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# **Conspecific Attraction in a Low-Density Population of a Threatened Songbird**

A thesis submitted in partial requirement of the degree of Master of Science in Biology at  
Virginia Commonwealth University

By

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## ABSTRACT

### CONSPECIFIC ATTRACTION IN A LOW-DENSITY POPULATION OF A THREATENED SONGBIRD

By Daniel James Albrecht-Mallinger

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Many organisms use both vegetation structure and social cues in selecting habitats. Many species of songbirds use the presence of breeding conspecifics as a social cue and sign of habitat quality, and can be induced to settle in unoccupied habitats by artificially broadcasting breeding song, a process referred to as “conspecific attraction”. In our study, we tested response to conspecific attraction a low-density population of the threatened Golden-winged Warbler (*Vermivora chrysoptera*) in Highland County, VA. Response to broadcast song was observed, with a modest increase in mean male abundance at survey points within 250 meters of treatments, and mean abundance decreasing outside of this range throughout the study area. Recruitment to conspecific playback was lower in our study than observed in previous research on high-density systems. Our results suggest more research is needed of the effectiveness of conspecific attraction in low density species and that its use should be tailored to the spatial and demographic conditions of the managed population.

Virginia Commonwealth University, 2014.

Thesis Advisor: Lesley P. Bulluck, Ph.D., Assistant Professor, Department of Biology

## **Introduction**

In order to maximize fitness, animals must be able to assess and select suitable habitats in heterogeneous landscapes (Grinnell 1917, Hirzel and Le Lay 2008). Failure to locate optimal habitat can result in declines in body condition (Villafuerte et al. 1997), reduced reproductive success (King et al. 1996), and increased mortality due to physical stress (Ganzhorn and Schmid 1998), predation (Tupper and Boutilier 1997) or lack of resources (Tschardt 1992). Given the consequences of occupying suboptimal habitat, there is strong selective pressure on organisms to accurately judge a habitat's quality. Previous research demonstrates that organisms can and do modify their behavior when in habitats perceived as suboptimal by decreasing physical reproductive investment (Walters et al. 1998, Lambrechts et al. 2004, Díaz et al. 2005) and increasing efforts to prospect for more optimal habitat (Breininger and Oddy 2004). While some ability to discern habitat quality is heritable (Feldman and Cavalli-Sforza 1984, Kokko and Sutherland 2001), numerous studies have demonstrated that personal information regarding site quality (i.e., personal breeding success and failure, resource abundance) also affects individuals' dispersal and settlement decisions (Petit and Petit 1996, Switzer 1997, Haas 1998, Citta and Lindberg 2007, Chalfoun and Martin 2010).

Such trial and error collection of "personal information" can be costly to the organism in terms of both resources and time. Species with short breeding periods (Zicus and Hennes 1989), long migrations (Slagsvold 1987, Reed et al. 1999, Jones 2001) or preference for transient habitat (Doligez et al. 2003) have limited time to (1) learn to identify optimal environments and (2) seek and establish territories in high quality habitats through direct sampling. In lieu of relying on genetic information or personal experience, animals can use public information of local conditions by observing how other organisms interact with the environment (Danchin et al.

2004). Such information can inform a wide variety of decisions for animals including foraging strategies (Templeton and Giraldeau 1995), mate-choice (Nordell and Valone 1998, Otter et al. 1999), and nest site selection (Reed et al. 1999, Citta and Lindberg 2007).

Public information has proven to be an important factor in habitat selection across taxa (Danchin et al. 2004, Rudolph and Rödel 2005, Forsman et al. 2008), with research in avian use of social cues being particularly prolific (Ahlering et al. 2010). The density and recruitment of dozens of bird species have been experimentally manipulated using conspecific attraction (i.e., attraction to broadcast conspecific social cues). Research on the perception of habitat suitability in birds historically focused on structural cues of environment quality, such as dominant vegetation and successional stage (Holmes et al. 1996, Jones 2001), which in turn informed management decisions for species of concern (Ahlering et al. 2010). The shift to incorporate social information of site quality into habitat models has allowed biologists to more accurately explain local recruitment (or lack thereof) of many species (Ahlering and Faaborg 2006, Campomizzi et al. 2008, Farrell et al. 2012).

Social cues of habitat quality are critical during species' "prospecting" period, during which they are actively searching for potential breeding sites (Boulinier et al. 1996, Ward 2005, Dale et al. 2006). For first-time breeders—particularly migratory species that have only a brief period following fledging or preceding the subsequent breeding season—efficient prospecting is critical (Ward and Schlossberg 2004, Nocera et al. 2006, Mitchell et al. 2010, Pärt et al. 2011). Both direct social cues of breeding success—e.g., presence of active nests or vocalizations of fledglings (Mönkkönen et al. 1990, Boulinier 1996)—and indirect cues, such as breeding male song (Ahlering et al. 2006), can be effective signals to prospecting birds of habitat quality. Artificial simulation of these signals (placement of decoys, manipulation of fledgling density,

broadcast playback of male song, etc.) has been used to alter local recruitment and density in many species of birds (Ahlering et al. 2010), with artificial cues sometimes trumping vegetative and structural cues of habitat quality (Betts et al. 2008a, Farrell et al. 2012). The relative importance of the type (visual or auditory) and timing (preceding or following the breeding season) of cue varies substantially between species. (Arlt and Pärt 2007, Betts et al. 2008a, Farrell et al. 2012).

Given the growing understanding of how public information informs songbirds' territory selection, conspecific attraction has been proposed as a tool for the conservation of declining species (Ahlering and Faaborg 2006, Ahlering et al. 2010). The broadcast of male breeding song is relatively low-cost and simple, and has been used successfully to attract threatened species to new locations (Farrell et al. 2012, Virzi et al. 2012). However, questions and concerns remain regarding the efficacy and impact of using social cues to recruit songbirds to new or previously unoccupied habitats. Relatively few studies have investigated whether birds recruited to habitats by conspecific attraction experience breeding success comparable to established populations (Ward and Schlossberg 2004, Nocera et al. 2006, Ahlering et al. 2010, Farrell et al. 2012). This is important considering that conspecific attraction could act as an ecological trap by drawing individuals into suboptimal environments that land managers perceive as quality habitat or by only recruiting males, but not female mates (Giraldeau et al. 2002, Schlaepfer et al. 2002, Dall et al. 2004, Ahlering et al. 2010).

Additionally, the ecological and evolutionary value of social information at a landscape level has primarily received only theoretical consideration (Fletcher 2006, Fletcher and Sieving 2010). Field studies of localized geographic scale cannot address the effects of attenuating information predicted by increasing distance and landscape heterogeneity (Gould 1974, Johnson

1980). In a modeled system, Fletcher (2006) demonstrated that benefits to survival and fecundity from using social information in site selection diminish when landscape features— such as habitat fragmentation, edge effects and declining patch size – reduce the availability of social information. Additionally, field studies indicate that the recruiting range of social cues is significantly smaller than birds’ perceptual range (i.e., birds are not recruited by more distant signals, even when they can perceive them), indicating that signal value decreases with distance (Cornell and Donovan 2010).

Declining and threatened populations frequently exist at low densities (Brown 1984, Fuller et al. 1995, Purvis et al. 2000) and in fragmented landscapes (Temple and Cary 1988, Tschamtkke 1992, Herkert 1994, Harrison and Bruna 1999, Bregman et al. 2014). Moreover, landscapes of heterogeneous habitat composition pose barriers to dispersal of varying permeability. If conspecific attraction is to be used effectively in conservation, its influence on low-density populations in fragmented, heterogeneous landscapes must be investigated, both in terms of recruitment of target species and breeding success of recruited individuals.

We attempted to address these questions using a low-density Appalachian population of Golden-winged Warblers (*Vermivora chrysoptera*). Golden-winged Warblers are early- to mid-successional specialists with a preference for shrubby habitat bordering forest, although vegetative communities used vary widely across the species’ range (Confer et al. 2011). Golden-winged Warbler’s are migratory, engage in extra-pair paternity (Vallender et al. 2006), prefer ephemeral habitats (Confer and Knapp 1981), and have patchy population distributions (Confer et al. 2003): traits that are thought to be associated with a species’ use of social cues in habitat selection (Stamps 1988, Ahlering et al. 2010). Moreover, the Golden-winged Warbler is a species of conservation interest. Populations have rapidly declined over the last century as a

result of habitat loss both on breeding and wintering grounds (Confer and Knapp 1981). Their conservation status has stimulated substantial investment in creating and managing habitats to maintain threatened populations. Such habitat creation can be costly (Askins 1994, Litvaitis 2001, Brooks 2003, Oehler et al. 2003), and conspecific attraction may be one way to increase the likelihood that individuals will locate and use these created habitats. Specifically, we wanted to test the efficacy of conspecific attraction in recruiting Golden-winged Warblers to suitable unoccupied or low-density habitat.

## **Methods**

### Study Site Selection & Field Methods

We conducted our study in Highland County, Virginia. Golden-winged Warblers have been declining throughout Virginia; Highland County retains the highest density of males, and is thus the focus of the state's conservation interest for the species (Wilson et al. 2007). Golden-winged Warblers in Highland County are found in abandoned and minimally-grazed pasture land with abundant *Rubus sp.* bordered by deciduous forest. This population of Golden-winged Warblers persists at low densities, with less than 0.2 males per hectare of suitable habitat, as contrasted with estimates of 1 to 1.1 male per hectare in the core of the species' range (Streby et al. 2012). Small patches of suitable brushy habitat in Highland County are separated by large tracts of grazed pasture in valleys and forested slopes, creating a complex and highly fragmented landscape (Figure 1). Patches of early successional habitat were identified from Google Earth imagery and known locations (Wilson 2007, Bulluck and Harding 2011) in March to April of 2012. Only patches with high *Rubus* cover (~40%) were considered to be suitable habitat. Patches were delineated visually with aerial imagery from Google Earth and ArcMap (Figure 1), and assumed to extend 20m into the bordering forest margin, based on known foraging habitat

(Streby et al. 2012), but not extending beyond the shrub cover farthest from the forest edge (ie., not into open pasture). Survey points were established 200 to 300m apart in order to effectively sample the entire area of all patches. A total of 176 points were surveyed across 61 distinct habitat patches, with patches ranging in size from 2.2 to 108 hectares (1 to 13 survey points per patch). All surveyed habitat patches were higher than the 600m (~2000ft) above sea level, which has been suggested as altitudinal refuge from introgressing Blue-winged Warblers (Bakermans et al. 2011). The study site spans ~500 mi<sup>2</sup>.

From late spring through summer of 2012, patch occupancy surveys were conducted across three separate survey periods (Period 1: April 28<sup>th</sup>-May 16<sup>th</sup>, Period 2: May 17<sup>th</sup>-June-1<sup>st</sup>, Period 3: June 2<sup>nd</sup>-June 18<sup>th</sup>). Surveys were only conducted on mornings without precipitation and when temperatures were above 45°F (7°C). Occupancy surveys were performed between 5:30 and 10:00 AM at each point within a patch using a modified Cornell Golden-winged Warbler Atlas protocol, and consisted of three 3-minute segments:

1. Three minutes of silent observation
2. Two minutes of broadcast Type 1 Golden-winged Warbler breeding song (Confer et al. 2011) followed by one minute of silence.
3. One minute of broadcast Type 2 Golden-winged Warbler breeding song (Confer et al. 2011) followed by two minutes of silence.

Playback of male song was used to increase detection probability for this species with known low rates of detection (Kubel and Yahner 2007). The number, sex, and species (Golden-winged Warbler, Blue-winged Warbler, or hybrid) were recorded for warblers detected during each survey segment when individuals were visible. As male Blue-winged Warblers and hybrids were responsive to Golden-winged Warbler song, we considered them as equivalent to Golden-winged Warblers in terms of point occupancy; these non-Golden-winged Warbler observations only represented 4.13% of all individuals observed. Males present at a point could be detected

more than once within a survey, but not within a survey segment. Three unique detection periods allowed for estimation of detection probability (see below). To enhance detection of breeding behavior, during the second and third survey periods, additional mobbing surveys (Gunn et al. 2000, Doran et al. 2005) were conducted at occupied points. Mobbing surveys were conducted in the same location as occupancy surveys when points were positioned close to the central singing perch of the breeding male. When occupancy survey points were located between two territories or at the territory edge, mobbing surveys were conducted in the best estimate of the territory's center. These surveys consisted of 5 minutes of mixed Carolina Chickadee (*Poecile carolinensis*) and Tufted Titmouse (*Baeolophus bicolor*) mobbing calls, which have been demonstrated to increase the chance of observing reproductive behaviors within breeding territories (Gunn et al. 2000, Doran et al. 2005). Mobbing was followed by 5 minutes of silent observation. All birds and breeding behaviors observed in both mobbing and silent periods were recorded. A second mobbing survey was repeated 24-72 hours following the occupancy survey using the same protocol, such that each occupied point received four total mobbing surveys per field season. A reproductive index (Vickery et al. 1992) for each point during the field season was assigned as follows:

1. Male observed in the same point in two separate survey periods, indicating true territory establishment.
2. Male and female seen in close association (suspected pair).
3. Adults seen carrying nesting materials or flushed from the nest.
4. Adults seen carrying food.
5. Adults feeding fledglings or fledglings observed.

Where possible, territorial males were captured using song playback and a male warbler

model adjacent to a mist-net. Birds were fitted with U.S. Fish and Wildlife Service aluminum bands and individually marked using color bands. Males were aged by shape of the primary coverts (Pyle 1997). Patches and points that had no warblers detected on 2 or more surveys were considered unoccupied. Patches that had two or more points without warblers detected on multiple surveys were considered under-occupied. Patches at which all points had warblers for multiple surveys—or only had one point that was unoccupied on multiple surveys) were considered fully occupied. An unequal-variance ANOVA ( $F_{2,57} = 24.2, p = <0.001$ ) and post-hoc comparison showed that mean densities of males in 2012 (adjusted for detection probability) differed significantly across fully ( $0.17 \pm 0.086$  males/hectare) and under-occupied ( $0.09 \pm 0.045$  males/hectare) patch groups.

#### Vegetation Surveys

From June 10-30 of 2012 and 2013, we collected vegetation data at each survey point. Forty ocular tube readings were taken (both towards ground and azimuth) along 20m transect lines extending from in the cardinal directions from the survey point (10m in each direction). At each reading, presence of grass, forb >20 cm in height, shrub <1m, shrub >1m, saplings <2m, saplings >2m and canopy were recorded, along with the three most dominant species for each of those vegetative types. To ensure that vegetation structure did not differ at occupied, under-occupied and unoccupied patches, a series of equal variance 1-way ANOVAs were used to see if mean grass, shrub, canopy or sapling cover varied between 2012 patches; due to non-constant variance, a Welch's ANOVA of unequal variance was used to test for differences in sapling <2m cover across occupancy levels (Table 1). No significant differences were found across patch occupancy levels, and further analysis revealed no significant difference between the vegetative structure of treatment and control groups (Table 1, and discussed below).

## Playback Protocol

### *I. Treatments and Set-up*

Conspecific playback treatments were applied to either unoccupied or under-occupied patches in an effort to increase male density in sites where male density was lowest. We assigned patches to experimental treatments using a balanced randomized stratified design, with stratification occurring over under- and un-occupied sites. Treatment groups were assigned to post-breeding season ( $n = 15$ ), or pre-breeding season ( $n = 15$ ) treatments, with 29 control patches split that were either fully occupied ( $n=12$ ), under-occupied ( $n=8$ ), or unoccupied ( $n = 10$ ) (Figure 1). While mean patch size does not vary across the three treatments, we had hoped to stratify our sites by patch size; however, no small patches ( $<10\text{ha}$ ) were under-occupied, and no large patches ( $>30\text{ha}$ ) were unoccupied. Despite this, the three treatment groups do not differ with regard to patch size ( $F_{2,57} = 0.33$ ,  $p = 0.7171$ ). The treatment groups were also evenly distributed across Highland County (Figure 1). Neither raw nor adjusted male density per hectare ( $p = 0.7917$ ,  $p = 0.7832$ ) differed among treatment groups. Vegetation structure did not differ among treatment groups (Table 1). Distance to closest suitable habitat as estimated using 2009 aerial imagery from Google Earth did not vary significantly among treatment groups ( $p = 0.2454$ ).

Following Betts et al. (2008) and Farrell and Campomizzi (2011), component systems were constructed for broadcasting Golden-winged Warbler song in treatment sites. Two separate playback files for broadcasting were designed using recorded Golden-winged Warbler song from Maryland, which was the closest readily available recording. While there may be some regional variation in song, Golden-winged Warblers responded strongly to these recordings during our occupancy surveys. The post-breeding season (late summer) playback consisted of infrequent

Type-II (60% of sound-time), Type-I (35% sound-time) and chip-notes (5% sound-time) interspersed with 30-90 second periods of silence. The pre-breeding season (early spring) track consisted of Type I (70% sound-time), Type II (20% sound time), and chip notes (10% sound-time) played at greater frequency, interspersed with 20-60 seconds of silence. These different tracks are reflective of seasonal changes in Golden-winged Warbler vocalizations (Confer et al. 2011), and comparable to other conspecific attraction protocols used in related warbler species (Farrell et al. 2011).

### *II. Post-breeding season treatment - 2012*

From July 1<sup>st</sup> until August 20<sup>th</sup>, playback systems were placed in trees approximately 2m above the ground near unoccupied survey points in the post-breeding season treatment patches (N = 15). Post-breeding season sound files were played as a looped track for 8 hours following sunrise (5:30-13:30). Song was broadcast at peak amplitude of 180 decibels for frequencies of 200 Mhz, the volume at which playback was clearly audible to human ears at ~200m from the point with ambient sound. Treatment sites received playback in three 16-day cycles, with 8 days of broadcast followed by 8 days of silence for a total of ~192 hours of playback during the post-breeding treatment period per treatment. For two 30-minute periods during each broadcast cycle, playback and control sites were monitored for Golden-winged Warbler prospecting, for a total of 6 observation periods (3 hours) at each experimental and control site. Warbler sex and age (hatch year versus after-hatch year) were noted for all birds observed.

### *III. Pre-breeding Season Treatment - 2013*

From April 15<sup>th</sup> until the May 24<sup>th</sup>, playback systems were deployed in pre-breeding season treatment patches. Patches received playback in five 8-day cycles, with 4 days of playback followed by 4 days without, with 8 hours of playback from 5:30-13:30, for a total of 40

hours of playback per treatment. Two 30-minute observations were conducted during each of the first 4 playback cycles for each patch, for 4 hours of observation for each treatment and control patch, during which the sex and hybrid status of any observed Golden-winged and Blue-winged Warblers were recorded.

### 2013 Post Treatment Field Protocol

From May 1<sup>st</sup> until June 30<sup>th</sup> 2013, the three-period occupancy survey protocols described above were repeated across all survey points. We modified the mobbing survey protocol to include an additional 5 minutes of silent observation following mobbing playback to enhance our likelihood of detecting feeding behavior in treatment and naturally occupied sites. We were not concerned with this change in protocol because our interest was in comparing reproductive behavior in newly colonized and treatment sites, and not between breeding seasons.

### Statistical Methods

#### *Detection Probabilities, Adjusted Abundances and Adjusted Densities*

Detection probabilities ( $p$ ) for individual males in each segment of each survey were calculated using the Huggins closed-capture method in Program MARK (Huggins 1989 and 1991), using Julian date and time-of-day as covariates to account for temporal variation in detection probability. We used Akaike's Information Criterion ( $AIC_c$ ) to select the model with the most support. Models without temporal covariates performed substantially better than models which included them ( $\Delta AIC_c > 2$ ). Detection probabilities were then used to generate adjusted abundances for the total population and for each point by dividing the number of males observed by the cumulative survey period detection probabilities:

$$N_{adj} = \frac{N}{1 - (1 - p_1) * (1 - p_2) * (1 - p_3)}$$

For patch level analysis, abundances were summed and divided by patch area to calculate adjusted patch densities for each survey (males/hectare).

### *Response to Treatment*

Previous research on related migratory warblers has found that within-breeding season movement, and thus point occupancy likely cannot be considered static within a given breeding season (Betts et al. 2008b, Rota et al. 2009). To account for this, we used average densities and abundances across the three surveys of each season when calculating our response variables. For patch-level analyses, general linear models were constructed to test for the effect of treatment (artificial playback present or not present), treatment type (post-season playback or pre-season playback treatment), patch area, and 2012 male density on the change in mean male density (mean density 2013 – mean density 2012) as our response variable. As previous research on species that use social cues in habitat selection (Fletcher 2007) has found a positive association between patch area and density, as well as between natural and artificial social cues (i.e., existing density and conspecific playback), we included interaction terms between the presence of treatment and 2012 male density; treatment and patch area; and 2012 male density and patch area.

To test for localized response to conspecific playback treatment, general linear mixed models using change in point abundance (mean 2013 males/point – mean 2012 males/point) for points at discrete distance intervals (Table 5), with points within these radii being considered treatment points, and those that fell outside of radius considered as controls. The effect of treatment type (pre- vs. post-season) was also considered at these different radii. Patch identity was included as a random effect in all models.

All analyses were performed in R version 3.0.2 (R Core Development Team 2013) and we used Akaike's Information Criterion to rank model performance. The AICmodavg package

(Mazerolle 2013) was used for  $\Delta AIC_C$  model selection. Summaries of model parameters can be found in Table 2, and the nlme package (Pinheiro et al. 2013) was used to create mixed-effects models.

### *Breeding Level and Male Age on Treatment and Control Patches*

Breeding was considered “Successful” at points where adults were observed carrying food or fledglings were observed (reproductive index value 4 and 5); breeding was considered “Occurring” at points where a male was observed on multiple surveys, a male and female were observed interacting, or carrying nesting materials (reproductive index levels 1, 2, and 3).

Evidence for breeding was considered “Absent” at points where males were present for less than one survey; these points were excluded from subsequent analysis. We tested the hypothesis that the proportion of points with evidence of successful breeding would be greater in control patches than in treatment patches with a one-sided Fisher’s Exact Test with 1 degree of freedom. We also tested the hypothesis that the proportion of second-year males to after-second year males would be higher in treatment patches than in control patches using a Fisher’s Exact test with 1 degree of freedom.

## **Results**

### Survey Results

Average detection probability across all surveys was relatively high, with the use of playback in second and third survey segments substantially increasing detection probability (Figure 2). After correcting abundance for detection probability, maximum abundance across our study sites was  $118.78 \pm 2.25$  males, with a mean abundance of 104.5 males in 2012; maximum abundance in 2013 was  $104.3 \pm 1.69$  males, with a mean abundance of 84.8 males (Figure 3).

These abundance estimates show a population decline between our survey years. In 2012, three phenotypic Blue-winged Warbler and two hybrid males were detected in four separate patches, representing ~5% of the total males detected. In 2013, three phenotypic Blue-winged Warblers and four hybrid males were detected at 6 different patches, representing 6.7% of the total males detected for the year.

### Changes in Patch Density

Patch density in 2012 was found to be the strongest predictor of change in patch density between years. Although model selection did not provide a single best model (Table 3), the top two models ( $\Delta \Delta AIC_C < 2$ ) both included 2012 male density as a predictor. Change in density was significantly negatively correlated with 2012 male density ( $r = -0.2491$ ). This correlation is even stronger when an outlying leverage point from a small patch is excluded from the analysis ( $r = -0.5151$ , see Figure 4). This difference may be primarily related to the net loss of birds from our study population over the course of our study period. The second-best model ( $\Delta \text{Density} \sim 2012 \text{ Density} + \text{Treatment}$ ) did not show treatment to be a significant factor in predicting a change in density (Figure 5). Parameter estimates for the two top models can be found in Table 4.

A model that solely considered treatment as a predictor of change in male density (5<sup>th</sup> top performing model,  $\Delta AIC_C = 2.488$ ) did find the presence of treatment to be positively associated with change in density (estimate = 0.034, 95% CI = 0.0243, 0.0517), but this model was not among the top models ( $\Delta AIC_C > 2$ ). Models that considered pre-breeding and post-breeding treatments as different did not perform as well as models where they were treated as equivalent (Table 3).

### Changes in Point Abundance

Given the weak response to treatment at the patch level, we also investigated response to treatment at discrete spatial scales (250, 500, and 1000m from conspecific cue). Model selection identified one top model ( $\Delta AIC_C < 2$ ), indicating that the presence of playback treatment within 250m of a point was the strongest predictor of change in male abundance (Table 5, Figure 6). The presence of a treatment playback (treating pre- and post-season playback as equivalent) appears to be associated with a slight positive change—or, at least, non-loss of males—of males (mean change in abundance =  $0.1107 \pm 0.29924$  males), compared to points more than 250m away from playback treatments (mean change in abundance =  $-0.1637 \pm 0.5199$  males). Models that considered pre- and post-season treatments separately were not among top performing models, suggesting that pre- and post-season signals may be of comparable importance in recruiting male Golden-winged Warblers. The second-best model (Figure 7), which considered all points within a habitat patch contiguous with treatment as treatment points (again treating pre- and post-season playback as synonymous), performed significantly worse ( $\Delta AIC_C = 4.47$ ).

#### Detected Breeding Activity and Male Age in 2013

Strong evidence of breeding activity was detected at 14 of the 78 occupied points surveyed (out of 171 surveyed points) in 2013 (Table 7). Fisher's Exact test on occupied points did not find a significantly higher proportion of points with strong evidence of breeding in control patches than points in treatment patches ( $df = 1, p = 0.2368$ ). However, it should be noted that all 3 of the points within treatment patches with strong evidence of breeding were under-occupied patches the year before; none of the newly colonized un-occupied patches had strong evidence of breeding. We did not compare breeding between 2012 and 2013, as changes in breeding survey protocol increased our detection of breeding for 2013.

In 2012, 37 male warblers were banded, 17 (46%) of which were recaptured or re-sighted the next year; only one of these birds changed patches from 2012 to 2013 suggesting a high degree of breeding site fidelity (94%). Thirty-six warblers were captured and aged in 2013, thirty-two of which were first-time captures. While proportionally more males caught at treatment patches were second-year than control patches, a Fishers' exact test did not show any statistical differences ( $df = 1, p = 0.1606$ , Table 7), although this may be due to our small sample size.

## **Discussion**

We broadcast male song as a social cue to try to recruit male Golden-winged Warblers into under- and unoccupied patches of suitable habitat in a fragmented landscape with low population density. We predicted that we would observe lower recruitment compared to previous studies on species with similar natural histories (migratory, dependent on ephemeral habitat, preferring aggregated populations) in higher density populations. We also hypothesized that there would be disparities between male age and breeding success on treated and un-treated locations on the landscape. Our data generally supports our hypotheses; recruitment of warbler males to treatment sites did occur more often than in controls and these males were often first year breeders who did not successfully breed.

We initially investigated response to treatment on the patch level ( $N = 60$ ) by comparing changes in male density (males/hectare). In contrast to many other studies, this response to treatment was driven more by the *loss* of birds from non-treatment areas than the gain of birds from survey points near playback treatment—a result possibly driven by the decline of breeding males in our study population between the year preceding (2012) and following (2013) treatment. Moreover, model selection demonstrated that male density in 2012 alone was a better predictor

of change in density than treatment, with change in density negatively related with 2012 density. One interpretation of this is simply that population dynamics are density-dependent, whereby relatively higher density areas were more likely to lose breeding individuals and lower density areas were more likely to gain breeding individuals. However, nearly all sites in our landscape had a net loss in breeding individuals between 2012 and 2013 (Figure 3). Such stochastic changes in population density—due to unknown factors across the annual cycle of a migratory species—highlight the complexity and uncertainty that exists when interpreting only two years of density data. Indeed, environmental and stochastic effects are known to strongly affect short-term trends in avian populations and create false-positive detections of density dependence (Lande 1998, Bjørnstad and Grenfell 2001, Sæther and Engen 2002). In the absence of longer-term data of population dynamics, we hesitate to interpret the relationship between 2012 density and change in density.

Our investigation of the response to conspecific attraction at the point level ( $N = 171$ ) did reveal a significant difference between change in male abundance at points within 250m of treatments and points outside this radius, with no difference between pre- and post-breeding treatments. Model selection indicated that this restrictive 250m radius is the best predictor of recruitment and/or retention of existing males from the previous year in response to treatment. This result suggests that response to a conspecific cue is localized, at approximately the size of a male breeding territory, and does not generally affect recruitment across a larger habitat patch. This has implications for management because the management unit of interest is often the habitat-patch scale, and not necessarily the territory-scale. It is not known if a stronger conspecific cue (multiple playback stations in one patch and/or both pre- and post-season cues at the same location) would have a stronger effect at the patch scale.

Studies of recruitment by conspecific playback in higher-density territorial songbird populations have found comparatively stronger responses to treatments (Nocera et al. 2005, Hahn and Silverman 2006, Hahn and Silverman 2007, Betts et al. 2008a, Farrell et al. 2012). Hahn and Silverman (2006) found mean increases of more than 4 territorial males per treatment plot, as compared to our maximum recruitment of one male per treatment point. Farrell et al. (2012) found evidence of successful breeding in treatment sites, a behavioral component that is not often assessed in studies of conspecific attraction. We too found evidence of successful breeding in treatment sites, but at a much lower rate than in occupied controls (Table 7). The low density of our system may preclude the strong recruitment to conspecific playback seen in other studies by virtue of the paucity of males and/or the low probability of prospecting males passing within the signal radius of treatments. We feel the limited response of Golden-winged Warblers to conspecific cues is an important finding because ours is one of the only tests of conspecific attraction in a low-density population. The only other example we are aware of is with Baird's sparrow (*Ammodramus bairdii*) where they similarly found limited recruitment among unoccupied treatment patches, but no recruitment to unoccupied controls (Ahlering and Faaborg 2006).

Much discussion has been devoted to how conspecific attraction can be used to manage threatened populations of songbirds (Hahn and Silverman 2007, Ahlering et al. 2010, Cornell and Donovan 2010, Fletcher and Sieving 2010) and potentially for other taxa (Lima and Zollner 1996, Anthony and Blumstein 2000, Zeigler et al. 2011). Many threatened species exist in very low population densities and are thought to be good candidates for the use of conspecific attraction to either boost population density or recruitment into apparently suitable but unoccupied sites. Our results suggest that conspecific cues may only have moderate success in

these systems; specifically, they may only be effective in close proximity to known occupied sites for populations existing at low-densities in fragmented landscapes—conditions that are typical of many threatened species. Ahlering et al. (2010) highlighted the importance of establishing the best spatial arrangement of treatments for maximizing sustainable recruitment, which is largely unknown. Our results indicate that arrangement and strength of treatment must be calibrated by the density of and geographic distribution of the population being managed. When individuals are sparsely distributed and their likelihood of encountering a treatment is low, playback signal may require amplification either spatially—multiple treatments in suitable habitat—or temporally—extended signal period post- and or pre-breeding season—in order to recruit sufficient individuals to establish a successful local population. Moreover, we found establishment was most likely immediately adjacent to treatments, and we therefore suggest that conspecific cues either be placed centrally or at a density that would promote—but not mimic—saturation of the target patch. Future studies should explicitly address response to treatment at different distances and across habitats of differing permeability to prospecting birds. Current management guidelines for Golden-winged Warblers recommend habitat creation take place within one mile of existing populations (Bakermans et al. 2011), which may only be appropriate in high density populations with a high-proportion of first-time breeders prospecting across the landscape. In lower-density systems with smaller likelihood of a prospector encountering a playback treatment, a better understanding of response range needs to be established. If the distance of signal attenuation is well documented, broadcast playback along dispersal corridors at reliable intervals may help draw populations to suitable un- or under-occupied habitat. Such an understanding of species response range will also inform where management should be prioritized even in the absence of artificial conspecific attraction.

Our study was limited by several factors. As 31.7% based on our population estimates of surveyed areas, Figure 3) were color-banded in 2012, we could not extensively track individual movement within and between patches from 2012 to 2013. However, 17 of 37 color-banded individuals (46%) were re-sighted in 2013; of those individuals 16 (94%) were re-sighted in the same patch area they were banded the year before, suggesting a high degree of site fidelity in older males.<sup>1</sup> The movement of unbanded birds, particularly young males and females, is unknown; banding fledglings the season prior to conspecific attraction treatment may aid in future studies of recruitment. Proportionally more young males were found in treatment patches than in occupied controls (Table 6), suggesting, as previous research has shown (Nocera et al. 2006), that conspecific attraction is most effective at attracting first-time breeders.

An exciting part of our study is that all surveys were conducted on private properties; understanding the challenges that populations face on private lands is critical if we are to effectively conserve species of concern (Knight 1999, Norton 2000). Working on private lands did present a major challenge in that we had limited access to properties across a large study area, and—given the brevity of the breeding season (May-June)—we were unable to sample or quantify all available habitat. Other studies have found the importance of functional connectivity in a species' response to conspecific cues (Cornell and Donovan 2010, Zeigler et al. 2011); in the absence of explicit information regarding patch isolation and meaningful measures of local and landscape fragmentation, we are unable to quantify how landscape features impact the accessibility and value of broadcast social cues to prospecting individuals. A thorough landscape classification of suitable habitat (if possible) would allow us to assess (1) the proportion of the landscape that was sampled and (2) the degree of patch isolation of suitable (though unknown

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<sup>1</sup> One third-year male reappeared in 2013 in a new habitat patch 9.84 km from where it was as a first-year breeder.

occupancy) habitat which would strengthen this substantially. Another challenge is that private landowners changed cattle densities on experimental plots throughout the study—a variable we did not quantify. It is possible that the presence of intensive grazing may have affected habitat and warbler movement on the landscape, reducing occupancy where grazing was intensified. Future studies in this population should be conducted over several years and account for changes in livestock management and annual variation in warbler abundance that may result.

The use of conspecific attraction as a conservation tool may play an integral role in managing threatened and declining species. Our results demonstrate that, even in a low-density system, male songbirds may be recruited by broadcast song. However, response to such treatment may be limited to a small area surrounding treatment, and may be strongly affected by the strength of the broadcast social signal and the number of individuals capable of being recruited. As such, before conspecific attraction is used as a management tool for this and other low-density species, more study is needed to understand what the strength and scale of treatment would be most effective to increase the abundance of successfully breeding individuals.

Table 1: Sample sizes, mean total shrub cover (%) and forb cover (%) for treatment and control patches, and *p*-values for ANOVA comparisons between treatment groups, with Welch's ANOVA for sapling <2m, due to non-constant variance.

Patch Type	Control Patch	Pre-season Treatment	Post-season Treatment	<i>p</i> -value
<i>N</i>	30	15	15	-
Playback Regime	None	15-April to 16-May 2013	1-July to 20-Aug 2012	-
2012 Male Density (excluding fully occupied patches)	0.053 (±0.013)	0.023 (±0.018)	0.030 (± 0.017)	0.2454
Patch Area	21.84 (±4.105)	16.90 (±5.17)	16.68 (±5.50)	0.6659
Mean Grass Cover (%)	78.045 (± 18.269)	77.59 (± 10.00)	74.45 (±14.765)	0.7318
Mean Shrub Cover <1m (%)	26.06 (±8.335)	27.42 (±8.102)	31.48 (±12.380)	0.2165
Mean Shrub Cover >1m (%)	23.74 (±11.880)	28.15 (±10.443)	27.90 (±12.315)	0.3841
Mean Forb Cover (%)	50.42 (±20.48)	48.89 (±11.70)	48.70 (±12.21)	0.2184
Mean Sapling Cover <2m (%)	0.99 (±1.26)	1.36 (±1.779)	3.49 (±4.786)	0.1154
Mean Sapling Cover >2m (%)	5.067 (±4.67)	5.46 (±4.81)	5.34 (±6.269)	0.9834
Mean Canopy Cover (%)	24.63 (±12.52)	26.67 (± 16.81)	26.32 (±13.19)	0.8303

Table 2: Model parameters for analyses of point- and patch-level responses to treatment.

Analysis	Parameter	Summary
Point	$\Delta$ Mean Abundance	Change in abundance of males at survey point adjusted for detection probability
	Treatment<250m	Survey point <250m from treatment
	Treatment<500m	Survey point <500m from treatment
	Treatment<1km	Survey point <1000m from treatment
	Pre-Season<250m	Survey point <250m from Pre-season treatment
	Pre-Season<500m	Survey point <500m from Pre-season treatment
	Pre-Season <1km	Survey point <1000m from Pre-season treatment
	Post-Season<250m	Survey point <250m from Post-season treatment
	Post-Season<500m	Survey point <500m from Post-season treatment
Post-Season <1km	Survey point <1000m from Post-season treatment	
	Treatment	Survey point is found in a habitat patch contiguous with a playback treatment
Patch	$\Delta$ Mean Density	Change in density (males/hectare) from 2012 to 2013, adjusted for detection probability
	Treatment	Survey point is found in a habitat patch contiguous with a playback treatment
	Pre-Season Treatment	Pre-season treatment present in Patch
	Post-Season Treatment	Post-season Treatment present in Patch
	Pre/Post/Control Patch	Categorical consideration of Control, Pre-season and Post-season Patches
	Patch Size	Area of suitable habitat within patch (hectare)
	2012 Density	Mean density of males in patch during 2012 surveys (males/hectare)

Table 3: AIC<sub>C</sub> values used in model selection for mean male abundance from 2012 to 2013.

Model	K	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	Model Likelihood	Model Weight
Density 2012	3	-185.08	0.000	1.000	0.299
Treatment + Density2012	4	-184.93	0.157	0.925	0.277
Treatment + Density2012 + PatchArea	5	-182.92	2.160	0.340	0.102
Treatment + Density2012 + Treatment*Density2012	5	-182.75	2.335	0.311	0.093
Treatment	3	-182.60	2.488	0.288	0.086
Pre/Post/Control + Density2012	5	-182.55	2.528	0.282	0.085
Pre/Post/Control	4	-180.34	4.742	0.093	0.028
Treatment + PatchArea	4	-180.30	4.784	0.091	0.027
Patch Area	3	-176.25	8.835	0.012	0.004

Table 4: Parameter estimates for top-performing models of mean change in patch density from 2012 to 2013

Model	Parameter	Estimate	SE	95% CI
Δ Density ~ 2012	Intercept	0.0015	0.00825	-0.0146, 0.1775
Density	Density Males 2012	-0.2491	0.08192	-0.4097, -0.0886
Δ Density ~ 2012	Intercept	-0.0131	0.01349	-0.0396, 0.0133
Density +	Density Males 2012	-0.189	0.09208	-0.3700, -0.0090
Treatment	Treatment	0.0201	0.01455	-0.0084, 0.0485

Table 5: AIC<sub>C</sub> values used in model selection for mean change in point abundance from 2012 to 2013, with patch identity as a random effect in all models.

Model	K	AIC <sub>C</sub>	ΔAIC <sub>C</sub>	Model Likelihood	Model Weight
Treatment <250m	4	251.09	0.000	1.000	0.660
Treatment Patch	4	255.56	4.474	0.107	0.070
Pre-Season <250m	4	255.64	4.550	0.103	0.068
Post-Season <250	4	256.26	5.177	0.075	0.050
Treatment<1km	4	256.49	5.401	0.067	0.044
Post-Season	4	257.64	6.551	0.038	0.025
Post-Season<1km	4	257.87	6.783	0.034	0.022
Treatment<500m	4	258.67	7.582	0.023	0.015
Post-Season<500m	4	258.93	7.839	0.020	0.013
Pre-Season	4	259.04	7.954	0.019	0.012
Pre-Season <1km	4	259.20	8.110	0.017	0.011
Pre-Season <500km	4	259.59	8.503	0.014	0.009

Table 6: Comparison of detected evidence of breeding behavior at points between control and treatment patches

	Evidence of Breeding			Total
	Successful	Occurring	Absent	
Control	11 (12.8%)	41 (47.7%)	34 (39.5%)	86
Treatment	3 (3.5%)	23 (27.1%)	59 (69.4%)	85
Total	14	64	93	171

Table 7: Comparison of male age observed in control and treatment patches.

	Male Age		Total
	Second Year	After-Second Year	
Control	5 (29.4%)	17 (70.6%)	22
Treatment	6 (42.9%)	8 (57.1%)	14
Total	11	25	36

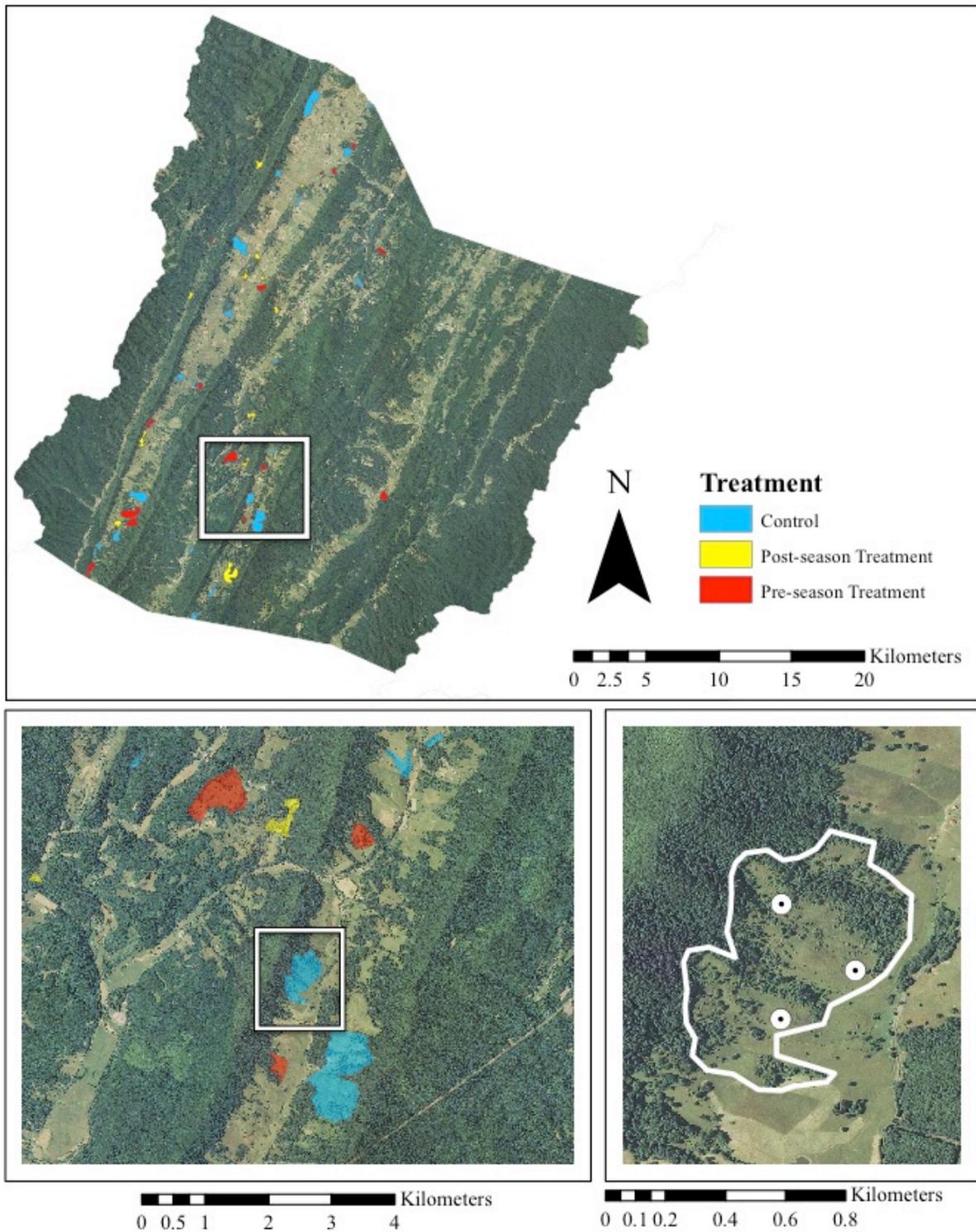


Figure 1: Study area in Highland County, Virginia. Bottom right panel indicates a patch of suitable habitat, denoting location of survey points.

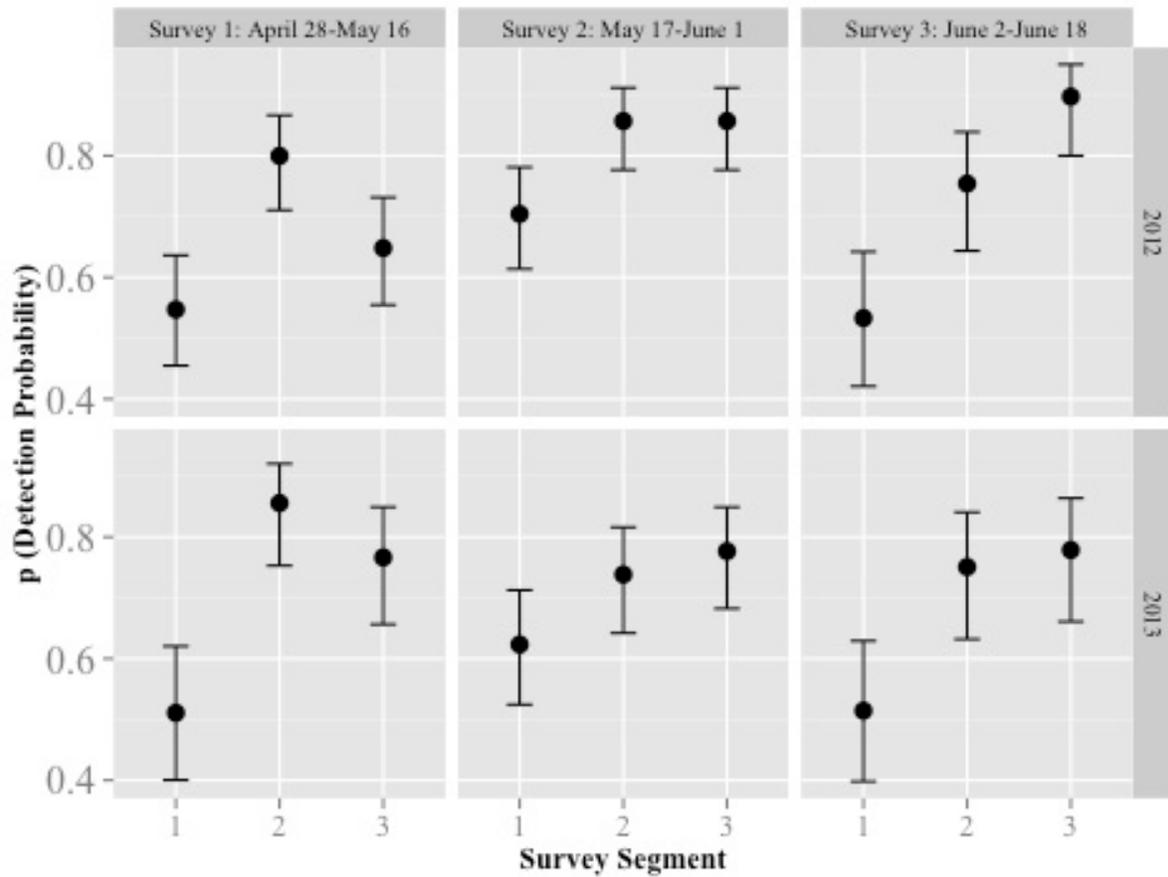


Figure 2: Detection probability with 95% confidence intervals for survey segments in each survey period, estimated using the Huggins Robust Closed Capture Method in Program MARK. Survey segment 1 was a silent listening period while segments 2 and 3 used playback to increase detection.

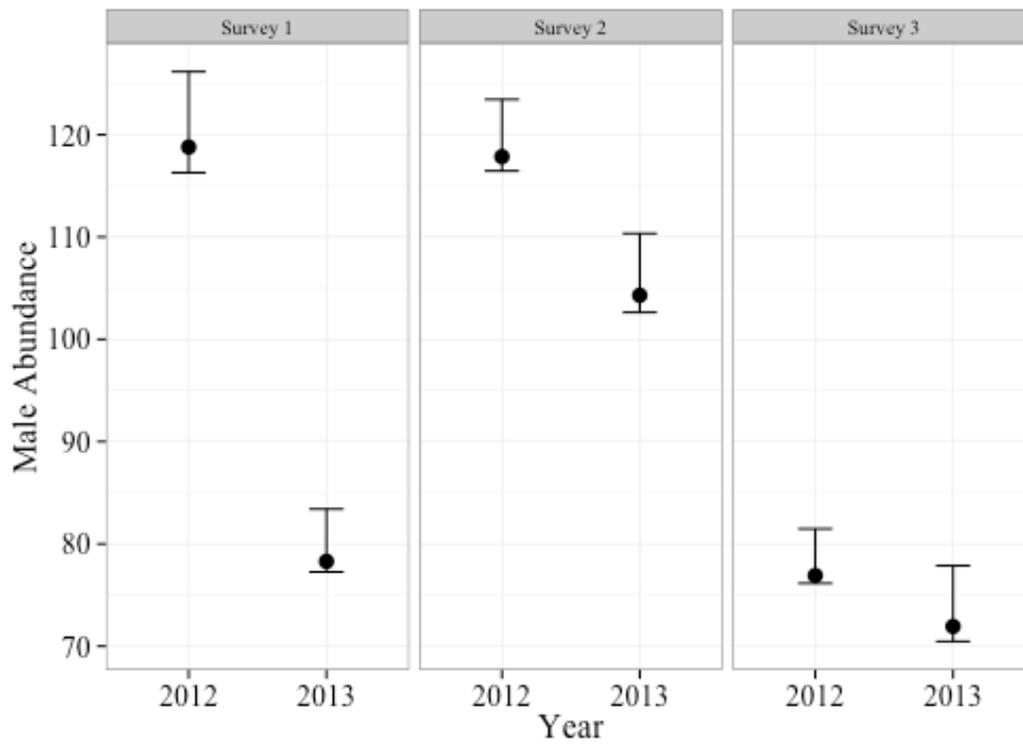


Figure 3: Total male abundance across the entire study area by each survey period 2012 and 2013, corrected for detection probability with 95% confidence intervals.

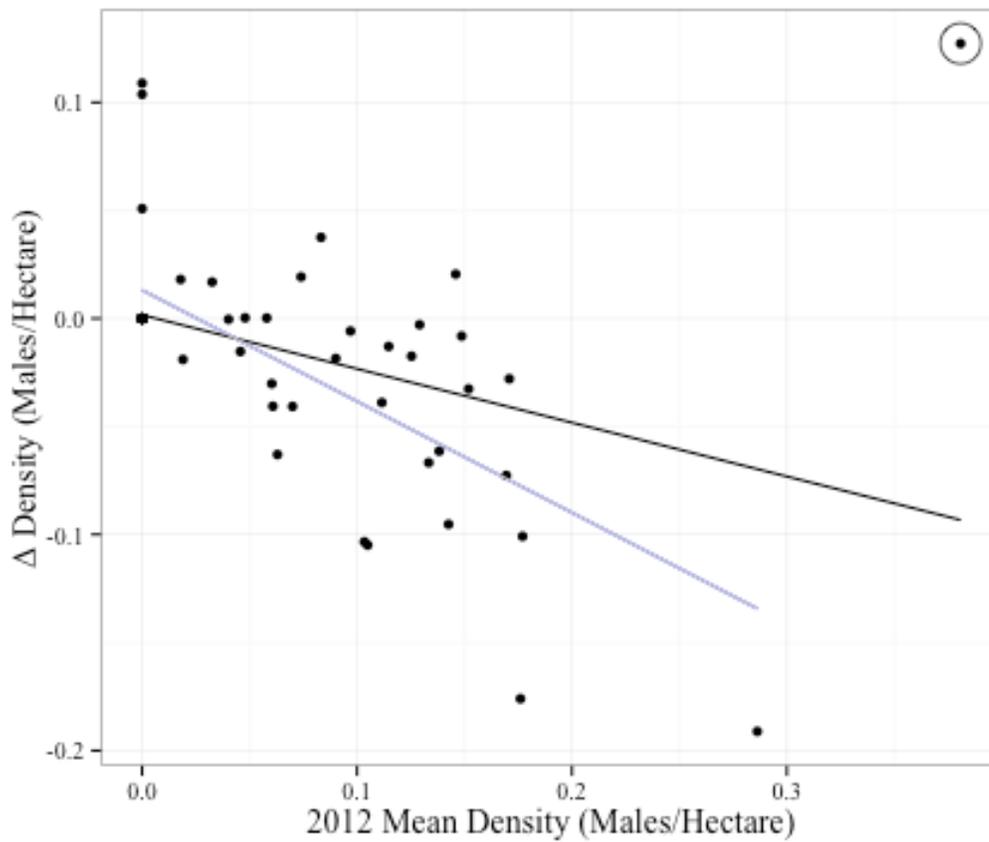


Figure 4: Change in patch male density from 2012 to 2013 as a function of 2012 male density. Note the leverage point (circled) and the increased strength of the relationship (plotted in grey).

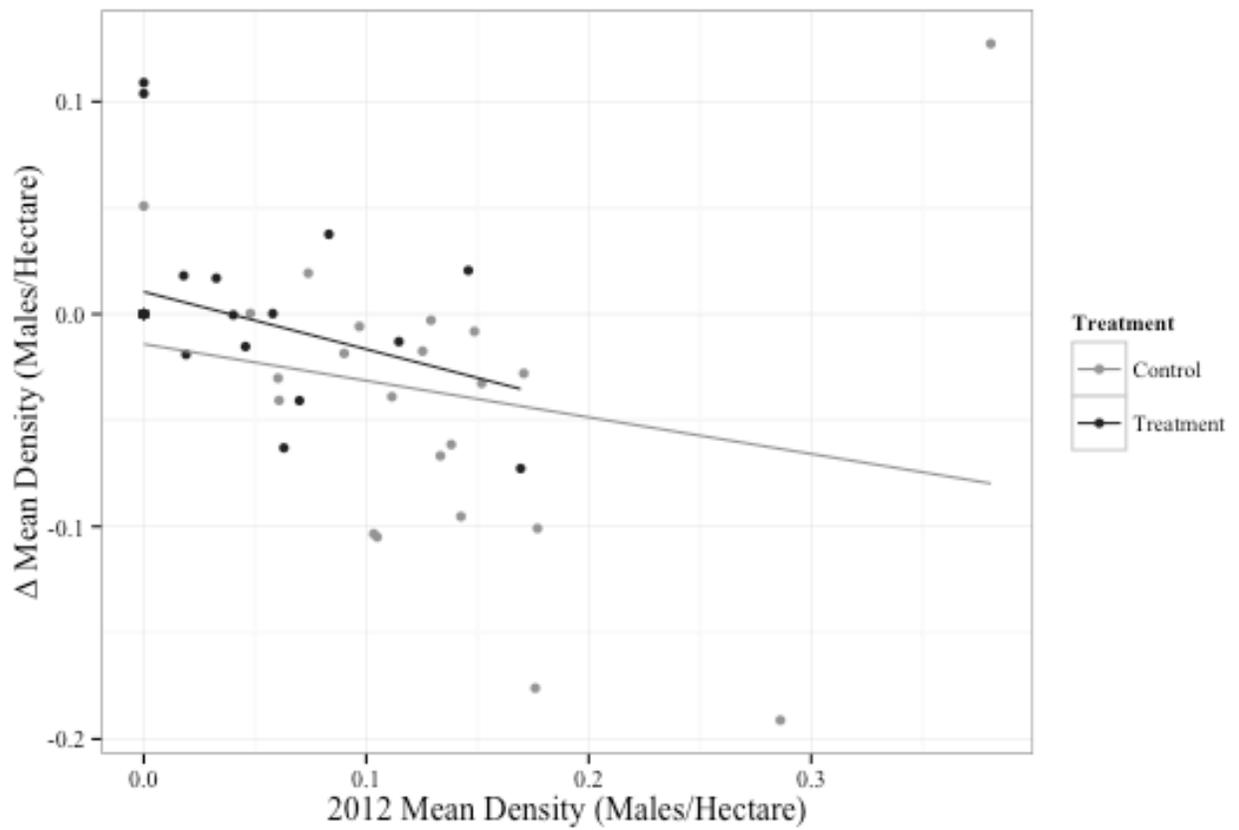


Figure 5: Change in mean patch density (males/hectare) as a function of 2012 Density for treatment and control patches.

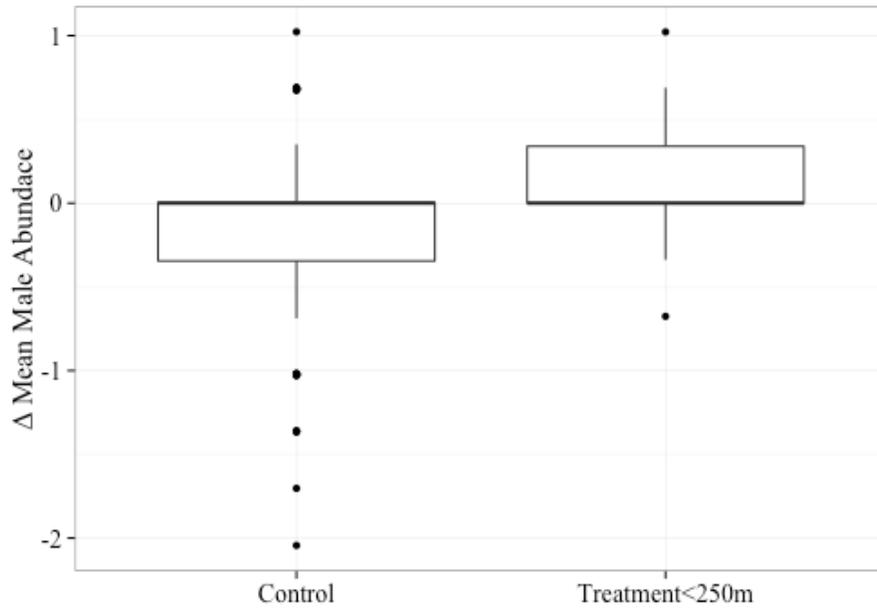


Figure 6: Change in male abundance (males/survey point) for points within 250m of playback treatment or more than 250m from playback treatment (control points).

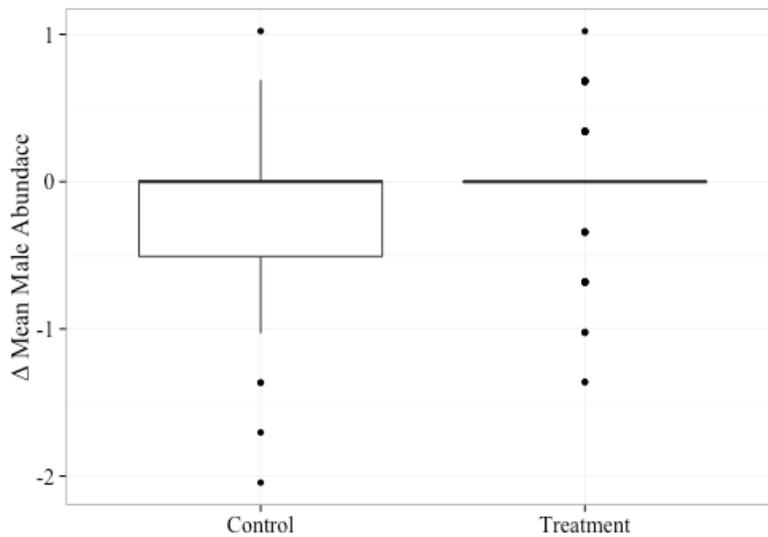


Figure 7: Change in male abundance (males/survey point) for points within treatment and control patches without playback treatment.

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