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Conspecific Attraction and the Conservation of Territorial Songbirds

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Abstract: *Conspecific attraction, the tendency for individuals of a species to settle near one another, is well described in colonial species, especially birds. Although this behavior may occur in territorial birds, evidence has been lacking. If territorial birds do exhibit this behavior, it would have major conservation implications. Birds could potentially be attracted to specific sites with artificial stimuli, making conservation of those species more efficient. In 2001 and 2002, we tested whether conspecific attraction occurs in an endangered, territorial songbird, the Black-capped Vireo (*Vireo atricapilla*) by playing vireo vocalizations in unoccupied habitats at Fort Hood, Texas. We were successful in attracting 73 birds to five experimental sites in 2001 and 75 birds to seven experimental sites in 2002. No birds settled on comparable control sites. Many birds attracted to the vocalizations paired and bred. At most research sites the primary threat to the species, the brood-parasitic Brown-headed Cowbird (*Molothrus ater*), was controlled, allowing vireos to achieve high nesting success relative to a nearby, unmanipulated population. Second-year birds were more responsive to conspecific vocalizations than older birds, as they were more common on experimental sites than in the established population. In 2002 birds recolonized experimental sites from 2001 where vocalizations were not played in 2002, indicating that 1 year of playbacks may be sufficient to establish a population. Our results provide the first experimental evidence that territorial songbirds use the presence of conspecifics when deciding where to settle and suggest that conspecific attraction may provide a valuable conservation tool.*

Key Words: Black-capped Vireo, conspecific attraction, endangered species, habitat selection

Atracción Conespecífica y la Conservación de Aves Canoras Territoriales

Resumen: *La atracción conespecífica, tendencia de los individuos de una especie a establecerse cerca de otro de la misma especie, está bien descrita en especies coloniales, especialmente aves. Aunque este comportamiento puede ocurrir en aves territoriales, se carece de evidencia. Si aves territoriales muestran este comportamiento, tendría implicaciones mayores en la conservación. Las aves potencialmente serían atraídas a sitios específicos mediante estímulos artificiales, haciendo más eficiente la conservación de esas especies. En 2001 y 2002, probamos si ocurre la atracción conespecífica en una especie de ave canora territorial, en peligro, *Vireo atricapilla*, con la reproducción de vocalizaciones de vireo en hábitats desocupados en Fort Hood, Texas. Tuvimos éxito al atraer a 73 aves a cinco sitios experimentales en 2001 y 75 aves a siete sitios experimentales en 2002. No se establecieron aves en sitios controles comparables. Muchas de las aves atraídas a las vocalizaciones formaron pareja y se reprodujeron. En la mayoría de los sitios, la principal amenaza para la especie, el parásito *Molothrus ater*, fue controlada, lo que permitió un elevado éxito de anidación a los vireos en comparación con una población no manipulada cercana. Las aves de dos años tuvieron mayor respuesta a las vocalizaciones conespecíficas que las aves más viejas, porque fueron más comunes en los sitios experimentales que en la población establecida. En 2002 aves recolonizaron sitios experimentales de 2001 en los que no se reprodujeron*

‡Order of authorship determined by coin flip.

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vocalizaciones en 2002, lo que indica que 1 año de repetición de vocalizaciones puede ser suficiente para establecer una población. Nuestros resultados proporcionan las primeras pruebas experimentales de que aves canoras territoriales utilizan la presencia de conspecíficos al decidir donde se establecen y sugieren que la atracción conspecífica puede ser una valiosa herramienta de conservación.

Palabras Clave: atracción conspecífica, especies en peligro, selección de hábitat, *Vireo atricapilla*

Introduction

Understanding an animal's behavior may be just as important for conservation as understanding its environment (e.g., Clemmons & Buchholz 1997; Sutherland 1998; Caro 1999; Gosling & Sutherland 2000). Traditionally, animal populations have been conserved by identifying and controlling threats such as habitat destruction or predators. Recently, however, conservationists have recognized that simply focusing on an animal's external environment may not be sufficient to conserve certain species. Reed (1999) describes numerous examples of how behaviors such as predator naiveté or avoidance of gaps during dispersal have contributed to the extinction and endangerment of birds. In cases where behavior affects demography, understanding behavioral processes may allow managers to develop improved methods for conserving species at risk. As an example, behavioral training in skills such as predator avoidance and foraging has been used to improve the success of animal reintroductions (e.g., Biggins et al. 1999; McLean et al. 2000; Meretsky et al. 2000).

One of the best examples of the in situ application of behavioral techniques is work on colonial seabird reintroduction by Kress (1997). Many colonial seabirds exhibit conspecific attraction, a tendency to settle near individuals of their own species. To reestablish colonies of Atlantic Puffins (*Fratercula arctica*) and Arctic Terns (*Sterna paradisaea*) on uninhabited islands, Kress used models of birds, mirrors, and playbacks of calls to create the appearance of an occupied colony. As a result, birds were attracted and founded new colonies. This technique has been used successfully on a number of colonial bird species (Podolsky 1990; Podolsky & Kress 1992; Blokpoel et al. 1997; Jeffries & Brunton 2001; Martinez-Abraín et al. 2001).

Although these results show promise for conservation, this technique has only been applied to birds that breed in groups. The majority of bird species are territorial (Lack 1968), and conspecific attraction has never been demonstrated conclusively in territorial birds. In fact, habitat-selection theory predicts that individuals of territorial species should eschew conspecifics to avoid density-dependent fitness losses (Fretwell & Lucas 1970). Nonetheless, anecdotal and observational evidence suggests that conspecific attraction may occur in territorial species (Stamps 1988). Observers have reported a ten-

dency for birds to aggregate their territories, even in continuous habitat (Møller 1983; Herremans 1993; Poysa et al. 1998; Tarof & Ratcliffe 2000; Arsenault et al. 2002). In an observational study of nest-site selection by House Wrens (*Troglodytes aedon*), Muller et al. (1997) found that new breeders at a site select nest boxes based on their proximity to established males' territories. To our knowledge, the only previous experiment on conspecific attraction in a territorial bird is that of Alatalo et al. (1982). They found that Pied Flycatchers (*Ficedula hypoleuca*) are somewhat more likely ($p = 0.07$) to settle at sites where vocalizations had been played than at comparable control sites.

If territorial birds use the presence of conspecifics to determine where to settle, this behavior would have significant conservation implications (Smith & Peacock 1990). By reproducing the appropriate cues, birds could be attracted to specific, preselected sites known to be high-quality habitat or managed to mitigate limiting factors such as predators or parasites (Reed & Dobson 1993). The ability to attract endangered or declining birds to specific sites could dramatically change the way these species are managed. Currently, the only option for conserving many species is to protect existing habitat or to control limiting factors where birds choose to settle. Being able to attract individuals to predetermined locations would allow managers to more effectively and efficiently manage endangered or declining species.

Here, we report the results of an experimental study of conspecific attraction in an endangered, territorial songbird, the Black-capped Vireo (*Vireo atricapilla*). This Neotropical migrant breeds in early successional shrublands over a small range in Texas and Oklahoma (U.S.A) as well as northern Mexico (Grzybowski 1995). The vireo is threatened by loss of habitat due to fire suppression and livestock grazing and by brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). We suspected that vireos may select habitats based on the presence of conspecifics because the birds are often patchily distributed and can take several years to colonize new habitat (Graber 1961). We addressed four questions: (1) Do Black-capped Vireos preferentially settle where conspecific vocalizations are played? (2) Will birds attracted by artificial cues establish territories, pair, and nest? (3) What are the demographic characteristics of populations established through conspecific attraction? (4) Do populations

Table 1. Study sites and experimental design for the study of conspecific attraction in Black-capped Vireos.

Site	Location	Cowbird control	Experimental treatment	
			2001	2002
41	Fort Hood	yes	playback	control
51	Fort Hood	yes	playback	playback
1	Fort Hood	yes	playback	control
27	Fort Hood	yes	playback	playback
36	Fort Hood	yes	control	playback
Murry	off base	no	playback	playback
Barton Creek	off base	no	control	playback

established through conspecific attraction persist for more than 1 year?

Methods

We selected five study sites at Fort Hood (a U.S. military base), Texas, and two other sites on private property in central Texas that had one or no pairs of vireos for at least 2 years before 2001. These sites ranged in size from 15 to 71 ha and were appropriate habitat for vireos based on consultations with experienced vireo researchers (G. Eckrich, personal communication). Fort Hood has one of the largest populations of Black-capped Vireos, and Brown-headed Cowbirds have been systematically removed from this location for the past 13 years (Eckrich et al. 1999). Cowbirds were not controlled at the two sites on private property.

In 2001 we played recordings of vireo vocalizations at four sites on Fort Hood and at one site on private property (Table 1). Two sites, one on the base and one off, were controls where we did not play vocalizations. In 2002 we played vocalizations at the two control sites from 2001, making them experimental playback sites. To determine whether a second year of playbacks would be necessary for vireos to recolonize experimental sites from 2001, we did not play vocalizations at two of the five former experimental sites in 2002. At the other three experimental sites from 2001, we conducted playbacks in the previous locations.

Playback of Vocalizations

At each experimental site, we played prerecorded vocalizations of Black-capped Vireos on two to four portable stereos (call boxes), spaced approximately 200 m apart. Vocalizations were not played at the control sites. At the experimental sites, vocalizations were played at maximum volume (approximately 80 db) from 0400 to 1030 daily throughout the settlement period and the breeding season (mid-March through early July). We mounted the stereos on wooden platforms, approximately 2 m above

the ground, and a solar panel powered the system. The stereos played compact discs that were 74 minutes long and included approximately 50 minutes of Black-capped Vireo song recorded at Fort Hood, 4 minutes of vireo alarm calls, 10 minutes of silence, and 10 minutes of songs of other species that co-occur with vireos: Bewick's Wren (*Thryomanes bewickii*), Scissor-tailed Flycatcher (*Tyrannus forficatus*), Painted Bunting (*Passerina ciris*), Field Sparrow (*Spizella pusilla*), and Rufous-crowned Sparrow (*Aimophila ruficeps*). We included the silent periods and heterospecific songs to prevent the vireos from habituating to the playbacks. Vocalizations were divided into tracks approximately 1 minute long. The stereo played the vocalizations in random order, playing each track on the disc once before repeating.

In 2001 we placed plastic resin models of vireos near some call boxes. This was done because we were unsure whether vireos would respond to the song playbacks without a visual stimulus. We never observed vireos interacting with the models, and there was no difference in settlement patterns between sites with and without models. Consequently, we did not use models again in 2002.

Field Methods

We visited all sites at least once a week throughout the breeding season and recorded the locations of all vireos seen or heard. We monitored all sites except one control site in 2001, when personnel from The Nature Conservancy conducted the bird surveys. We determined the age of males by plumage characteristics (Grzybowski 1995). Males were classified as either second-year (hatched the previous year) or after-second-year. In addition, we captured some vireos with mist nets and banded them with a unique combination of color bands. Where vireos established territories and paired, we located nests and monitored them at 2- to 7-day intervals.

Analysis

We plotted all vireo sightings on maps of the study areas to determine the number of second-year and after-second-year males and the number of females present. Population estimates were based on numbers of banded birds and simultaneous sightings of individuals, analogous to the spot-mapping technique (Bibby et al. 2000). In 2002, observations of previously banded vireos allowed us to determine the return rate of individuals. We used Fisher's exact test to compare return rates of birds at sites with and without cowbird control. We used the same test to compare the age structure of males in 2002 at sites with and without call boxes. Nesting success was estimated using the Mayfield (1975) technique. To determine whether or not birds attracted to experimental sites behaved typically for this species, we compared the nesting success

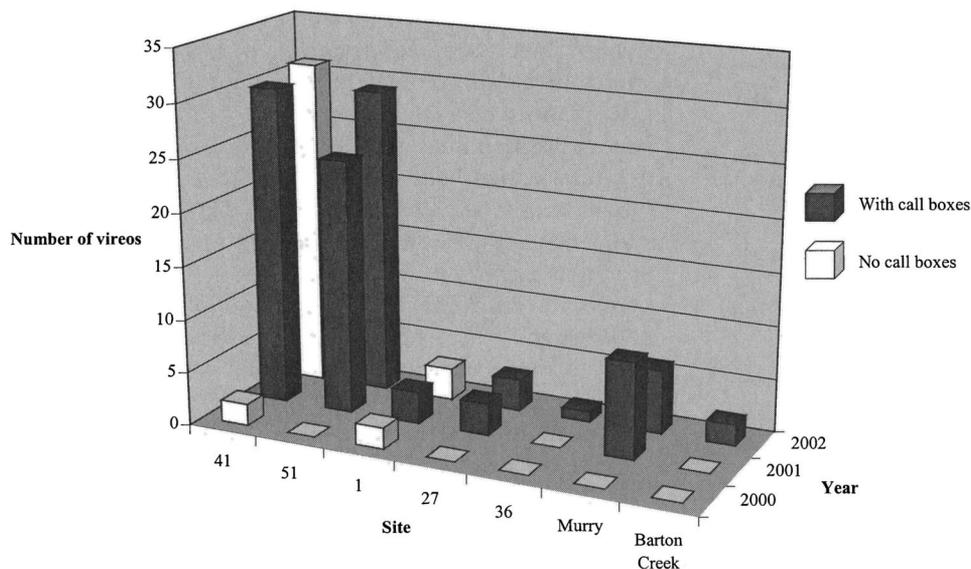


Figure 1. Estimated numbers of Black-capped Vireos on study sites.

and age structure of vireos on experimental sites with those of an established population at Fort Hood, which has been studied for the last 13 years (The Nature Conservancy 2001). We compared age structure between the experimental and established populations with the G test.

Results

Prior to 2001, four Black-capped Vireos had been observed on our seven sites over several years. In 2001 we observed 73 vireos on five experimental sites, whereas no birds settled on two control sites (Fig. 1). In 2002 we observed 75 vireos on the seven sites. At each site, the first year of playbacks led to an increase in the local vireo population relative to the previous year (Wilcoxon signed-rank test, $T = 0$, $p = 0.02$; Fig. 1). On the two sites that had call boxes in 2001 but no call boxes in 2002, the number of vireos remained nearly unchanged (29 vs. 30, 3 vs. 3, respectively). The sites that had call boxes

for a second year in 2002 also continued to have similar numbers of vireos (24 vs. 31, 3 vs. 3, 9 vs. 6).

We found 17 nests in 2001 and 16 nests in 2002. Nesting success was similar in both years, so we combined results for analysis. Overall nesting success was high, but sites differed based on whether or not cowbirds were controlled. On sites with cowbird control, vireos had high nesting success and low cowbird parasitism (Table 2). On the site without cowbird control, all nests were parasitized and unsuccessful in both years of the study (Table 2). The nesting success of vireos on sites with cowbird control at Fort Hood was even greater than that of the established populations (Table 2).

In 2001, 42% of the males on our experimental sites were in their second year ($n = 48$). In contrast, the age structure of males in the established population at Fort Hood was 28% second-year (The Nature Conservancy 2001). There was a marginally significant difference in the percentage of second-year males in the two populations ($G = 3.44$, $p = 0.06$). In 2002 at sites that had call boxes in both 2001 and 2002, 32% of males were second-year ($n = 26$). At sites where call boxes were used only in 2001, 26% of males were second-year ($n = 21$). This was not a significant difference (Fisher's exact test, $p = 0.23$).

Overall, 33% ($n = 33$) of the vireos banded as adults (second-year or after-second-year birds) in 2001 returned to the same sites in 2002. By sex, 41% ($n = 27$) of the males and 17% ($n = 6$) of the females returned. A higher proportion of males, 52% ($n = 21$), returned to sites with cowbird control than to sites without, 0% ($n = 6$; Fisher's exact test, $p = 0.03$). This relationship did not hold for females, 20% ($n = 5$) of which returned to sites with cowbird control and 0% ($n = 1$) of which returned to sites without cowbird control (Fisher's exact test, $p = 0.33$). The test, however, has low power because of the small sample size.

Table 2. Nesting success and brood parasitism rates of Black-capped Vireos on experimental sites (vocalization playbacks) and a nearby, established population.

Site	Nesting success ^a (%)	Brood parasitism rate (%)
All experimental sites ($n = 33$)	52	18
Fort Hood sites ($n = 29$)	61	7
Off-base sites ($n = 4$)	20	100
Established population ^b ($n = 132$)	32	5

^aEstimated using the Mayfield (1975) method for the entire nesting period of 26 days. For experimental sites, data from 2001 and 2002 are combined.

^bData from The Nature Conservancy (2001).

Discussion

Our results offer strong experimental evidence that territorial birds use the presence of conspecifics to select a habitat. Playing conspecific vocalizations invariably led to an initial increase in local vireo populations. Although our sample sizes were small, evidence leads us to believe that vireos were attracted specifically to the vocalizations. The increase in vireo numbers on experimental sites was not due to an influx of vireos into the region. In fact, the regional population of vireos on Fort Hood decreased between 2000 and 2001 (The Nature Conservancy 2001). Furthermore, the vireos appeared to treat the call boxes as if they were birds with very small territories. Early in the season, vireos frequently counter-sang with the call boxes. In some cases, vireos would sing while moving around the call box, a behavior reminiscent of birds' counter-singing at the edges of one another's territories. Later in the season, however, the birds appeared to have habituated to the call boxes. They no longer sang in response to the playbacks, just as birds are known to habituate to the calls of their neighbors once their territories are established (Brooks & Falls 1975).

The playbacks consisted of both conspecific and heterospecific vocalizations. Recent work suggests that some migratory birds are attracted to areas with high numbers of heterospecific residents when selecting habitats (Mönkkönen et al. 1990; Forsman et al. 1998; Mönkkönen & Forsman 2002). Although we cannot rule out the possibility that heterospecific vocalizations attracted vireos in this experiment, we find this conclusion unlikely. The 74-minute playback disc included only 10 minutes of heterospecific songs versus 54 minutes of Black-capped Vireo vocalizations. Furthermore, the vireos that did settle on the site were never observed responding to heterospecific song playbacks. They did, however, respond to conspecific songs with approaches and counter-singing. Thus, the vireos were likely attracted to conspecific rather than to heterospecific vocalizations, but further experiments would be necessary to confirm this conclusion.

Although vireos were attracted to playbacks in appropriate habitat, this does not imply that vireos could be attracted to any type of habitat. Our results suggest that habitat quality may be important in habitat selection by vireos, and this may influence the success or failure of this conspecific attraction technique. Two sites that only attracted a few birds (sites 1 and 27 in Fig. 1) had limited amounts of high-quality habitat surrounded by a larger area of low-quality habitat (Grzybowski et al. 1994). Thus, the presence of conspecifics may be just one cue in a suite of cues used by vireos to select habitats (Stamps 2001).

Unlike colonial seabirds, which can be attracted by models, vireos appeared to be attracted only by vocalizations. The vireos' lack of a response to models may have been due to the dense vegetation in their habitat. This scrubby, early-successional habitat is dominated by

oaks (*Quercus sinuata*) and other dense trees and shrubs, and vireos spend much of their time in the foliage. They therefore probably communicate primarily through vocalizations. Visual cues may be more important to passerines in other habitats, and models may be necessary for conspecific attraction in these species.

Demographic Patterns

Overall, vireos attracted to experimental sites behaved similarly to vireos in natural populations. Birds on our sites established territories, paired, and bred. At sites with cowbird control, vireos had high nesting success, indicating that populations founded through conspecific attraction can be productive and contribute to the recovery of the species.

Following removal of call boxes on two sites in 2002, many individuals exhibited site fidelity. Presumably, these returning birds acted as a seed for their local populations and attracted new birds to the sites (as described by Stamps 1991). Site fidelity, however, was strongly influenced by cowbird control. In many species, individuals that reproduce successfully one year are more likely to return to a site in the following year (e.g., Bollinger & Gavin 1989; Haas 1998; Hoover 2003). On our sites that lacked cowbird control, nesting success was extremely low, and none of the birds banded there in 2001 returned in 2002. In contrast, nesting success was much higher on sites with cowbird control, and return rates were correspondingly higher. This implies that populations established with conspecific attraction would not recolonize a site if Brown-headed Cowbirds were not controlled and if nesting success were too low. Thus, the success of conspecific attraction in establishing a population that persists for multiple years may require high nesting success.

Populations on experimental sites in 2001 contained a higher proportion of second-year males than did established populations. There are two possible explanations for this pattern. First, because they lack experience in selecting breeding habitat, young birds may be more likely than older birds to use conspecific attraction. Alternatively, all birds looking for new breeding sites may use conspecific attraction. Because some after-second-year birds will return to their previous breeding sites, second-year birds may simply make up a greater proportion of the birds settling at new sites.

Implications for Habitat Selection

Theoretical and empirical studies of habitat selection suggest that animals should avoid conspecifics because fitness decreases with density (Fretwell & Lucas 1970; Sinclair 1989; Newton 1998). In our study, birds behaved in direct opposition to this prediction. The fact that individuals of a species are attracted to one another when selecting habitat suggests that basic tenets of habitat-selection theory—competition and density

dependence—may need to be revised to include positive interactions among individuals (Stamps 2001).

Why would birds be attracted to one another if fitness decreases with density? Stamps (1988, 2001) suggests two potential explanations, conspecific cuing and the Allee effect. Conspecific cuing involves using the presence of others of one's species as an indicator of habitat quality (Stamps 1988). Allee effects occur when fitness increases with density (Stephens & Sutherland 1999). Our results support conspecific cuing; the main benefit vireos obtain from settling near conspecifics is the identification of suitable habitat. As discussed above, birds often exhibit site fidelity when they reproduce successfully and disperse after failing to reproduce. Thus, the presence of experienced individuals at a site could be an indicator of high-quality habitat. As a result, a good strategy for finding a high-quality nest site could be to locate one's territory near that of site-faithful males (Alatalo et al. 1982; Stamps 1988, 1991). For Black-capped Vireos, site quality is primarily influenced by the abundance of Brown-headed Cowbirds. Thus, conspecific attraction may be an effective defense against Brown-headed Cowbirds.

Using Conspecific Attraction in Conservation

One of the most significant benefits of the technique we tested is that it could be used to attract birds to high-quality habitat or locations where factors limiting survival and reproduction (e.g., predators or brood parasites) are controlled. In many cases where humans have altered landscapes, birds may be attracted to areas where they experience poor survival or reproductive success (e.g., Gates & Gysel 1978; Wilcove 1985; Robinson et al. 1995). These ecological traps are a serious conservation problem because birds cannot distinguish between high- and low-quality habitat (Schlaepfer et al. 2002). For species prone to use conspecific attraction, conservationists could use playbacks to attract birds to settle in high-quality habitats. This could be a major benefit for species that are declining due to selection of ecological traps.

Habitats to which birds will be attracted should be managed to ensure they are not population sinks. In our study, vireo nesting success and site fidelity were much higher on sites with than without cowbird control. Because cowbird control leads to higher reproductive success, it is critical to the persistence of vireo populations. With even moderate levels of cowbird parasitism (35%), vireo populations can be sinks (Tazik & Cornelius 1993; Eckrich et al. 1999). Thus, attracting birds to sites without controlling cowbirds would be pointless and potentially harmful to conservation efforts. When using conspecific attraction, the importance of management cannot be understated. Simply attracting birds to a new site will not provide conservation benefits unless limiting factors are controlled or the site is known to be of high quality.

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