information in low-quality habitats (Nocera et al. 2006).

In addition, there are numerous characteristics of the simulated cues themselves that could mitigate how individuals within a species respond (Table 1, topical area 3). For instance, cues may be ineffective if they are asynchronous with prospecting behavior, which could occur in either the pre-breeding or post-breeding periods. The duration of treatment applications could also influence how many individuals will encounter them (Betts et al. 2008, Ahlering et al. 2010). In addition, conspecific attraction experiments almost always use vocalization broadcasts in treatments, but some have hypothesized that visual stimuli might be equally important (Ward and Schlossberg 2004). Furthermore, treatment characteristics such as simulated conspecific density (Kelly et al. 2018), whether the cues imply the quality of the individual or habitat (Betts et al. 2008, Szymkowiak et al. 2016), and even the geographic origin of the cue (for species with geographically variable vocalizations; Ahlering et al. 2010) could mediate how prospectors perceive and respond to the information.

In the last decade, several reviews (Ahlering et al. 2010, Szymkowiak 2013, Buxton et al. 2020) have qualitatively examined the role of conspecific attraction in habitat selection of terrestrial breeding birds. None, however, has quantitatively assessed the mechanisms underlying this attraction. Here, we review previously published studies that evaluated the settlement of terrestrial breeding birds in response to experimentally simulated social cues. We aggregated the mechanistic hypotheses proposed in these studies and associated subject reviews (Ahlering et al. 2010, Szymkowiak 2013, Buxton et al. 2020, Lewis et al. 2020) and grouped them into broad topical areas to examine if and how conspecific attraction is mediated by characteristics associated with the species, sites, and treatments being evaluated (Table 1). We also tested whether the strength of responses to social cues could be explained by variability in

TABLE 1. A summary of 4 broad topical areas with key hypotheses and their associated predictions regarding how focal species, study location, treatment, and response characteristics could mediate conspecific attraction in avian habitat selection. We use the term “Moderators” to describe the covariate used to test the hypotheses in the meta-regression (Table 2).

Topical area/focal hypothesis	Predicted effect on conspecific attraction	Moderators
(1) <i>Conspecific attraction is mediated by species traits</i>		
Attraction to conspecifics is an evolutionarily derived trait	Response more similar with decreasing taxonomic distance	Phylogeny
Short-lived species have less time to acquire nonsocial information	Decreases with life span	Longevity
Residents have more time to personally evaluate habitat than migrants	Greater for migrants than residents	Migratory status
Settling near conspecifics increases mating opportunities	Greater for polygamous species	Polygamy
Aggregated breeding clusters facilitate the use of conspecific presence cues	Greater for species that cluster	Clustered breeding
Ephemeral habitats are more difficult to locate and temporally variable	Greater for species with ephemeral habitat	Habitat preference
Late-arriving individuals are more likely to cue on conspecific presence	Greater for asynchronous breeders	*
(2) <i>Conspecific attraction is mediated by treatment site locations and characteristics</i>		
To avoid direct competition, individuals settle at a safe distance from the putative conspecific	Increases with site size (i.e. area sampled)	Size
To maximize benefits, individuals settle close to putative conspecifics	Decreases with site size (i.e. area sampled)	Size
Previously occupied sites are closer to carrying capacity and can support fewer new individuals	Greater in previously unoccupied sites	Previous occupation
Individuals personally assess habitat quality after locating conspecifics	Greater in quality habitat	Site quality
Individuals are more likely to use conspecific cues in regions with shorter breeding seasons	Increases with distance from the equator	Latitude
Conspecific cues provide little habitat quality information when habitats are regionally saturated	Decreases with regional abundance	Local distribution
(3) <i>Conspecific attraction is mediated by cue characteristics</i>		
Individuals assess habitat in the post-breeding period	Greater for post-breeding cues	Time of year
Individuals assess habitat in the pre-breeding period	Greater for pre-breeding cues	Time of year
Local conspecifics provide better information about local habitat	Greater for locally sourced cues	Signal origin
Performance information is more valuable information than location cues alone	Greater for performance information than location cues	Cue type
Treatments applied for longer periods are encountered by more potential prospectors	Increase with playback duration	Playback duration
Prospectors are attracted to high-density aggregations of conspecifics	Increase with density of simulated conspecifics	Density
Prospectors minimize competition by avoiding high-density aggregations	Decrease with density of simulated conspecifics	Density
Prospectors rely on visual cues to assess conspecific presence	Greater in studies using decoys	Decoys
Settling near high-quality conspecifics maximizes potential fitness benefits	Greater for cues from high-quality males	Conspecific quality
Settling near low-quality conspecifics minimizes competition (direct or indirect)	Greater for cues from low-quality males	Conspecific quality
(4) <i>Conspecific attraction metrics are influenced by researcher measurement approaches</i>		
More individuals are detected than settle at a site	Greater for studies that measure detections vs. settlement	Response measured
Sampling for longer periods increases the probability of detecting response	Increases with monitoring duration	Monitoring duration
Inexperienced individuals rely more on social cues	Stronger for yearlings than older birds	*

*Sufficient information for testing this hypothesis was lacking.

how responses are measured across studies (Table 1, topical area 4). We evaluated each hypothesis using phylogenetically controlled meta-regression (Nakagawa and Santos 2012) and used our findings to develop a research agenda for broadening our understanding of how terrestrial birds use social cues when selecting habitat. Adoption of this research agenda will maximize the conservation benefits of these methods in management settings (Farrell et al. 2012, Anich and Ward 2017, Schofield et al. 2018) and enhance our understanding of fundamental components of how birds use conspecific social information.

METHODS

Literature Review and Study Inclusion Criteria

We summarized evidence for conspecific attraction to breeding sites from studies that experimentally simulated conspecific social cues. These studies represent the most statistically rigorous tests of conspecific attraction, allow for direct quantification of social cue characteristics, and are of direct relevance to managers. We first conducted a literature review on May 20, 2020 in the ISI Web of Science, ProQuest, and OpenGrey databases. We used the search terms “bird” AND (“conspecific attraction” OR “social information” OR “public information”) over all years (1900–2020), yielding 592 studies. Searches with additional terms (e.g., “social cues” and “social facilitation”) and variants of the original terms yielded no additional studies.

We then adopted a multistep approach to identify studies for inclusion in our analysis (Figure 1). First, we excluded studies on colonial waterbirds because this group often nests in large aggregations and was not the focus of our review. We then selected those studies that used manipulative experiments of natural cues (i.e. vocalizations, decoys, or both) to simulate conspecific presence in wild bird communities. We specifically focused on this subset of studies for 2 reasons. First, doing so eliminated observational studies in which the quality of local habitat was likely confounded with the availability of conspecific social cues making it impossible to distinguish their relative effects on habitat selection. Second, by focusing on simulated social cues we were able to test predictions about cue characteristics (e.g., timing, frequency, and duration of cues) that are of direct relevance to managers. In addition, we only included studies that (1) compared presence–absence, density, or abundance between treatment and control sites in replicated sampling units during the settlement period (defined as ~2 weeks before breeding begins through the breeding season) and (2) provided sufficient information for calculating an effect size (see below). This ensured effect sizes were comparable among studies and relevant to focal hypotheses about habitat selection. After filtering studies based on these criteria, we selected the 10 most recently published papers and 2 comprehensive reviews on

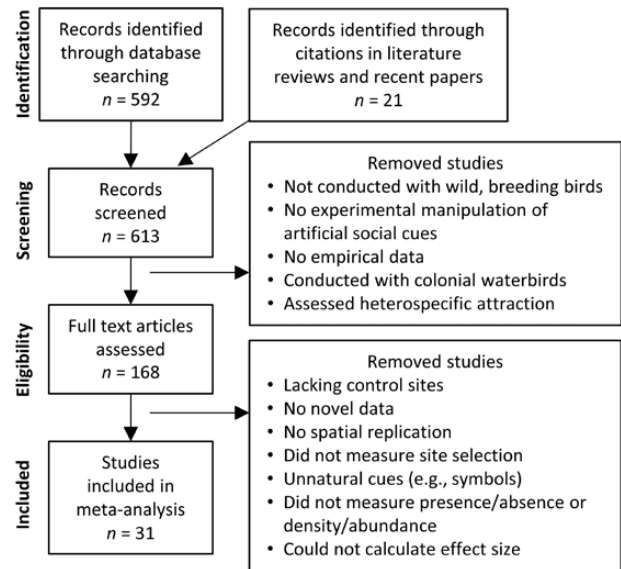


FIGURE 1. A flow chart describing how we identified and processed studies for inclusion in our meta-analysis of factors influencing avian attraction to simulated conspecific presence during habitat selection.

this subject (Ahlering et al. 2010, Szymkowiak 2013) and scanned their references for any studies we potentially overlooked. In total, we screened 613 unique studies and ultimately retained 30 published studies that were suitable for analysis (Supplementary Material Appendix A), in addition to one unpublished study to which we had access (Supplementary Material Appendix B).

Data Extraction

We developed a list of potential explanatory variables (hereafter moderators) based on our hypotheses (Table 1) and refined this list to information that could be obtained from studies that met our search criteria (Table 2; see Supplementary Material Appendix C for a description of how each moderator was defined). We then searched the text, tables, and figures of each selected paper to extract data for testing focal hypotheses. We recorded unique response values for each species and each combination of explanatory variables reported. For instance, if a study used 2 different playback densities (Kelly et al. 2018) or reported on both detections and territory establishment (DeJong et al. 2015), we recorded each result separately. Most studies did not distinguish between male and female responses, and for the few that did, we recorded estimates of male settlement because that was most comparable across studies (many others relied on simple counts of singing males). Though we hypothesized that individual age would influence the magnitude of the response (Table 1), few studies separated age classes (Nocera et al. 2006), so we aggregated

data across age classes. We were similarly unable to quantify asynchrony in breeding (Table 1) as such data were rarely available in published studies.

For studies that examined presence–absence, we recorded the total number of replicates for treatment and control sites as well as the proportion that was occupied in the first breeding season following treatment completion. For those that examined density or abundance, we recorded the number of sites, mean posttreatment density/abundance, and the standard deviation of those estimates. When authors reported both presence–absence and density/abundance, we recorded both, as these response variables were examined separately (see below). All values were either calculated from raw data or from univariate models; while some authors included other covariates (e.g., site, habitat covariates, pretreatment densities) or accounted for imperfect detection in their analyses, we did not include parameter estimates from these models as treatment effects may be incomparable between models with different covariates or structures (Koricheva et al. 2013). When studies alternated the same sites between treatments and controls in different years (Hahn and Silverman 2006), we only used the first year's data unless the authors demonstrated there were no carryover effects on previously treated control sites.

Analyses

We calculated standardized effect sizes for presence–absence and density/abundance studies separately. For each presence–absence effect, we calculated the log odds ratio and its variance (Koricheva et al. 2013) as:

$$\ln \text{OR} = \ln \left[\frac{(n_{T1} + 0.5) \times (n_{C0} + 0.5)}{(n_{C1} + 0.5) \times (n_{T0} + 0.5)} \right]$$

$$\text{VAR}(\ln \text{OR}) = \frac{1}{n_{T1}} + \frac{1}{n_{C1}} + \frac{1}{n_{T0}} + \frac{1}{n_{C0}}$$

Here, the values of n_{T1} and n_{C1} indicate the number of treatment and control sites where the species was detected, respectively, whereas n_{T0} and n_{C0} indicate sites where it was not detected. We added 0.5 to each value in the 2-by-2 contingency tables to prevent division by 0 (Hyatt et al. 2003). For each density/abundance effect, we calculated Hedges' d and its variance (Hedges and Olkin 1985) as:

$$d = \frac{\hat{Y}_T - \hat{Y}_C}{\sqrt{\frac{(n_T - 1)\hat{s}_T^2 + (n_C - 1)\hat{s}_C^2}{n_T + n_C - 2}}} \left(1 - \frac{3}{4(n_T + n_C) - 9} \right)$$

$$\text{VAR}(d) = \frac{n_T + n_C}{n_T n_C} + \frac{d^2}{2(n_T + n_C)}$$

Here n_T and n_C represent the number of treatment and control sites, \hat{Y}_T and \hat{Y}_C represent estimated mean bird densities among sites, and \hat{s}_T^2 and \hat{s}_C^2 represent estimated variance in density. The value of Hedge's d indicates the number of pooled standard deviations that separates the average treatment and control site. Values below 0.5 are considered small to medium effect sizes whereas values of 0.8 or greater are considered large and obvious (Cohen 1988). Increases in values for both the log odds ratio and Hedge's d correspond to stronger treatment effects. We conducted all calculations with the *escalc* function in the *metafor* R package (Viechtbauer 2010).

We fit 3 types of meta-regression models for each response variable using the *MCMCglmm* R package (Hadfield 2010); we used default vague priors on fixed effects and parameter-expanded priors ($V = 1$, $\nu = 1$, $\alpha = 0$, $\alpha.v = 1,000$) for all random effects to speed up model convergence (Hadfield 2010). We ran each model for 400,000 iterations with a burn-in of 200,000, thinned by 100 and evaluated model convergence by visually inspecting trace plots for convergence and signs of temporal autocorrelation. In all models, $ES_{i,j,k}$ is effect size k recorded in study j for species i .

Initially, we fit a *species model* designed to estimate mean effect sizes for each species across all moderators and studies:

$$ES_{i,j,k} = \theta_{i,j,k} + \text{STUDY}_j + e_{i,j,k}$$

$$\theta_{i,j,k} \sim N(\text{SPECIES}_i, \sigma_\theta^2), \quad \text{STUDY}_j \sim N(0, \sigma_{\text{STUDY}}^2), \\ e_{i,j,k} \sim N(0, \sigma_{i,j,k}^2)$$

Here, SPECIES_i represents a species-specific response to conspecific treatment, while σ_θ^2 , σ_{STUDY}^2 , and $\sigma_{i,j,k}^2$ represent within-study variation, between-study variation, and sampling error (estimated as the standard error of $ES_{i,j,k}$), respectively.

Next, we fit an *intercept model* that was designed to estimate the overall mean effect (μ) of social cue treatments on breeding birds:

$$ES_{i,j,k} = \theta_{i,j,k} + \text{SPECIES}_i + \text{STUDY}_j + a_i + e_{i,j,k}$$

$$\theta_{i,j,k} \sim N(\mu, \sigma_\theta^2), \quad \text{SPECIES}_i \sim N(0, \sigma_{\text{SPECIES}}^2), \\ a = [a_1, a_2, \dots, a_S] \sim N_S(0, \sigma_a^2 A)$$

Here we modeled random variation among species ($\sigma_{\text{SPECIES}}^2$) rather than directly estimating individual species effects. We also accounted for evolutionary history by incorporating phylogenetic effects (a_i) which we assumed come from a multivariate normal distribution. We constructed a phylogenetic tree by randomly sampling 1,000

TABLE 2. A description of moderators used in meta-regression analyses to test hypotheses listed in Table 1. These hypotheses examine how characteristics of the study species, sites, treatments, and response measured mediate the effects of conspecific attraction in avian habitat selection. Details on how moderator data were collected are found in Supplementary Material Appendix C.

Moderators	Type	Description
<i>Species characteristics</i>		
Longevity	Continuous	Maximum recorded age (years) of a wild individual
Migratory status	Discrete	Breeds and winters in the same region
Resident		Breeds and winters in different regions
Migrant	Discrete	Primarily pair-bonded, though may participate in extra-pair copulations
Polygamy		Most individuals primarily polygamous
Low		Evidence for aggregations that cannot be explained by habitat
High		No evidence for aggregation beyond what can be explained by habitat
Clustered breeding	Discrete	Habitat dynamic in space/time over life cycle (i.e. prefers wetlands or early successional stages)
Clustered		Habitat relatively stable in space and time over life cycle (e.g., mature forests, shrublands, grasslands)
No evidence	Discrete	
Habitat preference		
Ephemeral		
Static		
<i>Site characteristics</i>		
Size	Continuous	Spatial size (ha) of sites sampled by the researchers after treatment
Latitude	Continuous	Absolute value of latitude of the center of the study area (i.e. distance from the equator)
Local distribution	Continuous	Proportion of local eBird checklists reporting the species during the peak of the breeding season
Previous occupation	Discrete	All study sites are known to be unoccupied by study species prior to the experiment
Unoccupied		All study sites are known to be occupied by study species prior to the experiment
Occupied		Occupancy status of sites unknown prior to the experiment
Unknown		
Site quality	Discrete	All study sites placed in purportedly preferred habitat for the species
Presumed high		Study sites placed in areas that spanned a gradient in purportedly preferred habitat for the species
Gradient		
<i>Treatment characteristics</i>		
Playback duration	Continuous	Total hours of treatment applied to experimental sites
Playback density	Continuous	Number of treatments (i.e. playback units) per hectare (see site size above)
Time of year	Discrete	Treatments only applied ~2 weeks prior to breeding onset and/or during the breeding
Pre/breeding		Treatments only applied after the peak of breeding when nestlings and fledglings were locally active
Post		
Signal origin	Discrete	Vocal playback recordings made locally at the study site
Local		Vocal playback recordings made in the study region (e.g., within the same state or neighboring states)
Regional		Vocal playback recordings of unknown geographic origin
Unknown		
Cue type	Discrete	Treatment included post-breeding juvenile begging to indicate habitat quality
Performance info.		Treatment included only songs and calls in the pre- or post-breeding period
Location	Discrete	Experimental treatment included the use of visual decoys
Decoys		Experimental treatment did not include the use of visual decoys
Used		
Not used		
Conspecific quality	Discrete	Treatment indicates low fitness of cue provider (i.e. exclusively alarm calls or reduced song rate)
Low		Treatment does not demonstrably indicate low fitness of cue provider
Presumed high		
<i>Measurement characteristics</i>		
Monitoring duration	Continuous	Length of time (days) encompassed by posttreatment monitoring period
Response measured	Discrete	Response measured based solely on detections rather than territory establishment
Detected		Response measured based on territory establishment (e.g., repeated observations of the same male)
Territorial		Response measured based on known breeding activity (e.g., presence of nests)
Breeding		

Ericson backbone trees (Jetz et al. 2012; <http://birdtree.org/>) and calculating an average tree using the Robinson–Foulds distance (Robinson and Foulds 1981). With S total species, \mathbf{a} is a 1-by- S vector of a_i and \mathbf{A} is an S -by- S matrix of phylogenetic distances between species. All other parameters are as specified above.

Finally, we fit 19 *moderator models* to evaluate support for our predictions (Table 1). Each of these models built on the intercept model by including an additive effect of one of the moderators presented in Table 2. Because this analysis was largely exploratory, and because there are myriad combinations of moderators and interactions that could be tested, we chose not to attempt any stepwise model-building or model comparison procedures. Instead, we designed models to evaluate each hypothesis independently. We omitted individual effect sizes from a model if we were unable to extract an appropriate moderator value from the study text. To mitigate model convergence issues, we standardized the values of all continuous moderators prior to model fitting by subtracting the mean and dividing by the standard deviation.

We evaluated support for our phylogeny hypothesis (Table 1) by calculating phylogenetic heritability, H^2 , which is the proportion of the variance accounted for by phylogeny divided by the sum of all variance components except sampling error (Lynch 1991). An H^2 value of 0 indicates no heritability of conspecific attraction in habitat selection, whereas a value of 1 indicates effect sizes are directly proportional to phylogenetic relatedness. We evaluated support for all other hypotheses by examining whether the moderator effect sizes were consistent with our predictions (i.e. if the direction of the estimated effect from presence–absence and density/abundance analyses were as predicted). We determined there was strong support for a moderator effect if the 95% CI (credible interval) for the effect size (continuous moderators) or the difference between any 2 groups (categorical moderators) did not overlap 0. Finally, we tested for evidence of publication bias by (1) visually evaluating funnel plots of the residuals from the intercept models plotted against the effect size standard errors (Nakagawa and Santos 2012), and (2) conducting Egger’s regression (Egger et al. 1997) on these residuals (*regtest* function) which statistically tests for funnel plot asymmetry, an indicator of bias in published studies.

RESULTS

In total, we recorded 31 presence–absence effects and 43 density/abundance effects for 29 unique species. Our review found data for only 2 non-passerine species: Little Owl (*Athene noctua*) of the order Strigiformes and Chimney Swift (*Chaetura pelagica*) of the order Apodiformes.

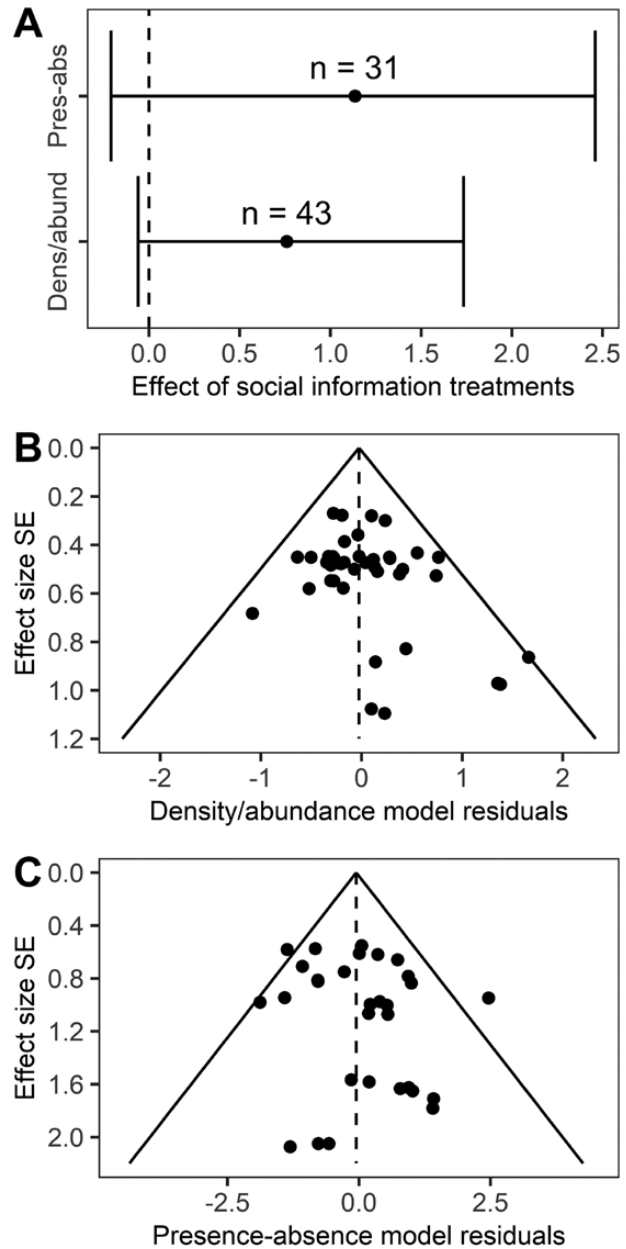


FIGURE 2. Results from intercept models examining the effects of social cue treatments on density/abundance or presence–absence of terrestrial breeding birds from 31 studies. In (A), the average log odds ratio (presence–absence) and the average Hedge’s d (density/abundance) were positive, indicating relatively strong effects of conspecific presence on settlement decisions across species and contexts. Funnel plots (B and C) indicated no evidence for publication bias given the relatively symmetric distribution of model residuals around their mean (dashed line) regardless of the standard error (SE) estimate. Solid lines indicate ~95% CI for residuals from the model at a given SE.

Experiments also targeted primarily temperate-breeding migrants; we found no studies that recorded data in tropical regions and only uncovered information on

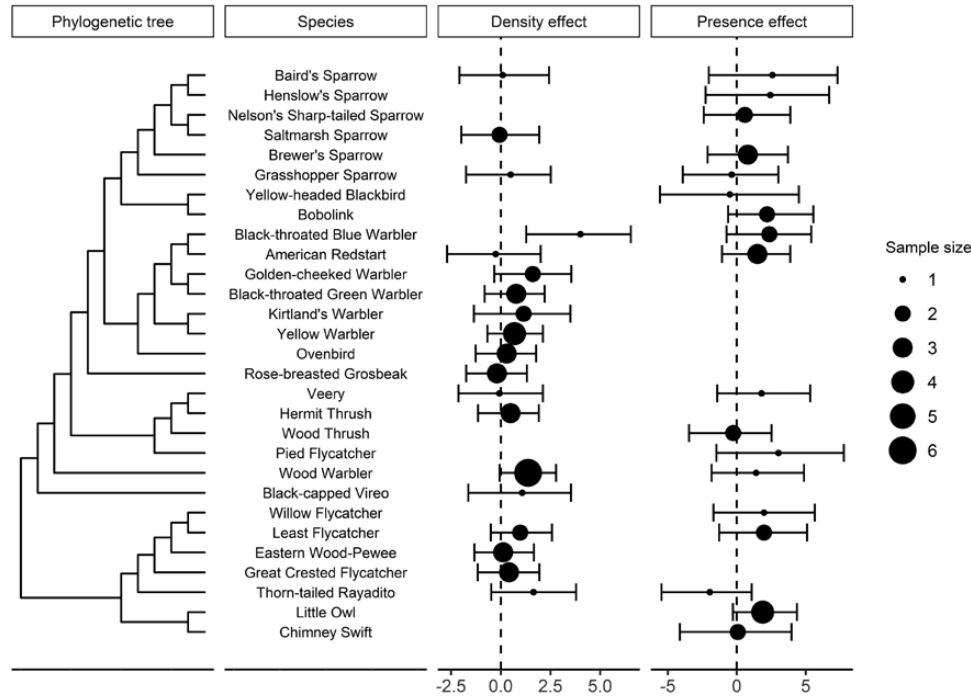


FIGURE 3. Estimated effects of experimental social cue treatments on settlement decisions of 29 species based on a meta-analytic model. We fit separate models for studies examining density/abundance and presence–absence. The number of effect sizes used to estimate each value is represented by point size.

2 non-migratory species, Little Owl and Thorn-tailed Rayadito (*Aphrastura spinicauda*).

Breeding birds generally exhibited a strong tendency to settle near conspecifics (Figure 2A). Analysis of the presence–absence data indicated that across studies the odds of detecting the target species were 3.12× (95% CI: 0.81–11.69) greater in treated than untreated sites. In addition, the density/abundance of breeding birds was on average 0.76 (95% CI: –0.059 to 1.73) standard deviations greater at treatment than control sites. Of note, only a single study documented significant negative effects of social cue treatments on settlement decisions of any species, the Thorn-tailed Rayadito (Quilodran et al. 2014). In all other studies, effects were positive or not different from 0 at the $\alpha = 0.05$ level. Importantly, we found no strong evidence for bias in publication of datasets measuring presence–absence ($z = 1.06$, $P = 0.29$) or density/abundance ($z = 1.37$, $P = 0.17$; Figure 2B and C).

We did find evidence that the use of conspecific social cues during habitat selection is an evolutionarily conserved trait. Results from the intercept models indicated that evolutionary history explained 25.47% (95% CI: 5.12%–65.37%) and 30.96% (95% CI: 9.04%–63.57%) of the variance in the presence–absence and density/abundance datasets, respectively. Warblers in the genus *Setophaga* ($n = 6$ species) tended to have the strongest responses, yet even within this group there was marked heterogeneity (Figure 3). For

instance, the Yellow Warbler (*Setophaga petechia*) showed a weak response to experimental cues, whereas the response for the American Redstart (*Setophaga ruticilla*) was positive in the presence–absence analysis, but negative in the density/abundance analysis. Sparrows in the genus *Ammodramus* ($n = 5$ species) also tended to show strong positive responses in the presence–absence analysis, but effects were generally weak or negative when examining density/abundance (Figure 3). Within-genus replication was lacking in all other cases except for *Empidonax* flycatchers ($n = 2$ species) and *Catharus* thrushes ($n = 2$ species), groups that showed relatively strong and weak positive responses, respectively, to social cue treatments (Figure 3).

We found no strong support for any of our hypotheses (Table 1) regarding the mediating effects of species, site, cue, or response measurement characteristics on conspecific attraction to breeding sites (Figure 4; Supplementary Material Table S1). The direction of estimated effects contrasted between the presence–absence and density/abundance datasets for 14 moderators (74%; Figure 4). For continuous moderators that means one effect size estimate was negative and the other was positive, and for categorical moderators that the ordered arrangement of groups by effect size differed between the 2 datasets (e.g., effect sizes were stronger for migrants than residents

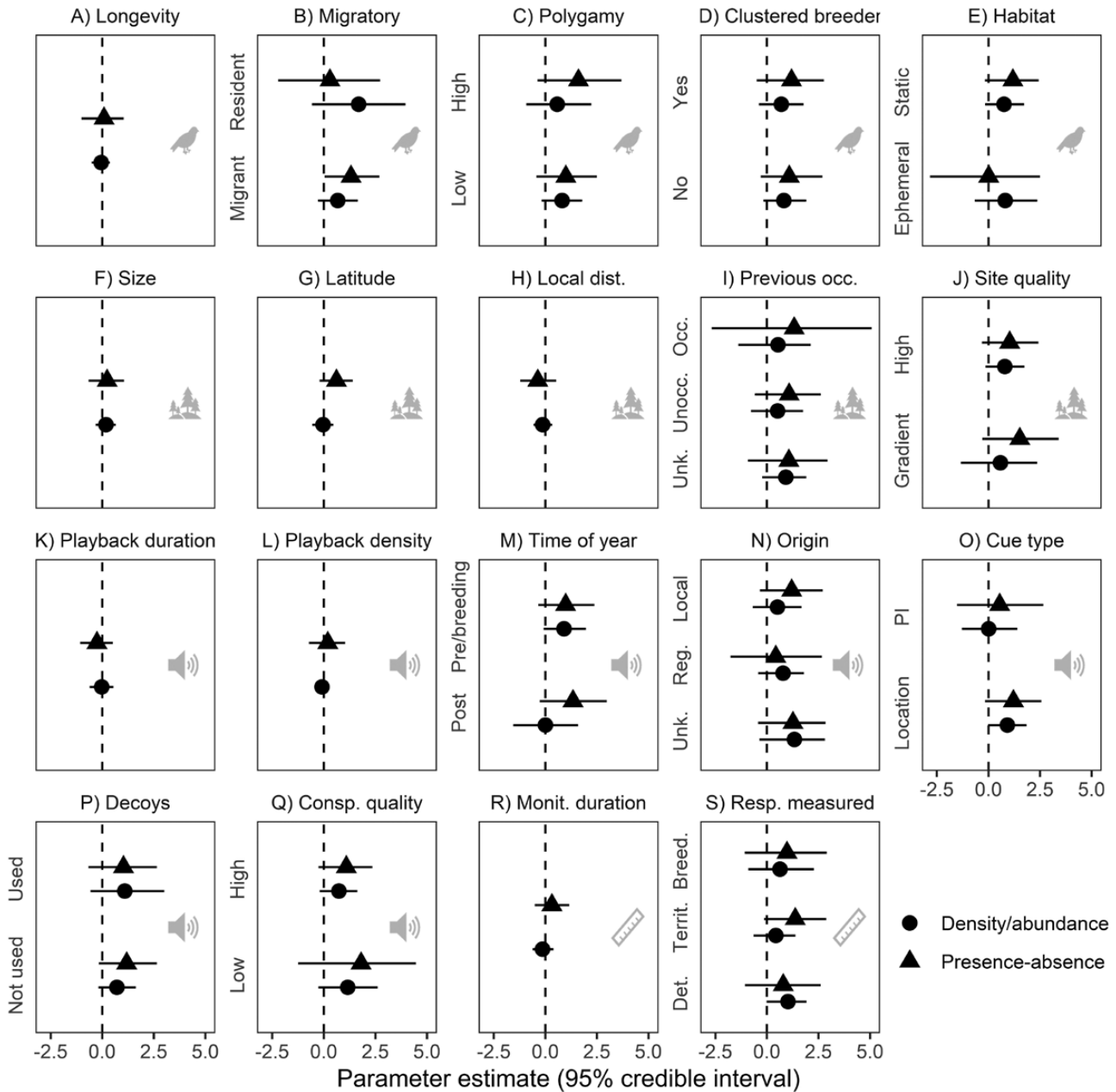


FIGURE 4. Effects of species (A–E, indicated by bird silhouette), site (F–J, tree silhouette), treatment (K–Q, speaker silhouette), and response (R–S, ruler silhouette) moderators on avian response to social cue treatments. Continuous moderators (A, F, G, H, K, L, R) were standardized, so the estimate represents the change in effect size for each 1-unit increase in the standard deviation of the moderator. Estimates for categorical moderators represent the average effect size within that group. Sample sizes can be found in [Supplementary Material Table S2](#).

in the presence–absence dataset, but stronger for residents than migrants in the density/abundance dataset; [Figure 4](#)). In many cases, the lack of strong moderator effects may be due to relatively small sample sizes, a narrow range of values for some moderator categories, or both ([Supplementary Material Table S2](#), [Figure S1](#)). The effects of only 3 moderators were consistent with our predictions. Results

from both datasets indicated that the effect of treatment on settlement increased with site size (i.e. size of the area the researchers examined for settlement) and decreased as the relative abundance of conspecifics increased regionally. Settlement was also more likely when the treatment cues were produced by a low-quality individual than a high-quality individual. However, all these effect sizes were small relative to

their estimated error and 95% CIs overlapped 0 in all cases (Figure 4; Supplementary Material Table S1).

DISCUSSION

In this study, we reviewed the effects of experimentally simulated social cues on the attraction of terrestrial birds to potential breeding sites and found that treatments had relatively strong and positive effects on settlement across species, studies, and contexts. The odds of a site being occupied were more than 3 times greater for sites where social cues were experimentally simulated than at control sites; similarly, density/abundance was nearly 0.8 standard deviations greater at treatment sites. Such findings are considered large and biologically significant treatment effects (Cohen 1988), and although the 95% CIs overlapped zero slightly for both estimates, we posit this is a function of the generally small sample sizes and large methodological variability across these studies. Given that we found no evidence for publication bias, attraction to conspecifics during breeding habitat selection appears to be strong and widespread among the terrestrial species on which rigorous experiments have been conducted. However, the species represented in these experiments are still predominantly migratory passerines that breed in North America, and thus our scope of inference is constrained to this group. Even within this species subset, we found that we still lack basic information about the traits, contexts, and cue characteristics that mediate conspecific attraction which limits our ability to use it efficiently for management.

We hypothesize that experimental conspecific attraction research has tended to focus on passerines because, for most species within this order, vocalizations are integral to mate attraction and territory defense. Using song broadcasts to attract breeding conspecifics thus seems intuitive and straightforward. Furthermore, we suspect researchers target migrants because they hypothesize that socially influenced habitat selection should be particularly adaptive for these species (Ahlering et al. 2010, Buxton et al. 2020) and because there is a clear, finite time window when social cue treatments should be applied (between arrival from and departure to the wintering grounds). Non-migratory species, on the other hand, could theoretically prospect at any time of year making the appropriate timing for treatment ambiguous. Regardless of the reason, conspecific attraction appears to be widespread across birds and indeed many animal taxa (Buxton et al. 2020), and future research should examine whether simulating conspecific cues will be useful for the management of species other than colonial waterbirds and migratory passerines (Pöysä et al. 1998, Finity and Nocera 2012, Parejo et al. 2012, 2018).

In our review, we found no experiments examining conspecific attraction to breeding sites in the tropics,

the region home to the highest concentration of threatened bird species (BirdLife International 2017). Tropical species can use social information to identify foraging locations (Martínez et al. 2018) and predation risk (Hua et al. 2016); thus, it seems likely some species may use social information to select breeding sites, which could have clear management applications. For example, while forest restoration is urgently needed to protect tropical biodiversity (Lamb et al. 2005, Betts et al. 2019), native avian species often remain absent from restored tropical forests for many decades after they provide ostensibly suitable habitat (Catterall et al. 2012). Simulated social cues could be useful in attracting native colonizers to newly restored and potentially underutilized habitats. On the other hand, tropical birds tend to be located on the slower end of the fast–slow life history continuum than temperate-breeding passerines (Moreau 1944, Lack 1947, Skutch 1949, Martin 1996, Cardillo 2002), which may make them more inclined to use nonsocial information in habitat selection (Table 1). At present, it is thus ambiguous whether conspecific attraction methods can be used to manage distributions of tropical species, and this too requires further investigation.

Despite these limitations, our results did yield several generalities that should prove useful to practitioners. First, restoration and management of avian habitat often rely on the “Field of Dreams” assumption that if the habitat is provided, it will be colonized (Ahlering and Faaborg 2006). We found that broadcasting social cues is likely to enhance settlement for migratory passerines and in some cases may be required to facilitate local breeding (Ward and Schlossberg 2004). In addition, conspecific attraction in habitat selection appears to be an evolutionarily conserved trait within this group. Managers seeking quick information about whether simulated social cues could be used to attract their target species should examine results from conspecific attraction experiments on phylogenetically related species and may consider using analogous methods from those studies. At present, evidence suggests that species in the genera *Setophaga* and *Ammodramus* tend to respond strongly to simulated social cues, though generalizing for other taxonomic groups is difficult due to lack of replication.

The use of simulated social cues to manipulate distributions of terrestrial breeding birds thus has great potential as a management tool. Not only can this approach be used to expand distributions of target species (Fletcher 2009, Anich and Ward 2017, Schofield et al. 2018), it can also encourage successful breeding in high-quality sites that continue to be used in subsequent years (Ward and Schlossberg 2004, Anich and Ward 2017). We caution, however, that attraction to conspecifics can be so strong as to result in settlement of poor-quality habitat (Nocera et al. 2006, Betts et al. 2008, Farrell et al. 2012). Thus, we

re-emphasize the need for a priori habitat assessments and posttreatment monitoring, as both are critical steps to ensure species of conservation concern are not inadvertently drawn into ecological traps (Ahlering et al. 2010, Szymkowiak 2013, Anich and Ward 2017).

A Research Agenda for the Study of Conspecific Attraction in Birds

Despite a decade of calls to improve management efficiency by developing a more mechanistic understanding of the factors influencing conspecific attraction in breeding birds (Ahlering et al. 2010, Szymkowiak 2013, Lewis et al. 2020), we still lack broad support for any of 26 mechanistic hypotheses we uncovered in the literature (Table 1). We suggest that these findings are most likely because there have been few empirical investigations specifically designed to test these hypotheses (see below). Of course, it is also possible that some of the moderators we selected were weak proxies for the mechanisms they were designed to represent (e.g., eBird checklist frequency may poorly represent local abundance), or that we could not discern consistent effect sizes due to more complex interactions among moderators. Yet this is even more reason to encourage carefully designed experiments that can explore these interactions and measure covariates locally. Below we outline 3 major themes for future research that we expect will lead to the greatest progress in the conspecific attraction field.

Theme 1: Evaluating the characteristics of social cues that attract breeding birds. Currently, it is difficult to interpret results from experiments that report no response to simulated social cues because one cannot distinguish between the equally plausible explanations that (1) social information is not used by the target species in the context examined or (2) the cue provided by the researcher lacks information that is relevant to targeted individuals. Thus, the first priority is to uncover the proximate characteristics of the cues themselves to which individuals respond. The limited evidence generated thus far indicates that the types of social cues used, and the way they are presented, can influence the strength of conspecific attraction. For example, responses may be stronger when cues are simulated during the pre-breeding (Farrell et al. 2012) or post-breeding period (Nocera et al. 2006), depending on the species. Potential settlers can also be influenced by the implied quality of the cue producer; in some studies, this resulted in higher settlement rates near cues produced by successful breeders (Betts et al. 2008, Kelly and Ward 2017), and in others, settlement was greater near cues from low-quality competitors (Szymkowiak et al. 2016). Kelly et al. (2018) also demonstrated that the density of simulated cues can alter settlement patterns. We know of no studies that have evaluated the effects of broadcast duration or geographic origin of the cue on settlement, or

whether combining multiple cues (e.g., audible sounds and visual decoys) can strengthen the response.

Identifying the characteristics of social cues that attract birds will require experiments purposefully designed to test the response of species to different types of treatments. Researchers interested in such questions will have the most success by starting with a group of species known to exhibit conspecific attraction in habitat selection and then systematically varying cue characteristics. These experiments will be a critical precursor to developing effective management and designing robust experiments for examining how conspecific attraction varies across species and contexts.

Theme 2: Assessing the role of life history in conspecific attraction. There is a strong need to increase the breadth of life history strategies in species included in rigorous conspecific attraction experiments. This information will help identify potential species that can be targeted for management with simulated social cues. The greatest advances in this area are likely to be made by implementing multi-species studies that directly compare responses across life history strategies. To date, few studies have adopted a multi-species exploration of conspecific attraction and those that have typically did not select focal species for the explicit purpose of evaluating how life history variation influences conspecific attraction. A notable exception comes from Nocera et al. (2006) who compared settlement responses of a social (Bobolink, *Dolichonyx oryzivorus*) and a more solitary (Nelson's Sparrow, *Ammodramus nelsoni*) species to conspecific playback. Similar experiments following this precedent will be important for addressing the other hypotheses related to life history presented in Table 1.

Because there is evidence that conspecific attraction is phylogenetically conserved, any cross-species comparisons will need to control for phylogenetic relatedness. This can be accomplished by explicitly incorporating phylogenetic distance into models. Alternatively, researchers may initiate comparisons of closely related species that have differing life history traits (e.g., migratory strategies or habitat preferences) to isolate the trait differences as the most likely explanation of observed variability in conspecific attraction. Importantly, any cross-species comparisons should, as much as possible, control for heterogeneity in the social cues (Theme 1) and spatial context (Theme 3) to reduce potential confounding effects on inference.

Theme 3: The influence of spatial context on conspecific attraction. Finally, there is a need for within-species research examining contexts in which social information is prioritized. Birds use both social and nonsocial information when selecting habitat (Pärt et al. 2011), and the

relative value of social information is likely to vary with environmental predictability and conspecific density (Giraldeau et al. 2002, Doligez et al. 2003, Rieucou and Giraldeau 2011). Spatial context is therefore likely to affect the degree to which birds are attracted to conspecifics and thus is an important consideration for managers considering the use of simulated social cues. In addition, understanding how conspecific attraction varies in space will be critical for developing studies that are ecologically comparable across species (Theme 2).

Several of the studies we examined investigated conspecific attraction across a spatial gradient in habitat structure or quality resulting in strong evidence that targeted species prioritize social information over nonsocial information (Nocera et al. 2006, Betts et al. 2008, Farrell et al. 2012). Beyond these studies, however, we found few investigations that examined how other spatial patterns or processes mitigate conspecific attraction. For example, all studies we reviewed measured habitat selection at a single spatial scale, typically centered on the treatment locale. We also found no studies that explicitly compared socially influenced habitat selection for the same species in different regions. Although some intraspecies comparison may be possible across studies (Hahn and Silverman 2007, Betts et al. 2008, Cornell and Donovan 2010), it is typically impossible to know whether the variability in responses is driven by spatial context or differences in treatment characteristics. Thus, we have no direct evidence regarding the appropriate spatial scale for measuring settlement in response to simulated cues, or how regional habitat availability or conspecific density moderate its effects on settlement.

Studies examining how conspecific attraction varies across spatial context should standardize experimental treatments to allow for direct comparison of species responses in different areas. They should also target species that are known to exhibit conspecific attraction to eliminate the possibility that the species does not use social information when selecting habitat. By carefully varying the systems in which these studies are conducted for a single species, we will begin to understand why conspecific attraction appears to be strong in some contexts and not in others (Hahn and Silverman 2007, Cornell and Donovan 2010).

Conclusions

Because conservation resources are often limited, managers require an understanding of when and where potential management tools are likely to be successful. Research focused on examining whether a single species does or does not select habitat based on social cues has been critical for advancing our understanding of avian habitat selection,

and it will continue to play a role in the conservation of many species. Nevertheless, the greatest advances to the field will come from studies that move beyond evaluating whether a single species responds to treatment in a single location and instead compare settlement responses across species, cues, and contexts. The above themes and the hypotheses we have aggregated (Table 1) should serve as a useful starting point, although we encourage others to develop and explore alternative mechanistic hypotheses. By testing such ideas through carefully crafted experiments, we expect to enhance our understanding of how and when birds use social information, and thus when it can be used as an effective tool for avian conservation and management.

SUPPLEMENTAL MATERIAL

Supplemental material is available at *Ornithological Applications* online.

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Ethics statement: This research did not require any permits and we have appropriately cited all data we used in our analyses.

Author contributions: All authors helped to formulate the questions and develop the research hypotheses. J.J.V., C.L.L.-R., and A.M.T. collected the data and J.J.V. conducted analyses. J.J.V., C.L.L.-R., and J.W.R. drafted the first version of the manuscript, and all authors contributed extensively to editing.

Data availability: All data and code for reproducing analyses can be found in the work of Valente et al. (2021).

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