

RESEARCH NEEDS AND RECOMMENDATIONS FOR THE USE OF CONSPECIFIC-ATTRACTION METHODS IN THE CONSERVATION OF MIGRATORY SONGBIRDS

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Abstract. Numerous studies have confirmed that when selecting habitat birds can use social information acquired from observing other individuals, and many aspects of this social information can be capitalized upon to manage bird populations. The conservation implications of attraction to conspecifics are especially promising for management, and as research progresses it is important to consider how this behavior can be applied to conservation practice. The biological underpinnings of conspecific attraction and the repercussions of manipulating species' distributions with attraction methods are not well understood, but conservation decisions often cannot wait for scientific research. Here we synthesize the current research on manipulation of songbirds by conspecific-attraction methods and review our knowledge gaps critically. We reviewed the published literature on conspecific-attraction experiments in songbirds and found that of 24 studies in which they were attempted, 20 were successful in attracting birds. Although many experiments have been successful in attracting conspecifics with various cues, we outline issues to be considered before songbirds are manipulated by attraction methods, and we highlight areas of research necessary to enhance the understanding of conspecific attraction and its use in conservation.

Key words: avian conservation techniques, conspecific attraction, endangered and threatened species, habitat selection, playbacks, social information.

Necesidades de Investigación y Recomendaciones para el Uso de Métodos de Atracción de Individuos Coespecíficos en la Conservación de Aves Canoras Migratorias

Resumen. Se ha confirmado mediante numerosos estudios que las aves pueden utilizar información social adquirida mediante la observación de otros individuos al seleccionar el hábitat y muchos aspectos de esta información social pueden emplearse para manejar las poblaciones de aves. Las implicaciones de la atracción entre individuos coespecíficos para la conservación son especialmente promisorias para el manejo y a medida que la investigación progresa es importante considerar cómo se puede aplicar este comportamiento a la conservación en la práctica. Las bases biológicas de la atracción entre individuos coespecíficos y las repercusiones de manipular la distribución de las especies mediante métodos de atracción no se entienden adecuadamente, pero las decisiones de conservación a menudo no pueden esperar al desarrollo de investigaciones científicas. En este trabajo, sintetizamos la investigación actual sobre la manipulación de aves canoras mediante métodos de atracción de individuos coespecíficos y revisamos nuestros baches en el conocimiento de forma crítica. Revisamos la literatura publicada sobre experimentos de atracción de individuos coespecíficos en aves canoras y encontramos que, de 24 estudios en los que éstos fueron emprendidos, 20 tuvieron éxito atrayendo a las aves. Aunque muchos experimentos han tenido éxito atrayendo individuos coespecíficos usando varias señales, esbozamos algunos asuntos que deben considerarse antes de manipular a las aves canoras mediante métodos de atracción. Además, resaltamos áreas en las que es necesario realizar investigaciones para mejorar el entendimiento de la atracción de individuos coespecíficos y su uso en conservación.

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INTRODUCTION

Avian habitat selection is a hierarchical progression of choices that leads to a distribution of habitat use (Jones 2001). For migratory birds, the hierarchy begins at a regional scale and the focus increases toward microhabitat selection for nest sites and feeding locations; this process is then repeated annually. Numerous factors can influence the decision process. Traditionally, research has concentrated on correlations between vegetation structure and occupancy (e.g., Cody 1985). However, it has become increasingly apparent that inadvertent social information—information acquired from observing the interactions of individuals with their environment—can play an important role in the process of habitat selection (e.g., Danchin et al. 2001). Social information can be derived from the performance of other individuals (i.e., public information; Valone 1989) or merely the presence or abundance of other individuals (i.e., “location” or social cues; Danchin et al. 2004), and both of these types of information can arise from conspecifics or heterospecifics. Knowledge about which factors influence habitat selection at different stages in the hierarchical decision process is desirable for management and conservation strategies (Swaisgood 2007) because management and conservation of a species are often aimed at increasing populations and promoting settlement in new habitats.

Research into all aspects of social information and avian habitat selection has recently increased. A search of the ISI Web of Science (last updated 20 Dec 2008) for the terms “social information” and “habitat selection,” “public information” and “birds,” “conspecific attraction” and “birds,” and “heterospecific attraction” and “birds” shows a sharp increase in the number of research papers published since 1990 (Fig. 1). This increase is not an artifact of increased volume of publication, as papers using these terms have increased dramatically in proportion to the overall number of papers published on “habitat selection” and “birds,” particularly in the last 3 years. Thus it is not surprising that there is a growing interest in applying social-information concepts to conservation and management, particularly in the case of conspecific attraction, because of its ease of application (see below). Despite the growing body of literature, knowledge in this area is still rudimentary and has not been synthesized to address conservation issues. A large problem, however, is the gap between the questions researchers address and the answers required by practitioners (Campomizzi et al. 2008). Our goal is to aid managers in government agencies and nonprofit organizations as well as academic researchers by providing a critical review of our current knowledge and knowledge gaps, giving some guidance for practitioners interested in applying conspecific-attraction methods, and explicitly linking management needs with research needs.

For the purposes of this review, we focus on migratory songbirds because very little conspecific-attraction research has addressed nonmigratory songbirds. We focus specifically on conspecific attraction during the breeding season because more information and research is currently available for

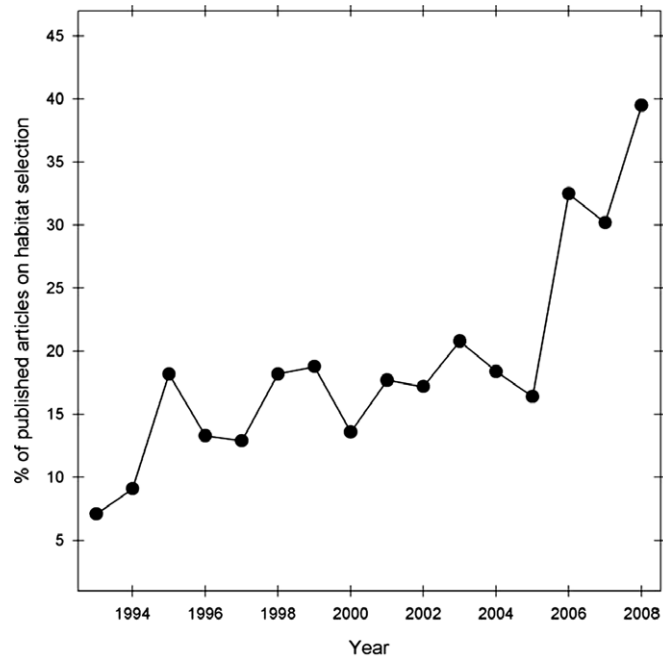


FIGURE 1. The percentage of peer-reviewed articles on habitat selection and birds published before 20 Dec 2008 and catalogued in the ISI Web of Science that could be traced with the following pairs of search terms: “social information” and “habitat selection,” “conspecific attraction” and “birds,” “public information” and “birds,” and “heterospecific attraction” and “birds.”

conspecific attraction than for heterospecific attraction and almost all research has been conducted during the breeding season. We focus on two simulated social cues, playbacks and decoys, because they are easily manipulated and have been shown to increase local bird populations effectively. Nonetheless, many issues we address are relevant in other situations and for other types of social information. We emphasize recent experiments on migratory songbirds and contrast these results with results from long-standing experiments on colonial waterbirds (see Kress 1997 for a thorough review on waterbirds).

STATE OF KNOWLEDGE

Experimental tests for conspecific attraction in waterbirds date back to the late 1970s and early 1980s (e.g., Kress 1983), but the integration of conspecific attraction into the study of habitat selection for songbirds has been relatively recent. Here we summarize the state of knowledge regarding the ultimate and proximate factors involved in the conspecific attraction of migratory songbirds. We highlight three hypotheses regarding the ultimate causes of conspecific attraction and discuss some of the proximate factors involved, such as the type of cue used (e.g., auditory and visual) and the time of year at which the information is collected. If individuals monitor others’ behavior or performance at the end of a breeding season and act upon that information the following year, we refer to these

as “post-breeding” season cues. If individuals monitor behavior at the start of the current breeding season, we refer to these as “pre-breeding” season cues. We also review which species have been tested with playback or decoy experiments and the reported consequences of these manipulations.

ULTIMATE FACTORS IN CONSPECIFIC ATTRACTION

In habitat selection, ultimate factors are those that influence fitness directly (Hildén 1965). In some capacity, intraspecific interactions (such as those elicited by conspecific attraction) influence the habitat-selection process in all species. What has become increasingly clear is that for some species or individuals conspecific cues can be as important as (and sometimes more important than) environmental cues. Conspecific cues are used when they are expected to increase fitness, but the mechanisms by which conspecific cues are linked to fitness may vary by species, individual, or life-history stage within an individual. However, most mechanisms remain hypothetical. We highlight three potential benefits that the use of conspecific attraction might confer: (1) increased mating success, (2) protection from predators, and (3) selection of higher-quality habitat. These benefits can be manifested alone or in concert (i.e., they are not mutually exclusive). Depending on the mechanism of a cue, its benefits to fitness may be immediate or delayed (e.g., to a future breeding season; Stamps 1988). In general, whether individuals benefit from delayed advantages depends on their longevity and the temporal autocorrelation of the environment (see literature on public information, e.g., Doligez et al. 2003).

Settling close to conspecifics may increase fitness by improving the mating success of both males and females. Males settling in clusters may attract more females or attract them faster than do isolated males (Lack 1948, Allee 1951, Stamps 1988). Selecting aggregations of males could also increase the efficiency of mate choice by females. Furthermore, extra-pair paternity is widespread in birds (Petrie and Kempenaers 1998, Griffith et al. 2002), and settling in aggregations could increase opportunities for extra-pair copulation by both sexes. The hidden-lek hypothesis (Wagner 1998) formalizes these ideas and suggests that the clustering of territories of socially monogamous birds is driven by extra-pair mating. For instance, there is evidence that conspecific attraction of the Least Flycatcher (*Empidonax minimus*) could be driven by a hidden-lek strategy (Wagner et al. 1996, Tarof et al. 2005, Fletcher 2007). However, not all individuals may benefit from increased paternity by settling close to conspecifics, and some males (e.g., subordinate males) might benefit from avoiding settling close to dominant males (Greene et al. 2000, Formica et al. 2004).

Theoretical and empirical evidence also suggests that settling in conspecific aggregations provides protection from predators by decreasing the risk per capita of predation (Turner and Pitcher 1986, Stamps 1988, Perry et al. 2008); predation might also be reduced as a result of neighbors warning of the presence of predators (Beletsky et al. 1986, Smith 1986, Stamps

1988). However, aggregations could also attract predators or brood parasites (Krause and Godin 1995, Ioannou and Krause 2008). For this mechanism to favor conspecific attraction, the benefits of neighbors' warnings and reduction of an individual's probability of predation would have to outweigh the costs of potentially attracting more predators.

Conspecific cues may also yield information about the quality of a location (Kiestler 1979, Stamps 1988, Stamps and Krishnan 2005). This hypothesis assumes that the presence, density, or activity of conspecifics is positively correlated with past habitat quality or an individual's experience and thus fitness (Kiestler and Slatkin 1974, Pérot and Villard 2009). After the breeding season, conspecific cues may provide information about the performance (i.e., habitat quality) of individuals at a site that year (Boulinier and Danchin 1997, Doligez et al. 2002), allowing individuals to select higher-quality habitat the following year. Before the breeding season, the presence of conspecifics is assumed to be correlated with previous experience and success at that location. In some species, the first birds to return to the breeding grounds are older, experienced individuals (e.g., Møller et al. 2004) that likely base their decision to settle on their own experience at a site. Many studies have shown that site fidelity is related to breeding success experienced at the site the previous year (Harvey et al. 1979, Haas 1998, Hoover 2003, Porneluzi 2003, Arlt and Pärt 2008). In species in which site fidelity by successful breeders that return to the breeding grounds early is strong, and if habitat quality is spatially autocorrelated, a bird settling near these individuals should therefore be selecting high-quality habitat. This hypothesis predicts that it is primarily failed or first-time breeders (often arriving later) that respond to such cues; recent experiments on conspecific attraction have shown this to be the case (Ward and Schlossberg 2004, Hahn and Silverman 2006, Nocera et al. 2006, Betts et al. 2008). Finally, use of conspecific cues to locate habitat may be especially valuable if the costs of searching and settlement are high and the time spent searching can be reduced (Stamps 1988, 1991, Mönkkönen et al. 1999, Fletcher 2006).

PROXIMATE FACTORS IN CONSPECIFIC ATTRACTION

The proximate factors in habitat selection are the physical cues that release the response to settle (Hildén 1965). For conspecific attraction, the proximate factors, such as the type and timing of cues, may vary by species and individual. These factors are of particular importance to managers using conspecific cues for management because they are the factors that can be easily manipulated.

In selecting a habitat, birds use at least two types of conspecific-attraction cues: the presence and abundance of conspecifics (decoys) and conspecific song (Reed and Dobson 1993). Likely, because of the small size and cryptic nature of many songbirds, conspecific song has been tested more extensively than have decoys in experiments at attracting migratory songbirds (Table 1). Decoys in conjunction with conspecific

TABLE 1. Species tested for a conspecific-attraction response with playbacks and decoys.

Species	Location	Cue type ^a	Cue timing ^b	Attraction successful? ^c	Response ^d	Years of data			Territory ^e	Pairing ^e	Nesting ^e	Citation
						Pre	Treatment	Post				
Laysan Albatross (<i>Phoebastria immutabilis</i>)	Hawaii	VI, VO	Pre	Yes	IL	0	1	0	NA	Yes ^f	?	Podolsky 1990
Galapagos Petrel (<i>Pterodroma phaeopygia</i>)	Galapagos Islands	VO	Pre	Yes	ID, IL	0	2	0	NA	?	?	Podolsky and Kress 1992
Black-crowned Night Heron (<i>Nycticorax nycticorax</i>)	California	VI, VO	Pre	Yes	ID	1	1	1	?	Yes	Yes	Crouch et al. 2002
Fairy Tern (<i>Sterna nereis</i>)	Papakanui Spit, New Zealand	VI, VO	Pre	Yes	IL	0	1	0	NA	?	?	Jeffries and Brunton 2001
Least Tern (<i>Sterna antillarum</i>)	New Jersey	VI	Pre	Yes	IL	0	1	0	NA	?	?	Burger 1988
Arctic Tern (<i>Sterna paradisaea</i>)	New Jersey	VI	Pre	Yes	IL, CO	0	1	0	NA	Yes	Yes	Kotliar and Burger 1984
Common Murre (<i>Uria aalge</i>)	Maine	VI, VO	Pre	Yes	IL, CO	0	4	2	NA	Yes	Yes	Kress 1983
Atlantic Puffin (<i>Fratercula arctica</i>)	California	VI, VO	Pre	Yes	CO	8	2	9 ^g	NA	Yes	Yes	Parker et al. 2007
Least Flycatcher (<i>Empidonax minimus</i>)	Maine	VI	Pre	Yes	ID	2	9	0	NA	Yes	Yes	Kress and Nettleship 1988
	Ontario	VI, VO	Pre	Yes	CO	1	1	0	N	No	No	Mills et al. 2006
Black-capped Vireo (<i>Vireo atricapilla</i>)	Montana	VO	Pre	Yes	ID	1	1	0	Yes	?	?	Fletcher 2007
Pied Flycatcher (<i>Ficedula hypoleuca</i>)	Montana	VO	Pre	Yes	CO	0	1	0	Yes	Yes	Yes	Fletcher 2009
	Texas	VI, VO	Pre	Yes	CO	2	2	1	Yes	Yes	Yes	Ward and Schlossberg 2004
	Sweden	VO	Pre	Yes	CO	0	1	0	Yes	?	?	Alatalo et al. 1982

(continued)

TABLE 1. (Continued).

Species	Location	Cue type ^a	Cue timing ^b	Attraction successful? ^c	Response ^d	Years of data			Territory ^e	Pairing ^e	Nesting ^e	Citation
						Pre	Treatment	Post				
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	Michigan	VO	Pre	Yes	ID	1	1	0	Yes	?	?	Hahn and Silverman 2007
	New Hampshire	VI, VO	Post	Yes	CO	1	1	0	Yes	Yes	?	Betts et al. 2008
American Redstart (<i>Setophaga ruticilla</i>)	Michigan		Pre	Yes	ID	1	1	1	Yes	?	?	Hahn and Silverman 2006
Baird's Sparrow (<i>Ammodramus bairdii</i>)	Montana	VO	Pre	Yes	ID	1	1	0	Yes	?	?	Fletcher 2007
Nelson's Sparrow (<i>Ammodramus nelsoni</i>)	North Dakota	VO	Pre	Yes	CO	2	1	0	Yes	?	?	Ahlering et al. 2006
	Nova Scotia	VI, VO	Pre	No	—	1	2	0	—	—	—	Nocera et al. 2006
	Nova Scotia	VI, VO	Post	No	—	1	2	0	—	—	—	Nocera et al. 2006
Bobolink (<i>Dolichonyx oryzivorus</i>)	Nova Scotia	VI, VO	Pre	No	—	1	2	0	—	—	—	Nocera et al. 2006
	Nova Scotia	VI, VO	Post	Yes	CO	1	2	0	Yes	Yes	?	Nocera et al. 2006
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)	Illinois	VI, VO	Pre	No	—	1	2	0	—	—	—	Ward et al. 2010

^a VI, visual; VO, vocal.

^b Pre, cue presented before the breeding season; post, cue presented after the breeding season.

^c As determined by the authors cited.

^d IL (increased landings), birds visited the site more frequently than controls; ID (increased density), the additional cues increased the density of birds already at the site; CO (colonized), cues attracted birds to a previously unoccupied site.

^e Yes at least one individual reported responding with the behavior;?, no relevant data given; NA, species not territorial.

^f Copulatory behavior observed.

^g Decoys kept 9 years and not removed.

song have been successful in attracting birds to a site (Nocera et al. 2006, Betts et al. 2008), but, with songbirds, decoys have not been tested alone. After breeding, birds may also use the presence and abundance of fledglings (i.e., public information; Doligez et al. 2002, Valone and Templeton 2002, Danchin et al. 2004) to identify high-quality breeding sites for the following year (Doligez et al. 2002; e.g., Ward 2005, Parejo et al. 2007, Calabuig et al. 2008).

Both before and after the breeding season, conspecific-attraction cues (decoys and songs) can influence settlement patterns (Ward and Schlossberg 2004; Nocera et al. 2006). Little is known, however, about when pre- or post-breeding-season cues are more likely to be used and how often birds use both. Pre-breeding cues may be more likely if mating strategies are a mechanism underlying conspecific attraction. The presence of other individuals at the beginning of the breeding season could increase the opportunities for extra-pair copulations. However, if the bird uses conspecific cues to indicate the location of suitable habitat, then pre-breeding cues, post-breeding cues, or both could contribute. To date, the response to post-breeding conspecific attraction cues has been less studied, but post-breeding cues are expected to be used only when the habitat is similar the following year. In experiments, both Bobolinks (*Dolichonyx oryzivorus*; Nocera et al. 2006) and Black-throated Blue Warblers (*Dendroica caerulescens*; Betts et al. 2008) used post-breeding song (in combination with decoys) as a cue for habitat selection in the following year. The use of post-breeding cues may be more frequent among long-lived species, but it has been shown in relatively short-lived species also (Betts et al. 2008).

RESULTS AND CONSEQUENCES OF ATTRACTION EXPERIMENTS

Colonial waterbirds have been the subjects of conspecific-attraction experiments for decades, and the results of these experiments are a useful comparison for the emerging work with songbirds. Because many waterbirds are colonial, their use of conspecific-attraction cues is perhaps less surprising than it is for territorial songbirds (Table 1). Most of the studies on colonial waterbirds have been limited in spatial extent (e.g., Kress 1983) or in the response measured, often only flyover rates or birds' potential prospecting (e.g., Podolsky 1990). Nonetheless, some interesting and important results have emerged. For example, Burger (1988) showed that as the number of decoys increased, responses by Least Terns (*Sternula antillarum*) also increased. Parker et al. (2007) had similar results with the Common Murre (*Uria aalge*). Both decoys (Burger 1988) and playbacks (Podolsky and Kress 1992) have been successful at attracting waterbirds to settle. Two notable aspects of some of these experimental designs are the length of experimentation and monitoring (Kress 1983, Kress and Nettleship 1988, Parker et al. 2007) and that none used post-breeding cues.

Monitoring the demographic effects of these experiments on waterbirds is also relatively limited (Table 1).

Since the conspecific-attraction playback experiment with the Pied Flycatcher (*Ficedula hypoleuca*) in Sweden by Alatalo et al. (1982), playback experiments have been published on eight other territorial songbirds of six families, all of them migratory (Table 1; Ward and Schlossberg 2004, Ahlering et al. 2006, Hahn and Silverman 2006, 2007, Mills et al. 2006, Nocera et al. 2006, Fletcher 2007, Betts et al. 2008, Ward et al. 2010). All but two species, Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*) and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), responded with attraction to a conspecific cue. Although Nelson's Sharp-tailed Sparrow and Baird's Sparrow (*A. bairdii*) are congeners, they responded to conspecific playback differently.

From these eight territorial species, only three, the Least Flycatcher, Black-throated Blue Warbler, and American Redstart (*Setophaga ruticilla*), have been tested at multiple locations, with responses consistent at each. However, in contrast to the findings of Hahn and Silverman (2007), an experiment by Cornell (2007) found weak and variable effects of conspecific playback before the breeding season on the settlement of Black-throated Blue Warblers, although this difference may be attributable to differences in study design. Nonetheless, given the overall positive responses to date, it is likely that conspecific attraction is widespread among the songbirds.

Four major habitat types (forest, grassland, shrubland, and wetland) are represented among the species tested. The only two species not to respond inhabit wetlands. Temporal autocorrelation of the three terrestrial habitat types is likely greater than in wetlands, and in extremely dynamic systems, such as wetlands, it may be that environmental cues such as surface area or depth of water are more reliable than conspecific cues. However, Ward et al. (2010) found that several species of wetland birds appear to aggregate and may be using the presence of heterospecifics as well as that of conspecifics. Additionally, previous research has shown that when selecting a breeding site Yellow-headed Blackbirds use the number of conspecific young produced at the site previously (i.e., public information; Ward 2005).

Among the eight species of songbird that have been attracted to a site with playbacks, there is evidence of pairing success for only three species and evidence of nesting attempts and success for only two, the Black-capped Vireo (*Vireo atricapilla*) and Least Flycatcher (Table 1). Ward and Schlossberg (2004) showed that nest success of the Black-capped Vireo was relatively high where recordings were broadcast and Brown-headed Cowbirds (*Molothrus ater*) were managed. Such data on the demographic consequences of playback are often lacking because of limited effort or time available in experimental studies. Only two studies present data for the year after initiation of playback, and both demonstrated some carry-over effects with birds returning to the site (Ward and Schlossberg 2004, Hahn and Silverman 2006).

Finally, few studies have examined the effect of experiments with playback on community dynamics. Fletcher (2008) demonstrated a reduction in richness of migratory species where the Least Flycatcher's song was broadcast, most likely because the broadcasts deterred migratory birds from these sites. Addition of a target species to a novel habitat through conspecific playback may also result in existing community members emigrating from a site (Betts et al. 2010). In some instances, niche space may be limited to the extent that it is not possible to support all members of the previous avian community as well as the target species. Additionally, literature on heterospecific attraction suggests that effects of broadcasted song on nontarget species should be considered (Thomson et al. 2003, Parejo et al. 2004).

USE OF ATTRACTION METHODS IN CONSERVATION AND MANAGEMENT

Although decoys have been used for decades in waterbird conservation, the use of attraction methods for other species is quickly becoming a realistic possibility. One appealing aspect of conspecific attraction is its ability to manipulate the target species directly. Many other management techniques are more passive and rely on the philosophy "if you build it, they will come" (Ahlering and Faaborg 2006). Birds actively choose an area (rather than a manager forcing movement, as in translocation). Even so, conspecific attraction could be used to aid translocation, possibly preventing homing and dispersal of relocated individuals that may be searching for conspecifics in their new habitat (Stamps and Swaisgood 2007). Conspecific-attraction methods are also relatively cheap and easy to implement if appropriate habitat is available. Equipment to broadcast song can be assembled at low cost, but the ease of execution will depend upon the investigator's experience with the equipment. Finding the equipment appropriate for a site and designing a system effective for it can be complex. Finally, attraction methods seem to produce a quick response; published studies report that birds' response, after arrival, has been almost instantaneous. In general, this technique could be a relatively quick, cheap, and easy way to manipulate a species' presence or density directly.

One concern with the use of conspecific-attraction methods is the perceived success of these techniques and the perceived lack of failure (Dodd and Seigel 1991). We advise caution in such interpretation, as most published literature on conspecific attraction reports positive responses to playbacks or decoys even though the strength of the response varies (Table 1). Very few papers report no response to conspecific playbacks, and it is difficult to say whether this is because few studies have found no response or because papers reporting no response are less likely to be published. For conservation and management, it would be desirable for the literature to represent all results from similar methods so the method is

not wrongly perceived as a unanimous success. Furthermore, when no effects are observed, we need to acknowledge that lack of a response does not necessarily indicate the species is not attracted to conspecifics but rather that the experimental approach might be ineffective in eliciting a positive response. Indeed, given the myriad of potential conspecific cues, confirming a lack of response to such cues will be challenging.

CONSIDERATIONS FOR PRACTITIONERS

Although there are still many unknowns about conspecific attraction in birds, we acknowledge that conservation cannot wait for science. Therefore, our intention here is to use current knowledge to provide recommendations and cautions about issues a manager should consider when deciding whether attraction methods are appropriate. Conspecific attraction may still be too risky for use with threatened or endangered species, considering we often do not understand their true habitat requirements, but it may be less risky than translocation. Regardless, conspecific attraction is most likely to be considered as a management option for species with small or declining populations, and decisions will need to be made carefully.

We provide a chart of questions to be answered when conspecific-attraction cues are considered as a management strategy (Fig. 2). The first two boxes concern whether a species is likely to respond to a conspecific cue, whether a site is likely to favor survival and reproduction if birds are successfully attracted, and whether the addition of conspecific cues will affect the target species only. If the target species is known to dominate behaviorally over other species in the community that are also of concern, using conspecific cues to increase the density of the target species may affect other community members adversely (Fletcher 2008). If the answer to any of the questions in the first two boxes is no, then conspecific-attraction methods may not be appropriate for the target species. The second two boxes outline questions and issues that should be addressed if conspecific-attraction methods are still being considered, such as the factors of the treatment design (e.g., cue type and timing) and the long-term goals for the species at the site.

To determine whether a target species is likely to respond, the first step should be to compare the ecology and behavior of the target species to species that have shown strong positive responses previously (Table 2). As a prerequisite, a species or focal population needs to have some tendency to actively disperse or migrate so that individuals can be attracted to a site. On the basis of the ultimate factors for conspecific attraction outlined above, we suggest that tendencies toward extra-pair copulations and aggregations of territories within a habitat may be useful predictors for settlement in response to playbacks. Previous studies have hypothesized that aggregations, independent of underlying environmental variation, may be caused by conspecific attraction (Sherry and Holmes

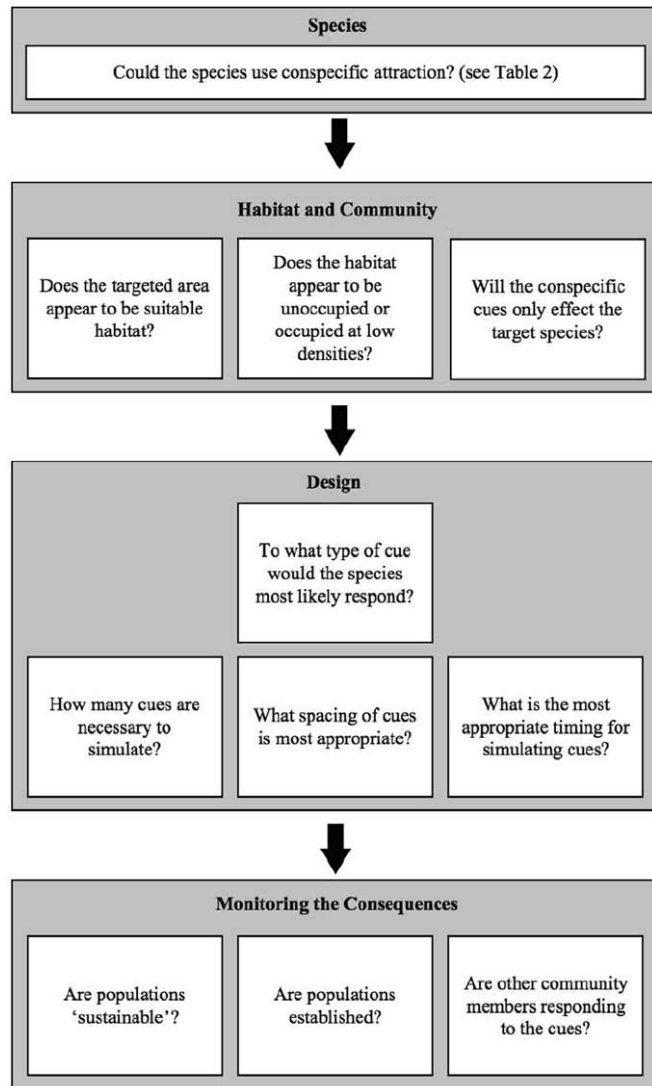


FIGURE 2. Flow chart of recommended questions before conspecific-attraction methods are applied in conservation.

1985, Stamps 1988, Betts et al. 2006, Bourque and Desrochers 2006, Nocera et al. 2009). Spatial techniques such as spatial-point-pattern analysis (Melles et al. 2009), autologistic regression (Augustin et al. 1996), or semivariogram analysis reveal the degree to which animals are aggregated while controlling for environmental gradients that may also influence distributions (Betts et al. 2009). Such patterns, however, may also be caused by other ecological or life-history traits such as limitation of dispersal, so evidence of spatial clustering does not ensure that a species uses conspecific cues.

Other characteristics that may favor conspecific attraction are a high ratio of juveniles to adults, a short lifespan (i.e., limited opportunities to breed), a short breeding season, and asynchronous or sequential breeding (Table 2). Juveniles and short-lived species may be more likely to take advantage of

TABLE 2. Clues for potential conspecific attraction by birds selecting breeding habitat.^a

Spacing
Coloniality
Aggregated territories/patchy distributions
Behavior and life history
Extra-pair mating behaviors
Large juvenile:adult ratio in population
Few breeding opportunities (e.g., low survival)
Migratory behavior
Breeding phenology
Short breeding season
Asynchronous breeding

^a From Kress and Nettleship (1988), Mönkkönen et al. (1990), Wagner (1998), Fletcher and Miller (2006), and Nocera et al. (2006).

information gained from older, more experienced individuals. Young birds and first-time breeders seem especially prone to using social cues to select a habitat, whereas older, more experienced birds may be more likely to settle on the basis of their own experience (Nocera et al. 2006, Betts et al. 2008, Nocera et al. 2009); how widely this principle applies to species beyond those tested remains to be seen. Similarly, short-lived species are less able to base decisions on their own experience and may be more likely to use conspecific cues (Table 2). Species with short breeding seasons that have to make quick decisions about where to breed may also be more likely to use conspecific information. To use pre-breeding conspecific cues, the species must breed asynchronously for later-arriving individuals to be attracted to early settlers. Many species of migratory birds have these characteristics; they breed asynchronously within a short season. Additionally, older, more experienced, and reproductively successful individuals often return first, and younger, inexperienced migrants return later (Møller et al. 2004), when there is less time to select a breeding location. To date, research suggests that most migratory species are likely to respond to some type of conspecific cue, but for resident birds the data are lacking. Although resident birds often breed sequentially, they frequently reside in or near their breeding location during the nonbreeding season and may have more time to assess a variety of cues to determine where to breed.

Site quality is an important consideration for successful attraction and population establishment (Fig. 2). It is especially important to ensure the habitats to which birds are drawn are not sinks (i.e., habitats where mortality exceeds reproduction; Pulliam and Danielson 1991). If attraction is planned at a site where a species occurred formerly, it is important to understand the original reason for the species' decline. Attracting birds to habitat from which they have disappeared is risky if the initial cause of decline has not been identified and addressed (Dodd and Seigel 1991, Fischer and Lindenmayer 2000). For any species, it is also important to evaluate expected habitat quality in terms of factors known to affect fitness (e.g., structure

of vegetation, availability of food, presence of competitors, and density of predators or nest parasites). Factors that are not visibly apparent, such as contaminants, could be an issue at some sites and should be considered. Finally, the location of the site within a species' geographic distribution may also be an important consideration. At the edges of a range, where populations are often small and habitats and bird densities are likely to be different (Mehlman 1997), behavior may differ in unexpected ways from that typical in the core of the species' range (Carbonell et al. 2003, Favaron et al. 2006).

The success of an attraction method can be affected by a project's design and implementation (Fig. 2). Depending on the selection mechanism, playbacks before or after the breeding season, or both, may be appropriate. The amplitude of the songs broadcast from the speakers and the density of the speakers at the site could influence a bird's decision to settle. Weak stimulation may not induce a response, and intense stimulation may act as a deterrent. Song type could also be influential, but the effects of song type on settlement have not yet been documented. In species whose song varies geographically, individuals with a song different from the one broadcast may not respond as expected. For example, individuals with a different song may be less likely to settle if their expected mating success with individuals with the different song is reduced (Bensch et al. 1998). In general, we recommend that all the above variables mimic natural conditions as closely as possible. The playback should contain only the songs of the target species because including other species' songs on the playbacks could have unintended effects on the target species. In some cases, the songs of other species could be interpreted as the presence of competitors (Mönkkönen et al. 1999, Thomson et al. 2003, Forsman et al. 2007, Fletcher 2008). There are many details to consider when selecting an attraction method, and many of them have yet to be tested. We recommend designing attraction experiments so variables of interest, such as the density of playback speakers per site (see Burger 1988 for an example with terns), can be evaluated, then publicizing or publishing the results for the benefit of others.

We strongly encourage, at the outset of an attraction project, establishment of a long-term strategy that includes a clear

plan for pre- and post-implementation monitoring (Fig. 2). The ultimate goal of the project should be established early so that success can be measured. If the goal is a self-sustaining population established at the site, expectations for what is considered "self-sustaining" and "established" need to be clear. Monitoring should then include measures of breeding activity, reproductive performance, and survival, in addition to settlement. A plan for population monitoring should be articulated clearly at the beginning and maintained throughout the duration of the project. Depending on the species' longevity and age of maturity, monitoring the project's results for >3 years after successful attraction will help determine whether the population can persist, given natural annual variation. Results of the monitoring should be published to add to our knowledge of the consequences of conspecific attraction.

RESEARCH NEEDS

There are many unanswered questions about the use of conspecific attraction in avian habitat selection. Here, we focus on five areas of research that are especially important for conservation: (1) the mechanisms and functional significance of conspecific-attraction behavior; (2) the intraspecific variation in the behavior (particularly ecological correlates with life history); (3) the relative importance of social and structural or environmental cues in habitat-selection decisions; (4) factors relating to the properties of the cues themselves (e.g., song frequency and timing), and (5) consequences of conspecific attraction for the population and community. To enhance the effectiveness of conspecific-attraction methods as a conservation and management tool, research questions and management needs should be linked (Table 3).

Understanding the ultimate factors involved in conspecific attraction is important to guide predictions of which species or individuals are good candidates for use of conspecific-attraction methods for conservation. Above, we summarized four potential mechanisms by which the fitness of migratory birds should benefit from conspecific cues, but knowledge of the extent to which these mechanisms apply in different species is very limited. We need to increase the

TABLE 3. Linking management and research questions for using social cues in conservation and management.

Management question	Research question
Is conspecific attraction necessary for restoration of species at a site?	What is the relative importance of social and environmental cues in habitat selection?
Which species use social cues?	What are the underlying causes of the conspecific-attraction behavior?
Should pre- and/or post-breeding season cues be used?	Does stimulus type influence the attraction response?
Should song and/or decoys be used as a cue?	Do species respond only above a threshold based on the number or density of simulated cues?
What density (intensity/spacing) of cues (i.e., playbacks or decoys) is necessary to attract birds?	What are the demographic consequences of attracting birds, and are they predictable?
Will conspecific attraction create a sustainable population?	What are the local versus regional population effects of attracting birds?

number of species tested to explore the life-history and ecological correlates of various mechanisms and to better understand the variation in the mechanisms. Expanding the suite of species tested to include permanent residents is especially necessary for understanding the mechanisms and ultimate factors involved in conspecific attraction. Because mechanisms of conspecific attraction may not be mutually exclusive, uncovering mechanisms will be a continuing challenge.

We need more research addressing which mechanisms the sexes or age classes within a species may use and how these can vary with different environmental or ecological conditions. Furthermore, we might expect the use of conspecifics as a cue for habitat selection to vary across a species' range. Only a few species have been tested in more than one location (Table 1), and more extensive surveys should be conducted to examine the response to conspecifics at the limits of a species' distribution. Such information will be particularly important if managers intend to use such techniques to facilitate range shifts to accommodate climate change (Thomas and Lennon 1999). Understanding the intraspecific variation in conspecific attraction should increase the power with which the effect of the playback technique can be predicted in new situations.

Another issue vital to the implementation of conspecific-attraction methods and needing extensive investigation is the relative importance of the types of cues used during habitat selection. The cues include not only social cues, such as the presence, abundance, or performance of conspecifics, and environmental cues, such as vegetation characteristics, but other factors such as landscape features and community composition. Betts et al. (2008) examined the relative importance of social and vegetation cues. They found social cues were able to lure Black-throated Blue Warblers into habitat not normally used by the species (see also Fletcher 2009). In a study of the same species, however, Cornell (2007) reported vegetation cues to be more important than social cues. Clearly, the relative importance of different cues may vary both between and within species (e.g., depending on the relative availability and variability of the cues), and more studies are needed to clarify where conspecific attraction fits in the habitat-selection hierarchy. The limited results thus far provide support for an important caution: if social cues are strong enough to attract birds to poor-quality habitats, we need to be especially careful about the situations in which this technique is implemented.

The properties of the cues themselves (e.g., amplitude, frequency, timing, song type) may affect birds' decisions to settle. However, these issues have been little explored. Birds respond to a cue only when they perceive it as salient, yet we have devoted surprisingly little effort to investigating how and when cues become important as well as how birds search for these cues. For instance, there is little empirical evidence suggesting which species assay their environment for auditory cues (playbacks), visual cues (decoys), or both. Although some research is starting to suggest that age and habitat may

be a factor, we know little about which birds act more on pre-breeding or on post-breeding cues. Research to answer these questions will be critical to determining how a conspecific-attraction program should be established.

The most prominent gap in our knowledge of conspecific attraction in songbirds is our lack of information about the consequences of attracting birds by such manipulations. Very few studies of songbirds have documented the post-settlement consequences of luring them to a site (Table 1). For the technique to be implemented successfully, information about the consequences at the levels of the individual, population, community, and landscape is essential. The immediate questions undoubtedly concern the effects on the fitness of attracted birds in terms of nest success, survival of juveniles and adults, and rates of return to these sites. It is also important to understand whether artificial attraction to a site could cause the individuals attracted to behave aberrantly (Reinert 1991, Rittenhouse et al. 2007). Many of these traits are difficult to study even in natural populations, but they are of particular interest and importance in situations where active conservation or population management is the goal. It is an open question as to whether playback-mediated shifts in a bird's distribution have the potential to alter population trends. Addressing this question will be challenging, but the answer is especially valuable for situations involving endangered or threatened species whose numbers are low. Color-marked populations may allow researchers to determine from where settlers are drawn and to evaluate the potential benefits of attracting these individuals to a new location. If playback simply redistributes existing birds, this may be a zero-sum situation. However, if playbacks provide opportunities for successful breeding to individuals that would have otherwise failed or not bred, then the manipulations may have positive consequences at the level of the population. The hypothesis that playbacks can increase a population's growth rate by altering its distribution is premised on the notion that individuals do not always have the capacity to find optimal habitat on their own. Although it is often assumed that individuals select the best habitats for settlement (Fretwell and Lucas 1969, McPeck et al. 2001), in reality individuals may make non-ideal choices and occupy poorer habitats before better ones (Misenhelter and Rotenberry 2000, Stamps and Krishnan 2005, Stamps et al. 2005, Arlt and Pärt 2008).

CONCLUSIONS

While research on conspecific attraction in avian habitat selection is growing, our review highlights the enormous amount of uncertainty regarding use of social attractants, like playbacks and decoys, for conservation. We considered only the use of social attractants for selection of breeding habitat, but similar approaches could be used to promote selection of non-breeding habitat (e.g., migratory stopover sites), foraging habitat, and/or movement through landscapes. Our intent is not to deter or promote the use of this technique but rather to inspire

participation in the progress of this developing field and to synthesize information useful for both conservation and research.

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