USE OF SOCIAL INFORMATION FOR HABITAT SELECTION IN SONGBIRDS

A Dissertation

by

SHANNON LEIGH FARRELL

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

May 2011

Major Subject: Wildlife & Fisheries Sciences

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Approved by:

Chair of Committee,	Michael L. Morrison
Committee Members,	James Cathey
	Jane Packard
	Gil Rosenthal
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ABSTRACT

Use of Social Information for Habitat Selection in Songbirds. (May 2011)
Shannon Leigh Farrell, B.A., Brown University; M.S., Texas A&M University
Chair of Advisory Committee: Dr. Michael L. Morrison

Habitat selection research has focused on the role of vegetative and geologic habitat characteristics or antagonistic behavioral interactions. Conspecifics can confer information about habitat quality and provide positive density-dependent effects that may result in improved fitness, resulting in positive behavioral responses to conspecifics as a habitat selection strategy. I conducted 3 replicated, manipulative experiments to investigate use of conspecific cues in habitat selection for the golden-cheeked warbler (*Dendroica chrysoparia*) using simulated conspecific vocalizations during pre-settlement and post-breeding periods, across a range of woodland canopy cover. I measured territory density, pairing, and fledging success in paired treatment and control units. Territory density was >2 times higher in treatment units across the range of canopy ($P = 0.02$). Pairing success was positively correlated with territory density ($P = 0.008$). Territory density response was higher for pre-settlement than post-breeding treatment ($P = 0.004$). I found pre-settlement and post-breeding conspecific cues influence golden-cheeked warbler habitat selection, inducing settlement in previously unoccupied areas, and producing aggregations within areas of similar vegetative characteristics. Better understanding of social information use in habitat selection can improve our understanding of species distributions, yielding more accurate predictive distribution models; improve our ability to predict impacts of habitat changes on habitat use, survival, reproduction, and ultimately fitness; and provide a potential tool for attracting individuals to restored or managed sites.

ACKNOWLEDGEMENTS

I thank the US Army Integrated Training Area Management (ITAM) Program, Office of the Secretary of Defense, Department of Defense for funding support and additional support from Central Texas Cattlemen’s Association, United Sates Department of Agriculture Natural Resources Conservation Service, the National Fish and Wildlife Foundation, and Texas Parks and Wildlife Department. I am grateful to the Texas A&M Institute of Renewable Natural Resources for boundless technical, logistical, and administrative support; I particularly thank N. Wilkins, B. Hays, L. Law, V. McCallister, B. Collier, T. Snelgrove, A. Snelgrove, H. Mathewson, and T McFarland. I am tremendously grateful to the landowners who generously granted me permission to conduct this research on their land and to S. Manning, D. Petty, and J. Tatum for facilitating connections with landowners, other logistical field support, and sharing their indispensible local knowledge. I thank field technicians M. Hague, D. Hardcastle, C. Lara Mendoza, J. Piispanen, and A. Stenman for their efforts.

I thank my graduate colleagues for their feedback and assistance; I am particularly grateful to A. Campomizzi for unmatched thoughtful discussion, constructive criticisms, encouragement, and support. I thank my committee members for their time and effort. I would especially like to thank my advisor, Dr. Michael L. Morrison, whose effort, time, and guidance has been immeasurable. Finally, I thank my family for providing the support and encouragement that made it possible to complete this challenging endeavor.

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INTRODUCTION

Wildlife habitat relationships are among the most intensively studied topics in ecology because understanding relationships between habitat and species occurrence, abundance, and distribution is important to both ecological theory and conservation and management efforts (Manly et al. 2002, Barry and Elith 2006, Guisan et al. 2006, Morrison et al. 2006). A species distribution appears to be the product of the hierarchical behavioral decision process of habitat selection (Hilden 1965, Block and Brennan 1993, Jones 2001, Dall et al. 2005). Organisms can use a variety of information to make habitat selection decisions, though most empirical and theoretical research on habitat selection has focused on vegetative, geologic, and geomorphic habitat characteristics (Grinnell 1917, Kendeigh 1945, Rosenzweig 1991, DeBoer and Diamond 2006). Research and theory addressing the role of inter and intra-specific behavioral interactions remains largely focused on negative density dependence and exploitative resource competition (Fretwell and Lucas 1970, Connell 1983, Dodds 1997; but see Darling 1952), though some ecologists have suggested an undue emphasis on the role of competition in explaining species distributions and habitat selection (Brawn et al 1987, Bertness and Callaway 1994, Gross 2008).

Positive interactions can play a role in habitat selection; for example, bird song is

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typically considered a behavior used for competitive exclusion or mate attraction (Falls 1992), but conspecific song can also function as a source of information for habitat selection that can attract conspecific males to an area (Doligez et al 2004b, Araujo and Guisan 2006, Hahn and Silverman 2006). Accurately identifying the information organisms use to make habitat selection decisions at various spatial scales (e.g., landscape, patch, territory) is necessary for understanding resulting distributions and the fitness consequences of habitat selection decisions (Jones 2001, Morris, 2003, Rodenhouse et al. 2003). Habitat selection behaviors can influence parameters such as adult survival, mating success, and reproductive success which, theoretically, can influence fitness (sensu Begon et al 2005, Alcock 2008, Dugatkin 2009).

Species distributions are constrained by physical and physiological limitations and innate evolutionary templates that drive coarse, first-order selection of a geographic region and vegetation type (Southwood 1977, Johnson 1980). Individuals can then use information from personal experience and from sampling of habitat to make selection decisions among sites within the range of potential habitat (Doliguez et al 1999, Danchin et al 2004, Seppanen 2007). For songbirds, information from personal experience can include previous success or failure at territory establishment, pairing, mating, nesting, and fledging young in previous breeding seasons; previous encounters with predators or food resources; and natal experience for second-year birds (Greenwood and Harvey 1982, Bollinger and Gavin 1989, Hoover 2003). Sampling potential sites can provide information about vegetation species and structure (Chalfoun and Martin 2007), predators (Fontaine and Martin 2006), food resources (Orians and Wittenberger 1991), and presence of conspecifics and heterospecifics (Fletcher 2007, Ahlering et al 2006). Individuals in several taxa use inadvertent social information, auditory, visual, or chemical location cues from conspecifics or heterospecifics in habitat selection (Stamps 1988, Monkkonen et al. 1990; Nocera et al. 2006, Donahue 2006, Hahn and Silverman 2007). Location cues can provide information about local habitat quality with varying reliability (Van Horne 1983, Valone 1989, Clark and Mangel 1984, Danchin et al. 2001). Alternatively, presence of conspecifics may neither provide nor be used for information about habitat quality but simply serve as a cue by which species can form aggregations that confer positive density-dependent benefits (Allee 1927, Stephens et al 1999, Courchamp et al 2009).

A bird with complete, perfect sampling information about all characteristics of all potential sites can make decisions that optimize both short-term survival and reproduction, and ultimately, lifetime fitness, but perfect information is rarely obtainable (Arlt and Part 2007, Seppanen et al 2007). Migratory bird species selecting breeding habitat are often constrained by a short breeding season, and may need to select a breeding site and establish a territory quickly. Sampling thoroughly is energetically and temporally costly and inefficient (Lima and Zollner 1996, Boulinier and Danchin 1997). Information about characteristics of a site that can affect reproductive success, including primary nest predators and food resources, may not be spatially or temporally detectable at the time when the bird makes a selection decision (Hilden 1965, Orians and Wittenberger 1991, Dall et al 2005). Conspecific location cues may be an efficient source of information for habitat selection decisions (Forbes and Kaiser 1994, Danchin et al. 2001). In habitats that vary unpredictably over space and time or where sampling information about food or predators is not readily accessible to an arriving migrant bird, the presence of conspecifics may be sufficiently or occasionally reliable enough to allow species to select profitable habitats during at least some of their breeding seasons to optimize fitness over the course of their lifetime (Clark and Mangel 1984).

Conspecific location cues detected during different temporal periods can provide different information content, with varying relative reliability and influence on decision-making. For migratory birds, particularly those in which older males arrive first to breeding grounds and show fidelity to sites where they had previous success, it is plausible that presence or abundance of conspecific males during the early breeding period may provide information indicating suitable or high-quality habitat areas for less experienced second-year males arriving later (Nocccera et al 2006). However, for many bird species, reproductive success at some occupied sites is low, some birds occupy poor habitat, and thus the presence of conspecifics in an area at the start of the breeding season is not always a reliable indicator of habitat quality (Arlt and Part 2007). For species that exhibit site fidelity at least some of the time even when unsuccessful in previous years, presence of after-second-year males at the start of the breeding season may not reliably indicate high-quality habitat (Bollinger and Gavin 1989, Pulliam and Danielson 1991, Sedgwick 2004).

Birds can also prospect neighboring territories during or after breeding for public information about the presence and reproductive success (e.g., presence, number, or condition of fledglings) of conspecifics for use in selection decisions in subsequent breeding years (Doligez et al. 1999, 2002, 2004a; Betts et al. 2008). Black-throated blue warblers (*Dendrioca caerulescens*) were found to use conspecific vocalizations detected during post-breeding prospecting to select territory locations in the subsequent year, including low-quality habitat areas (Betts et al. 2008). Thus, conspecific location cues observed during post-breeding prospecting may be more closely associated with actual performance measures (e.g., successful territory establishment, pairing success, or nesting) of conspecifics than simply presence of conspecifics at the start of a breeding season. Even presence of adult males in an area at the end of a breeding season may indicate the area was suitable enough to be occupied for the duration of the breeding season even if fledglings were not produced (Betts et al. 2008). However, post-breeding information may be temporally unreliable if habitat quality varies between years such that reliable signals of quality from one breeding season may not be correlated closely or at all to the quality of the habitat in the subsequent breeding season. Thus, uncertainty exists on the reliability of social cues for making habitat selection decisions.

In recent research, conspecifics location cues have primarily been thought of as potential source of information about habitat quality. Research addressing the influence of conspecific cues across varying habitat conditions has been limited and has focused primarily on post-breeding cues. Research has not addressed outcomes of conspecific cue use for pre-settlement or post-breeding social cues, in terms of mating success and reproductive success that can theoretically influence fitness. Neither theory nor research has addressed presence, prevalence, and potential fitness impacts of using unreliable cues. If conspecific cues are frequently unreliable and use of unreliable cues leads to deleterious fitness effects, we might not expect they serve primarily as indicators of habitat quality. Attraction to conspecifics cues may serve as a means to recruit conspecifics to an area to increase conspecifics densities and to form aggregations that confer positive density-dependent benefits (Courchamp et al 2008, Courchamp et al 2009, Brashares et al 2010, Gaston et al 2010). Aggregating in groups can provide benefits including group vigilance against predators, predation dilution, increased foraging success, increased probability of mating, and increased opportunity for extra-pair copulation (Forsman et al. 2002, Kokko and Rankin 2006).

Habitat selection decisions are often assumed to be adaptive (Jones 2001). But attraction to conspecific cues may be more influential in decision making than other habitat conditions, leading individuals to select suboptimal sites to be adjacent to conspecifics (Hilden 1965, Arlt and Part 2007). In systems where changes in habitat conditions have rendered once-reliable cues now misleading, individuals may inadvertently select sites that lead to poor short-term success and ultimately poor lifetime fitness (Schlaepfer et al. 2002). Investigating the use of conspecific location cues and the fitness consequences of these decisions is critical to predicting and understanding the potential impacts of positive and negative changes in habitat characteristics and habitat quality for species that use conspecific location cues for habitat selection (Fletcher 2006).

Although research on habitat use and predictive habitat modeling has been conducted for the federally-endangered golden-cheeked warbler (*Dendroica chrysoparia*; hereafter “warbler”) to inform management for the recovery of the species

(DeBoer and Diamond 2006), this research has not addressed the influence of conspecific interactions in habitat selection and consequent effects on distribution and habitat use (Campomizzi et al. 2008). Attraction to conspecifics can influence the spatial distribution of warblers and other species within available habitat, leading to clumped or aggregated distributions within available habitat (Clark and Evans 1954, Augustin et al. 1996, 1998; Donahue, 2006) and may lead to unoccupied sites with suitable habitat. Identifying aggregated distributions and understanding the underlying mechanisms will improve understanding of species distributions in relation to population size and amount of available habitat, create more accurate predictive habitat models (Augustin et al. 1996, 1998; Lichstein 2002) and make appropriate management decisions. Additionally, for species that show attraction to conspecifics in habitat selection, simulated conspecific cues may provide a tool for attracting individuals to restored or managed sites with suitable habitat for that species (Ahlering and Faaborg 2006, Hahn and Silverman 2007).

I conducted 3 replicated, randomized manipulative field experiments to: 1) investigate the use of conspecific location cues by the warbler, 2) examine the relative influence of conspecifics cues across a range of habitat vegetation conditions, 3) compare the influence of cues present at warbler arrival and settlement and those present during the post-breeding period, 4) examine mating and reproductive outcomes related to apparent use of conspecifics cues for settlement decisions.

STUDY AREA

The study region was located in east-central Texas, in the Cross Timbers and Southern Tallgrass Prairies ecoregion of the Edwards Plateau (Griffith et al. 2004) in Coryell, Hamilton, Bosque, and Bell counties, within the Leon and Bosque River watersheds, including 19 subwatersheds. The majority of land in the study region is privately owned; about 88% of the land in Coryell County is used for farming or ranching (U. S. Census Bureau 2005). I located sample units on study sites surveyed in 2005–2008 during previous presence-absence surveys of 33 properties within a 140,000 ha area study region (Collier et al. 2010). Vegetation in this region included improved or non-native pasture, grassland, mid-successional mixed woody vegetation, and mature oak-juniper woodland (*Quercus* spp. - *Juniperus asheii*). Sample units were located in the woodland and mixed woodland-shrubland habitat types. Woodlands were characterized by oak species including Texas oak (*Quercus buckleyi)*, post oak (*Quercus stellata*), live oak (*Quercus* virginiana), and shin oak (*Quercus sinuata*). Elevation ranged from 200-500 m.

METHODS

I conducted 3 replicated, randomized manipulative field experiments to investigate use of conspecific location cues by the warbler and to compare warbler response to cues present during different time periods and habitat characteristics as detailed below. I used broadcast of conspecifics vocalizations following the methods described below to simulate conspecifics location cues. In 2008, I conducted experiment 1 to test hypotheses regarding warbler use of pre-settlement conspecific location cues to select territories within known suitable habitat and reproductive consequences of response to conspecifics location cues. In 2009, I conducted experiment 2 to test hypotheses regarding warbler use of pre-settlement conspecific cues across a range of woodland canopy cover, considered important for habitat quality, as described below. In 2009-2010, I conducted experiment 3 to test hypotheses regarding warbler use of post-breeding conspecific cues across a range of woodland canopy cover. I sampled in 27 pairs of sample units during the 3 years of the study: 5 in 2008, 11 in 2009, and 11 in 2010.

Description of vocalization broadcast methods for the 3 experiments

To simulate conspecifics vocalizations for all 3 experiments, I used 3 broadcast stations placed 20-30m apart to simulate multiple territorial individuals in the center of the treatment sample unit area and to ensure that at least 2 broadcast stations were functioning at any time in the event of equipment failure at 1 of the broadcast stations. Broadcast stations consisted of a 36-cm × 24-cm × 16-cm lidded plastic box with drilled holes for sound to broadcast containing: 1 rechargeable 12-V direct current (DC) 12-A battery; 1 programmable digital timer; 1 portable compact disk (CD) player; 1 small, 200mW amplified speaker; 1audio cable with a ground loop isolator; and 2 power converters, 2 socket adapters, and 5 jumper wires to convert power and connect from the battery to the electronic devices (Farrell and Campomizzi 2011). Broadcast stations played a CD with one of several versions of a loop of warbler songs, calls, and periods of quiet to simulate typical warbler territorial male vocalizations from 06:00–11:00 daily during the experimental period. For experiments 1 and 2, I broadcasted vocalizations 2 weeks prior to expected bird arrival and for 4 weeks following arrival of the first male warblers. For experiment 3 broadcast vocalizations also included fledgling calls, and were broadcast beginning when the first warbler fledglings were observed in the study area, 15 May, until most warblers appeared to have left study sites on 8 August (pers. obs.).

I produced vocalization CDs using several audio files of warbler vocalizations publically available on the internet, as well as our own recordings and mixed tracks using free audio editing software (Audacity® Version 1.2.6, http://audacity.sourceforge.net, accessed 1 Feb 2008). In 2008, I observed warblers counter-singing with simulated song broadcasts indicating that the simulations had the desired effect, in that warblers perceive the simulated song as another male conspecific. I placed broadcast units in trees or tall shrubs and secured the units to branches with duct tape. I visited broadcast units at least twice per week to ensure proper functioning and to change batteries. Control sites did not have broadcast stations because I assumed the presence of the station did not influence warbler behavior. Additionally, I did not use broadcast of non-conspecific song or other sounds, to avoid potential confounding effects of response to heterospecific songs or anthropogenic sounds (Monkkonen et al. 1990, Nocera et al. 2006).

General sampling design for the 3 experiments

I used paired sample units and randomly assigned treatment to one of each pair of points. I established 250-m-radius circular sample units around treatment or control center points using ArcMap™ to serve as sample units within which I measured all response variables. A 250-m radius encompassed the approximate distance at which sound from the broadcast treatment units was to be audible and elicit response (Naguib 1996, Forman 2000); I confirmed that while some minor variation existed due in part to some variation in vegetation cover characteristics, sound attenuated at or near 250m, by listening for broadcast sound every 50 m at each of the 5 sites treatment sample units.

Description of response variables for all 3 experiments

I measured the response variables territory density, pairing success, and fledging success within each 250-m radius sample unit for experiment 1 and 2, and measured territory density only for experiment 3. I conducted territory spot-mapping (Bibby 1992, Shankar Raman 2003, Probst et al. 2005) in each sample patch ≥1 time per week from the time of the first male warbler arrival in the study region to 8 weeks after, approximately 15 March to 15 May. I recorded ≥3 sequential GPS locations of singing males, females, or pairs observed at each territory visit and delineated territories with ≥15 points taken on at least 3 visits to the territory using minimum convex polygons to delineate territory polygons using Hawth’s Tools (Beyer 2004) in ArcMap™.

I calculated territory density as number of territories within each 250-m radius buffer divided by the total woodland patch area within the 250-m radius buffer, excluding from the calculation area comprised of grassland, pasture, road, or other non-woodland habitat. I surveyed 1 time per week for 1-hr in each territory using a modified Vickery method (Vickery et al 1992, Christoferson and Morrison 2001, Butcher et al. 2010) to determine pairing status and whether fledglings were present. I considered a territory productive if ≥1 dependent fledgling was detected in the territory with one or both of the adults. I describe analyses specific to each experiment below. Additionally, I summarized territory density data for the 3 experiments combined, to explore the generalized pattern of territory density response to conspecific location cues for territory selection.

Experiment 1: Use of pre-settlement conspecifics cues within suitable habitat

I conducted a manipulative experiment to determine if warblers use conspecific location cues to select territories within patches of suitable habitat that were previously occupied by warblers, and whether reproductive outcomes varied between treated and control or as a result of consequent territory density. I tested the following hypotheses:

1a. Hypothesis. Density of warbler territories will be greater in the treated sample unit than control unit of each pair of sample units.

1b. Hypothesis. Percent of territories successfully paired will be higher in the treatment units than in control units of each pair of sample units.

1c. Hypothesis. Percent of territories successfully fledging ≥1 young will be higher in the treatment units than in control units of each pair of sample units.

1d. Hypothesis. Pairing success and fledging success are positively correlated with territory density.

Site selection — In 2008, I identified patches of oak-juniper woodland known to be occupied by warblers where pre-treatment warbler territory data was collected in 2006 and 2007 (M. L. Morrison unpublished data, Butcher et al. 2010). Among these I identified patches with woodland cover considered optimal warbler habitat (≥75% woodland cover; Texas Parks and Wildlife 2003, DeBoer and Diamond 2006) by running an unsupervised classification to estimate woody canopy cover using Spatial Analyst in ArcMap™ (ESRI® 2005, Redlands, California, USA). Patches varied in size so I limited study patches to those large enough to contain at least 4 warbler territories, a minimum of 8 ha based on average territory size reported by Ladd and Gass (1999). This minimum patch size excluded patches with low probability of occupancy (Butcher et al. 2010) and those too small to contain several territories and enable any experimental effect to be detectable between treatment and control unit.

Patches varied in relative deciduous- juniper (*Juniperus ashei*) composition, so I excluded monotypic stands and selected patches with at least 10% deciduous or juniper component to meet Texas Parks and Wildlife (2003) criteria for suitability for warblers. I randomly selected 5 of the patches that met the aforementioned criteria. I placed both sample units within one patch for this experiment. I systematically placed 2 points ≥500 m apart within the patch to ensure treatment and control areas did not overlap so that responses measured in each were independent. I randomly assigned treatment to one of each pair of points.

Analysis — I conducted descriptive statistics and plotted data to explore presence and magnitude of effects for all hypotheses. I was unable to find any literature or generate any reasoning based on theory or existing data indicating a difference in territory density that would result in biologically relevant implications so I considered a difference of 0.05 territories per hectare, or 1 additional territory per 250-m sample unit of woodland, between treatment and control as an *a priori* effect size I was willing to accept given some sites would have few territories.

I used paired sample Wilcoxon sign-rank tests (Zar 1999:538–539) to test hypotheses 1a-c, to for difference in the territory density, pairing success, and fledging success between paired control and treatment locations. I considered a 10% difference in fledging success as a biologically significant effect size, based on previous research suggesting that a difference in reproduction of 10% may have important consequences for population level breeding success, recruitment, and population dynamics (Porneluzi and Faaborg1999, Powell et al. 1999). I used a Spearman's rank correlation (Zar 1999:395–398) to test hypothesis 1d and 1e to determine if pairing and fledging success increased with increasing territory density. All analyses were conducted using SPSS (SPSS for Windows, Version 15.0.0. SPSS Inc. 2006. Chicago, Illinois, USA.) and R statistical software (R Development Core Team, R Version 2.11.1. 2010. R Foundation for Statistical Computing. Vienna, Austria.).

Experiment 2: Use of pre-settlement conspecifics cues across range of habitat

I conducted a manipulative experiment to investigate the relative influence of conspecific cues and habitat vegetation characteristics by determining if warblers will settle in response to conspecific songs in a range of canopy cover considered optimal to marginal or poor habitat based on Texas Parks and Wildlife habitat guidelines (see below; Campbell 1996, Texas Parks and Wildlife 2003), and whether reproductive outcomes vary between treated and control, as a result of consequent territory density, and with canopy cover. I tested the following hypotheses:

2a. Hypothesis. Density of warbler territories will be greater in the treated sample unit than control unit of each pair of sample units.

2b. Hypothesis. Difference in territory density between treatment and control will decrease with decreasing percent woodland canopy cover.

2c. Hypothesis. Percent of territories successfully paired will be higher in the treatment units than in control units of each pair of sample units.

2d. Hypothesis. Percent of territories successfully fledging ≥1 young will be higher in the treatment units than in control units of each pair of sample units.

2e. Hypothesis. If differences are observed as stated in hypothesis 2c and 2d, I hypothesize that pairing success and fledging success are positively correlated with territory density.

2f. Hypothesis. Difference in territory density between treatment and control will decrease with decreasing percent woodland canopy cover.

Site selection — In 2009, I used the same criteria for patch size and tree species composition described above for experiment 1 site selection. However, for this experiment, I did not require that sample units were placed within patches that were known to be occupied by warblers in previous years. I identified patches with woodland cover within the study region using the 2009 National Land Cover Dataset [NLCD] from the United States Geological Survey [USGS]. Texas Parks and Wildlife guidelines suggest that warblers can occur in sites with 35–100% woodland canopy cover, with areas < 35% unlikely to be occupied and patches with 50–100% canopy cover are highly likely to be occupied and additional data from the study region suggests that in areas with > 75 % canopy cover, probability of occupancy approaches 1, but is lower for areas with cover from ≈50–75% (DeBoer and Diamond 2006, M. L. Morrison unpublished data). Additionally, TPWD guidelines suggest that "marginal" habitat with low canopy cover adjacent or within 300m of high canopy cover areas may be occupied due to proximity, but this has not been empirically tested nor has any mechanism been described (Texas Parks and Wildlife 2003).

I ran an unsupervised classification using Spatial Analyst in ArcMap™ to identify patches of > 75 % canopy cover woodland with adjacent woodland within ≤ 300m in 2 categories of 35–50%, and 50–75%. Additionally, because research on effects of anthropogenic noise suggest that sounds and its concurrent effects attenuate within ≈300m (Forman 2000, M. L. Morrison unpublished data), placement within ≤ 300m will enable song broadcasts to be within audible distance from the > 75 % canopy cover woodland area. I systematically selected 6 pairs of sample sites for each of the 2 canopy categories, with pairing based on the continuous canopy cover values of each site. In some cases, both sample units of a pair fit and were placed with one patch, so I systematically placed 2 points ≥500 m apart within the patch to ensure no overlap in treatment and control 250-m buffer area. In cases where paired sample units were in different patches, I placed points systematically within each site to maximize the targeted woodland area (<35%, 35–50%, and 50–75%) within the sample unit. I randomly assigned treatment to one of each pair of points. I had to discontinue sampling in 1 pair of sample units in 2009 due to a change in access.

Analysis — I conducted analyses as described for experiment 1. I used descriptive statistics and plotted data to explore presence and magnitude of effects for all hypotheses. I used paired sample Wilcoxon sign-rank tests (Zar 1999:538–539) to test hypothesis 2a-d. I used a Spearman's rank correlation (Zar 1999:395–398) to test hypothesis 2d and 2e. I used scatter plots to explore hypotheses 2b and 2f, to determine if any relationship between the magnitude of difference between treatment and control units decreased with decreasing canopy cover.

Experiment 3: Use of post-breeding conspecifics cues across range of habitat

I conducted a manipulative experiment to determine if warblers use conspecific information (i.e., conspecific song and fledgling calls) gathered during post-breeding prospecting of neighboring territories to select territories in the subsequent year in a range of canopy cover considered optimal habitat to marginal or poor, based on Texas Parks and Wildlife habitat guidelines (Campbell 1996, Texas Parks and Wildlife 2003). I tested the following hypotheses:

3a. Hypothesis 3a. Density of warbler territories will be greater in the treated sample unit than control unit of each pair of sample units.

3b. Hypothesis. Difference in territory density between treatment and control will decrease with decreasing percent woodland canopy cover.

3c. Hypothesis. Difference in territory density between treatment and control will be greater in response to the pre-settlement conspecific cue treatment than for the post-breeding conspecifics cue treatment.

Site selection — For experiment 3, I used the same criteria and methods for selection of potential sampling sites as described above for experiment 2. From among the sites, I identified those where surveys in 2006-2009 did not detect warblers or detected warblers only on early survey visits during preliminary migrant arrival but did not continue to be occupied during subsequent survey visits. I systematically selected 6 pairs of sample sites for each of the 2 canopy categories. I established 250-m-radius buffers around treatment or control center points following the same methods described for experiment 1 and 2. I had to discontinue sampling in 1 pair of sample units due to a change in access.

Analysis — I used descriptive statistics and plotted data to explore presence and magnitude of effects for all hypotheses. I used paired sample Wilcoxon sign-rank tests (Zar 1999:538–539) to test hypothesis 3a. I used a scatter plot to explore hypothesis 3b, to determine if any relationship between the magnitude of difference in territory density between treatment and control units decreased with decreasing canopy cover. For hypothesis 3c, I used box plots to explore the data and conducted a Mann-Whitney U test (Mann and Whitney 1947).

RESULTS

For all 3 experiments combined, territory density was >4 times higher in treated sample units than control units (mean difference between treatment and control for each pair of sample units = 0.27 ± 0.04 territories per ha; paired samples Wilcoxon sign rank 1-tailed test, df = 27, V = 318, *p* <. 001). Twenty-three of the 27 pairs of sample units showed higher territory density in treated units than controls, an additional 2 of 27 had no territories in treatment or control units, and 2 of 27 had higher territory density in control than treated units.

Experiment 1: Use of pre-settlement conspecifics cues within suitable habitat

Territory density was 2 to 3 times higher in treatment units than controls in each pair (Fig. 1; mean difference between treatment and control for each pair = 0.25 ± 0.04; paired samples Wilcoxon sign rank 1-tailed test, df = 5, V = 15, *p* = 0.02). Density of warbler territories was overall 4.1 times greater in treatments than controls (mean treatment density = 0.33 ± 0.08 territories per ha, mean control density = 0.08± 0.05 territories per ha).

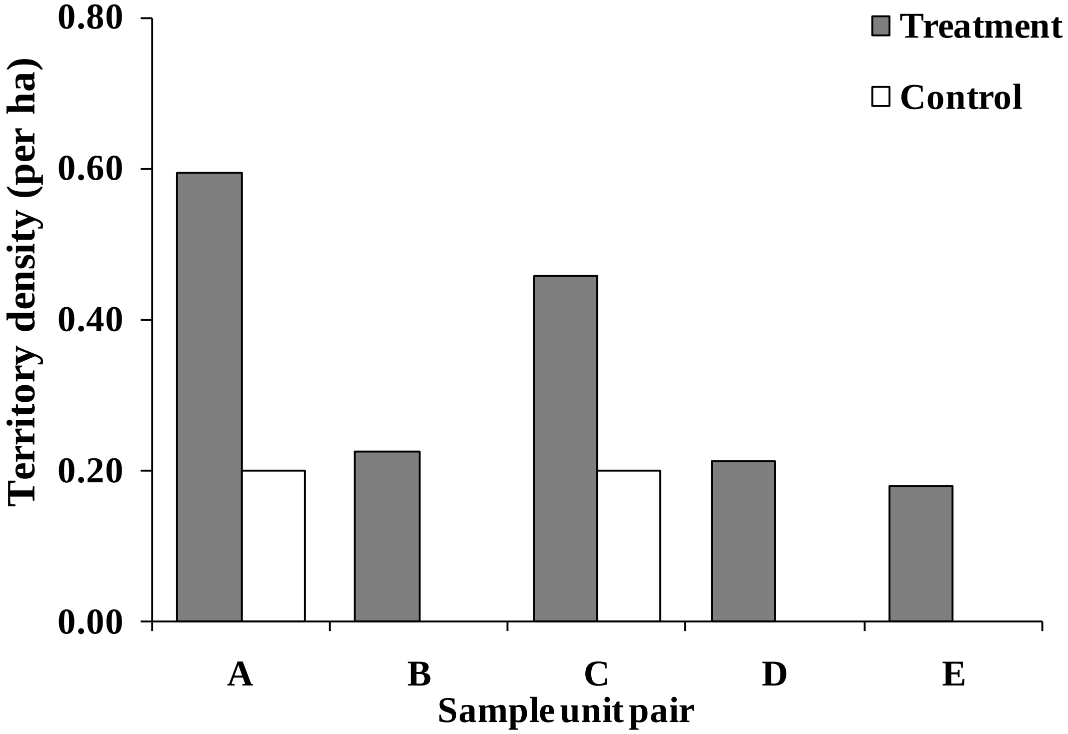

Figure 1. Territory density of golden-cheeked warblers in 5 pairs of experimental conspecific vocalization treatment and control sample units in > 75% canopy cover oak-juniper woodland patches in east-central Texas in 2008.

Mean proportion of territorial males that successfully paired was twice as high in treatment sample units as in control sample units (Fig. 2; mean proportion of males pairing in treatment units = 0.29 ± 0.18, mean proportion of males pairing in control units = 0.13 ± 0.13, paired samples Wilcoxon sign rank 1-tailed test, df = 5, V = 2, *p* = 0.33). Proportion of paired territories successfully fledging young was also twice as high in treatment than control sample units (mean proportion of pairs fledging ≥1 young in treatment units = 0.40 ± 0.24, mean proportion of pairs fledging ≥1 young in control units = 0.20 ± 0.20, paired samples Wilcoxon sign rank 1-tailed test, df = 5, V = 2, *p* = 0.16). Pairing success of males and fledging success of pairs showed evidence of a positive relationship with territory density (Fig. 3.; pairing success and territory density: Spearman's rho = 0.55, *p* = 0.05; Fig. 4.; fledging success of paired males and territory density: Spearman's rho 0.58, *p* = 0.04). But it should be noted that in 3 of 5 sample pairs, no males successfully paired in either treatment or control units, thus fledging success in these units was also zero.

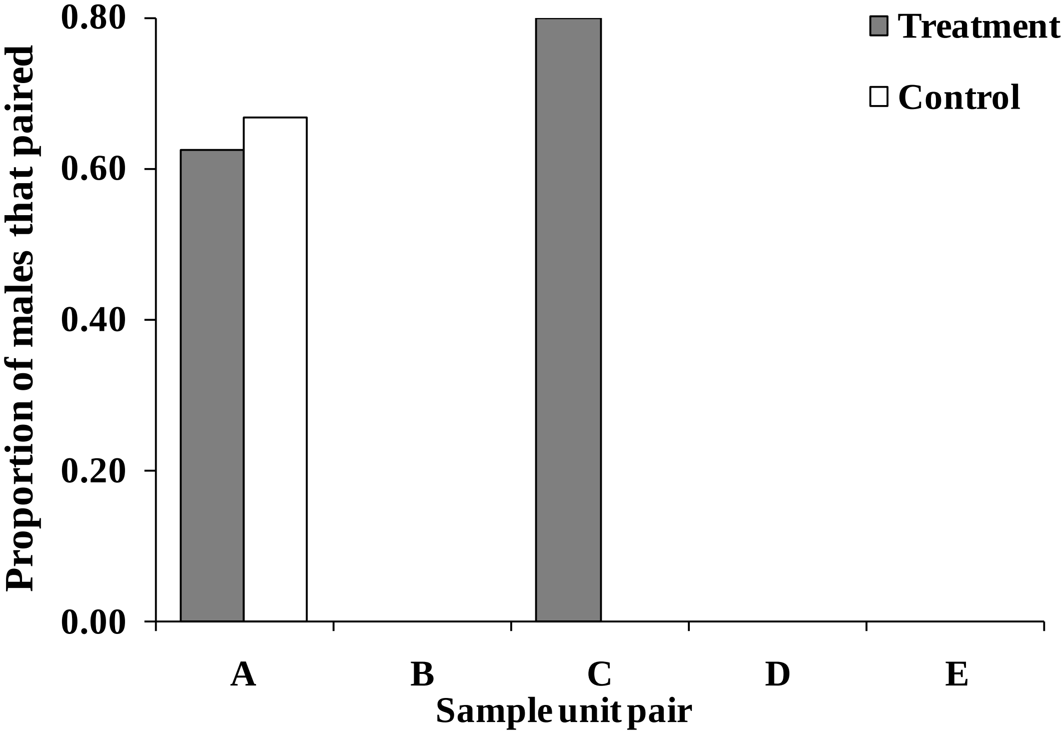

Figure 2. Proportion of territorial male golden-cheeked warblers that successfully paired with females in the 5 experimental conspecific vocalization treatment and control sample units in > 75% canopy cover oak-juniper woodland patches in east-central Texas in 2008.

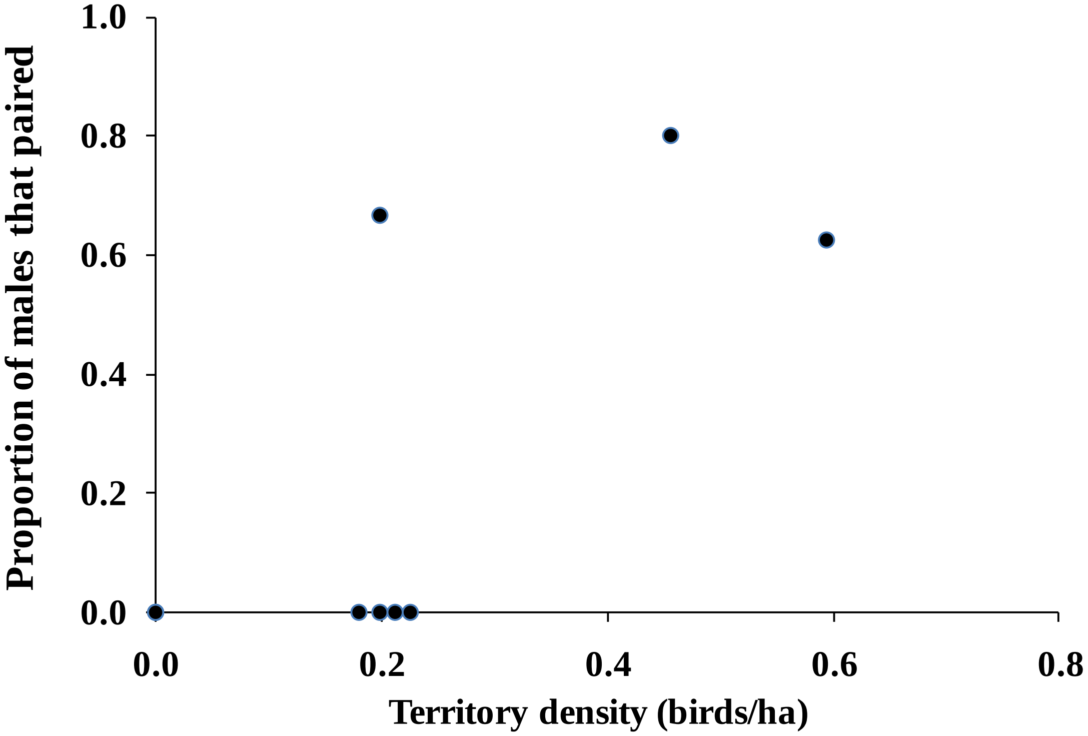

Figure 3. Proportion of territorial male golden-cheeked warblers that successfully formed pairs plotted against territory density in 5 pairs of experimental conspecific vocalization treatment and control sample units in > 75% canopy cover oak-juniper woodland patches in east-central Texas in 2008.

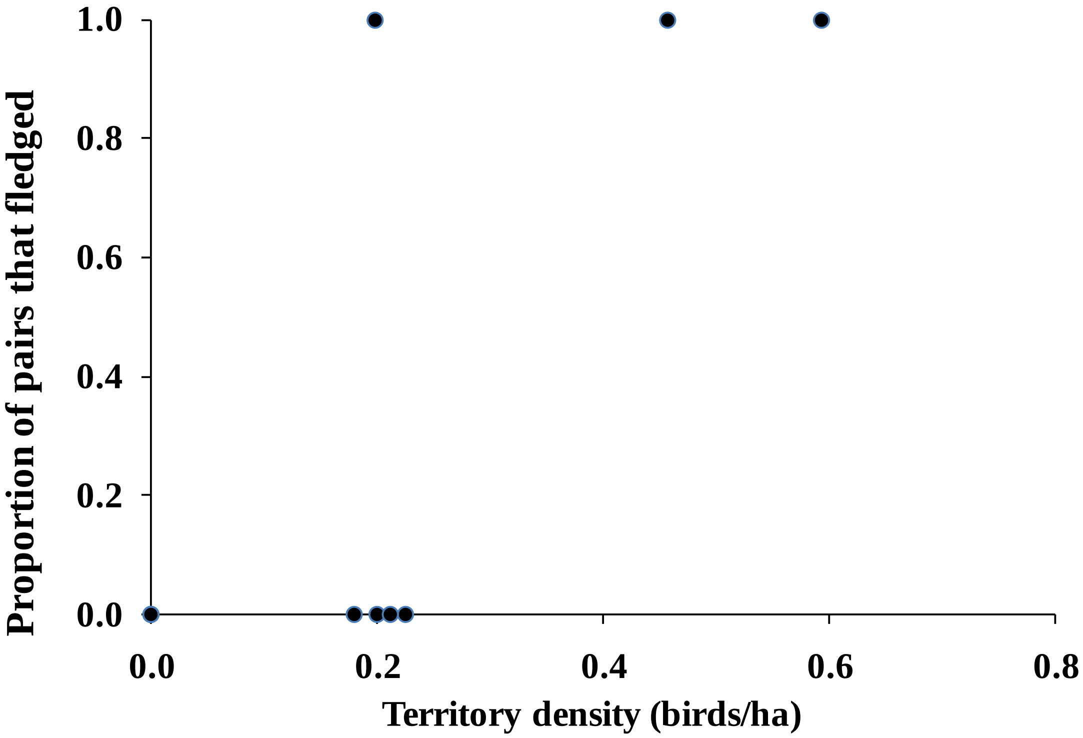

Figure 4. Proportion of golden-cheeked warbler pairs that successfully fledged young plotted against territory density in 5 pairs of experimental conspecific vocalization treatment and control sample units in > 75% canopy cover oak-juniper woodland patches in east-central Texas in 2008.

Experiment 2: Use of pre-settlement conspecifics cues across range of habitat

Density of warbler territories was greater in treatment sample units in 10 of 11pairs of sample units (Fig. 5; mean treatment density = 0.49 ± 0.06 territories per ha, mean control density = 0.1 ± 0.02 territories per ha). Territory density was an average of 5 times higher in treatment units than controls (Fig. 5; mean difference between treatment and control for each pair = 0.39 ± 0.05; paired samples Wilcoxon sign rank 1-tailed test, df = 11, V = 65, $p = 0.002$). The magnitude of difference in territory density between treatment and control units did not show a relationship with canopy cover (Fig 6; Spearman's rho = -0.064, $p = .426$), thus territory density was consistently higher in treatment units than controls regardless of percent canopy cover.

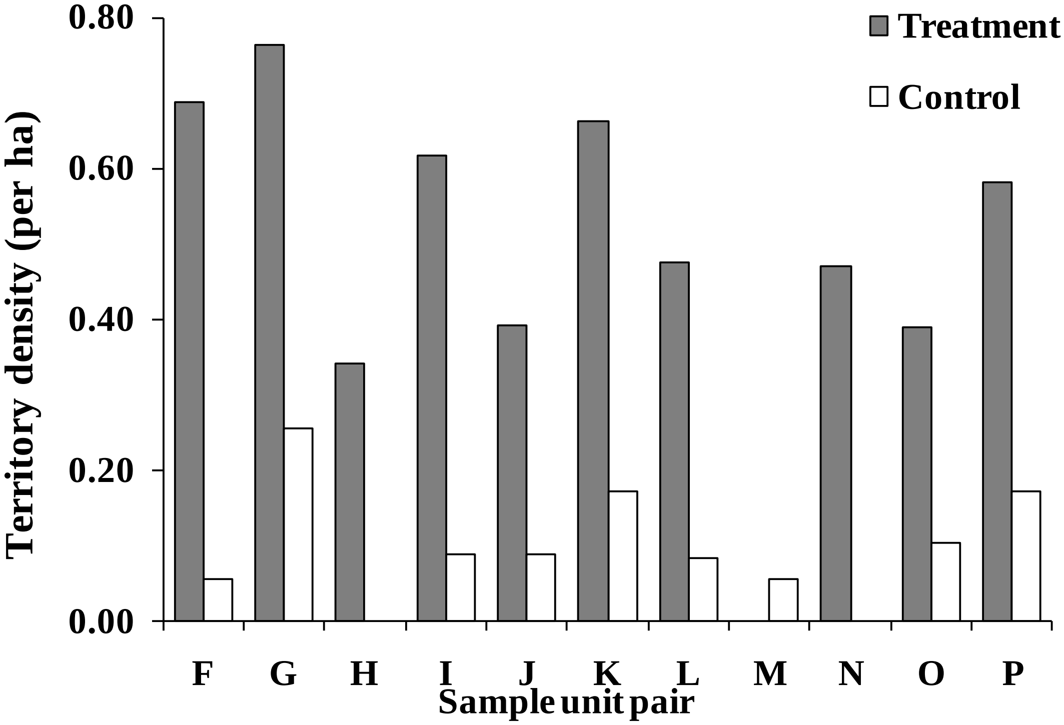

Figure 5. Territory density of golden-cheeked warblers in 11 pairs of experimental conspecific vocalization treatment and control sample units across a range of 25 to 70% canopy cover of oak-juniper woodland patches in east-central Texas in 2009.

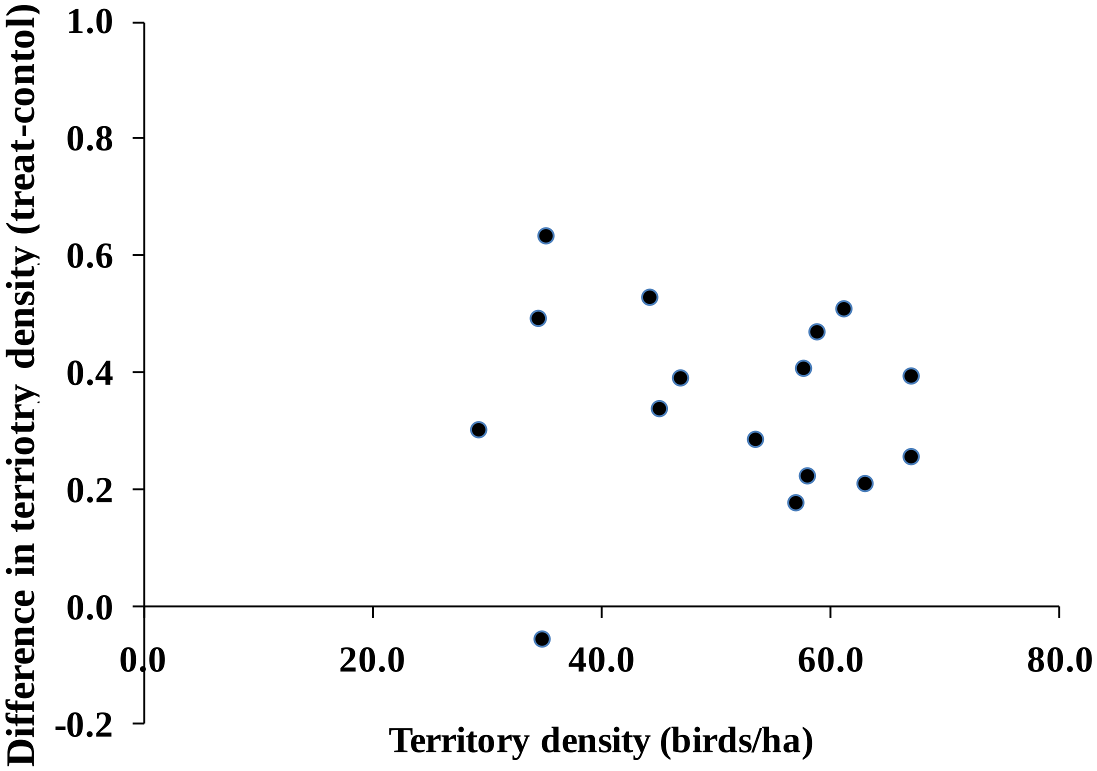

Figure 6. Difference in territory density of golden-cheeked warblers between treatment and control sample units in 11 pairs of experimental sample units plotted against percent canopy cover of oak-juniper woodland patches in east-central Texas in 2009.

Mean proportion of territorial males that successfully paired was 20% higher for treatment sample units than control sample units (mean proportion of males pairing in treatment units = 0.49 ± 0.07, mean proportion of males pairing in control units = 0.40 ± 0.13, paired samples Wilcoxon sign rank 1-tailed test, df = 11, V = 35, *p* = 0.22), but the difference was not statistically significant. Proportion of paired territories that successfully fledged young was also 20% higher for treatment sample units than control sample units (mean proportion of pairs fledging $\geq$1 young in treatment units = 0.49 ± 0.19, mean proportion of pairs fledging $\geq$1 young in control units = 0.40 ± 0.15, paired samples Wilcoxon sign rank 1-tailed test, df = 5, V = 2, *p* = 0.37), but the difference was not statistically significant. Pairing success of males was positively correlated with territory density (Fig. 7.; Spearman's rho = 0.506, *p* = 0.008); the correlation between pairing success and territory density suggested increasing pairing success with increasing density, perhaps above a density threshold of around 0.02 territories per hectare. Fledging success of paired males showed a statistical correlation with territory density (Spearman's rho 0.422, *p* = 0.03), but a scatterplot of data did not appear to suggest a clear pattern of correlation (Fig 8.).

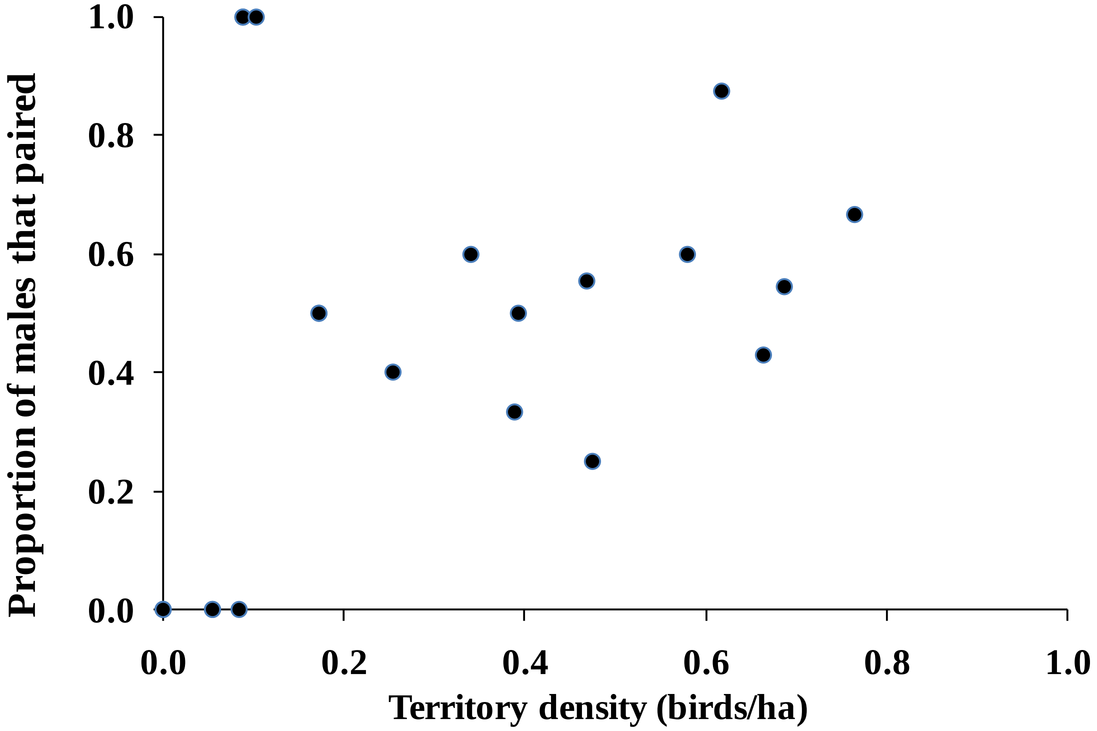

Figure 7. Proportion of territorial male golden-cheeked warblers that successfully formed pairs plotted against territory density in 11 pairs of experimental conspecific vocalization treatment and control sample units across a range of canopy cover oak-juniper woodland patches in east-central Texas in 2009.

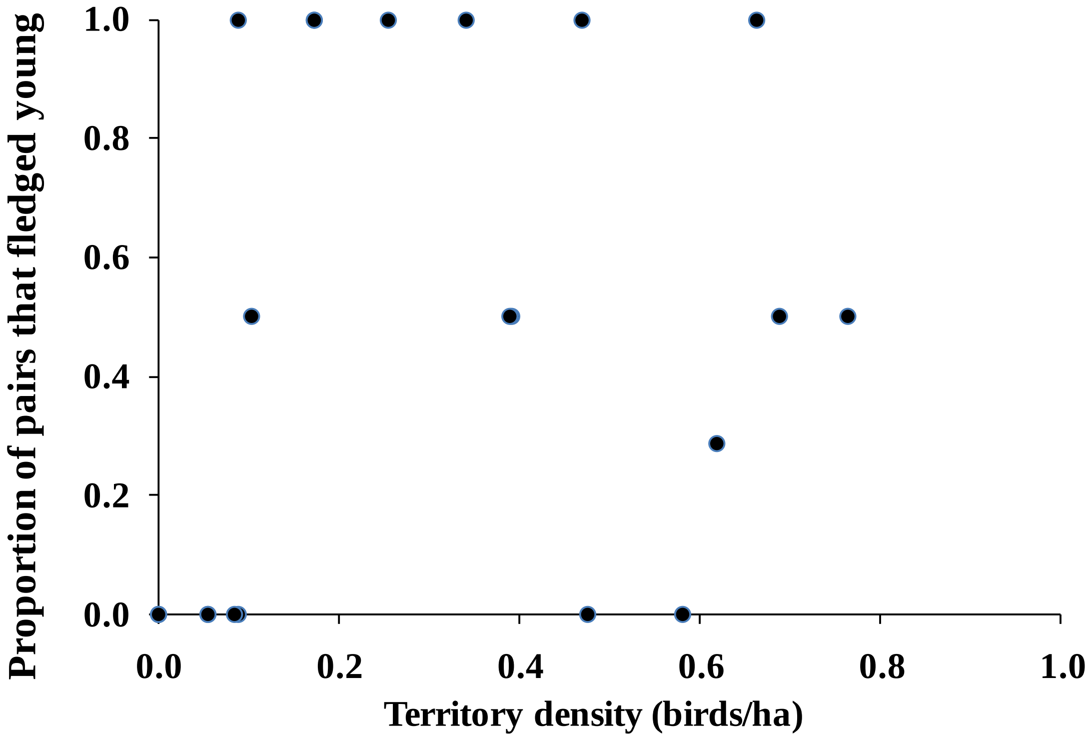

Figure 8. Proportion of golden-cheeked warbler pairs that successfully fledged young plotted against territory density in 11 pairs of experimental conspecific vocalization treatment and control sample units across a range of canopy cover oak-juniper woodland patches in east-central Texas in 2009.

Experiment 3: Use of post-breeding conspecifics cues across range of habitat

Density of warbler territories was greater in treatment sample units for 8 of 11 pairs of sample units in the post-breeding cue experiment, with 2 of the remaining 3 pairs of units having no territories in either the treatment or control (mean treatment density = 0.21 ± 0.06 territories per ha, mean control density = 0.06 ± 0.02 territories per ha). Territory density was 3 times higher in treatment units than controls (Fig. 9; mean difference between treatment and control for each pair = 0.15 ± 0.05; paired samples Wilcoxon sign rank 1-tailed test, df = 11, V = 41, $p = 0.01$). As in experiment 2, treatment units showed consistently higher territory densities than controls, regardless of percent canopy cover; magnitude of difference in territory density between treatment and control units did not show a relationship with canopy cover.

Although both pre-settlement and post-breeding conspecific cues elicited significant treatment responses of increased territory density in treatment units, the effect was significantly greater for pre-settlement treatment than for post-breeding treatment (Fig. 10; Mann-Whitney U 1-tailed test, W=100, $p = 0.004$).

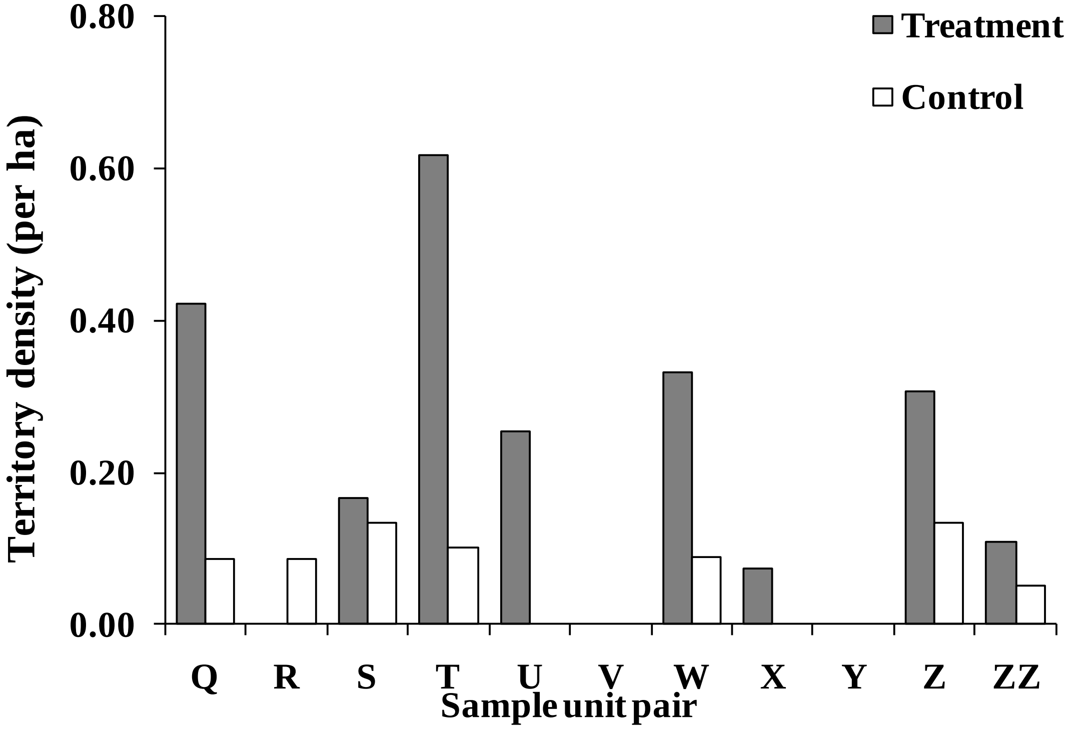

Figure 9. Territory density of golden-cheeked warblers in 11 pairs of experimental conspecific vocalization treatment and control sample units across a range of canopy cover oak-juniper woodland patches in east-central Texas in 2010.

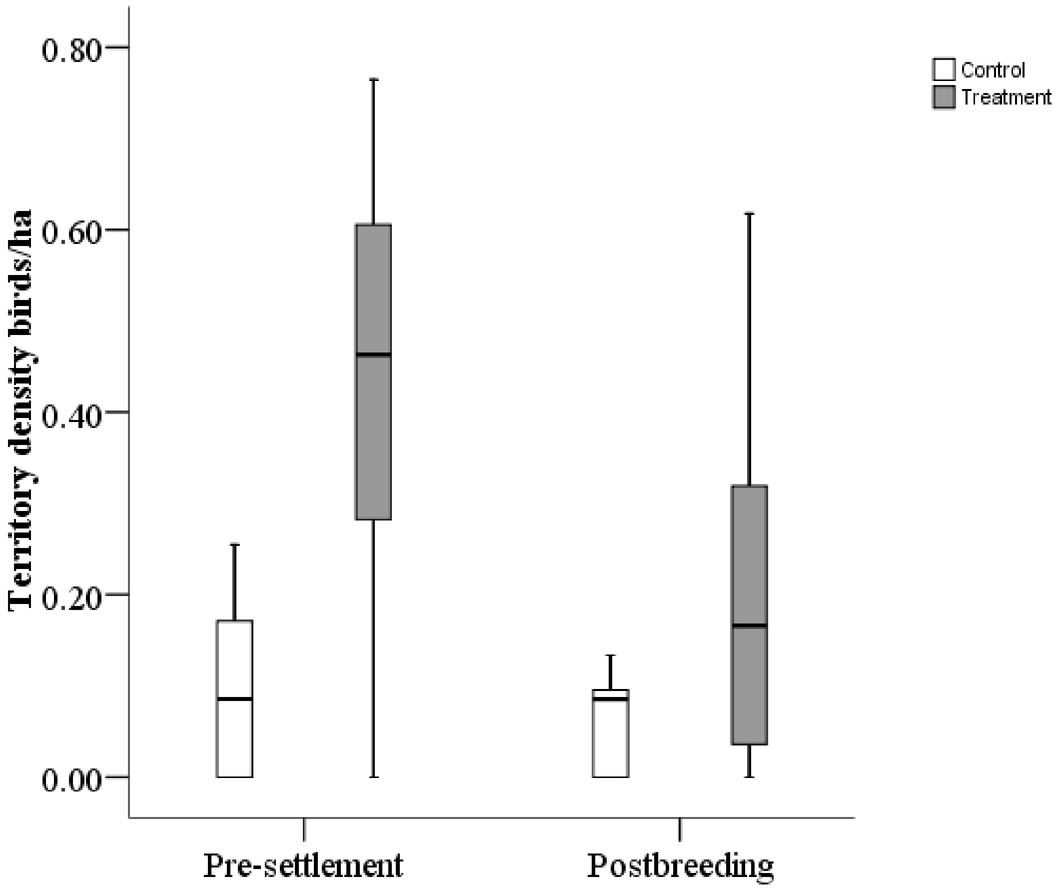

Figure 10. Difference in territory density of golden-cheeked warblers between treatment and control unit pairs and between pre-settlement and post-breeding conspecific vocalization treatment across a range of canopy cover oak-juniper woodland patches in east-central Texas in 2009 and 2010.

CONCLUSIONS

Territory density of warblers was, on average, 4 times greater in treatment than control sample units, supporting hypotheses 1a, 2a, and 3a. The magnitude of effect was greater than I expected and was observed even within patches known to be occupied by warblers (M. L. Morrison unpublished data, Butcher et al. 2010, Collier et al. 2010) where typically in the absence of experimental treatment, all but the very first warblers to arrive to the area are likely to encounter some conspecifics. We observed that for warblers and other breeding songbirds in the study area, males typically move around large areas and sing only intermittently upon initial arrival and within the first several days in a patch. If males then stay in the patch for several days or more, they typically substantially reduce the area they move within and begin singing more consistently. I suggest that conspecific vocalization behavior that may indicate the individual is not merely assessing the site but has selected the site and established a defined territory within it may be a more influential cue than conspecific vocalizations more generally in inducing settlement, and may also induce rapid settlement and territory establishment. Our broadcast treatment simulated this condition, and as additional males selected territories adjacent to treatment locations, the strength of this signal increased.

Data collected on some sample sites in experiments 1 and 2 in years prior to treatment suggest territory density in treatment units was higher following the experimental treatment than in pre-treatment years. But territory density in control units appeared to show a decrease following the treatment compared to pre-treatment (M. L. Morrison, unpublished data). Additionally, post-treatment territory distribution in control units was often characterized by large gaps in occupancy. The spatial pattern of territories in the control units and commonly reported return rates for male warblers of ≥ 40% (Peak and Lusk 2009) suggests males that previously held territories in the control unit area may have been drawn away from resettling in the control unit and settled in the treatment unit in response to the treatment. However, I did not age males or identify returning individuals because capturing and banding a large proportion of the birds was logistically infeasible for my short-term experiments so I cannot confirm individual territory shifts. Further research using conspecifics location cues with different characteristics, such as song frequency, spatial array of signals, or simulated density of individuals can help to investigate more precisely what information might be important for inducing settling responses. Additionally, researchers that are able to capture, age, and mark individuals pre-treatment may be able to address which individuals are most likely to use conspecifics cues, based on age class, previous reproductive success, or previous territory location and to assess finer patterns of timing and spatial distribution of territory settlement in response to conspecific location cues.

The magnitude of the territory density effect did not decrease with decreasing canopy cover as I had predicted in hypotheses 2b and 3b. In experiment 2, warblers settled in high densities in response to treatment in low canopy cover areas while adjacent patches of high canopy cover were also available suggesting that, at least within a range of vegetation characteristics, conspecifics location cues can be highly influential on settlement decisions in the hierarchical process of selection (Jones 2001, Dall et al. 2005). However, I did not test at the extremes of canopy cover characteristics, such as attempting to induce settlement in grasslands with few trees or shrubs. Nocera et al. (2006) found male bobolinks (*Dolichonyx oryzivorus*) settled in response to post-breeding conspecifics cues in unsuitable habitat, but in most cases left the sites after several weeks. However, Nocera et al. (2006) used an intermittent, rather than consistent, conspecific location cue treatment, and found that most poor quality sites settled in response to treatment were settled primarily by second-year males.

Theory would suggest that warblers should select habitat to sequentially fill the best available habitat until it reaches a saturation level at which point they may encounter competitive exclusion from accessing adequate resources and would then benefit from selecting the next best habitat area (Fretwell and Lucas 1970). My results suggest that the dynamic process of territory selection may not be substantially influenced by competition, that suitable areas may be left unoccupied or sparsely occupied while immediately adjacent areas, in some cases areas typically less likely to be selected or those considered less suitable, are densely filled in response to conspecifics location cues (Campomizzi et al 2008). Those sites in experiments 2 and 3 which were previously known to be unoccupied were typically considered unoccupied due to suboptimal or poor habitat quality on the basis of low woodland canopy cover. Birds that settled in these sites in response to conspecifics location cues might be expected to perform poorly, responding to an experimentally created ecological trap where a signal from conspecifics was unreliable and lead to a choice of poor habitat (Hilden 1965, Clark and Mangel 1984, Danchin et al. 2001).

However, birds who settled in areas of low canopy cover in response to treatment performed as well as those in higher canopy cover, in either pairing success or fledging success. Increasing territory density was correlated with increasing pairing success and, to a lesser extent, increasing fledging success, suggesting that warblers benefit from aggregating. This provides support for theory suggesting positive response to conspecifics cues may be, at least in part, as means for forming aggregations for species that exhibit positive density dependence. In such cases, conspecifics song may not serve mainly as a tool for competitive exclusion (Falls 1992), but a signal for recruiting conspecifics to an area, as an individual may experience benefits by increasing recruitment of conspecifics to an area (Araujo and Guisan 2006, Hahn and Silverman 2006). Treatment densities were significantly greater than control densities across pairs of sample units with similar habitat characteristics, often within the same woodland patch.

Where density of conspecifics has been considered as an important aspect of habitat quality, increasing conspecifics density is often considered to negatively impact the quality of a site for each subsequent individual. But our results suggest that increasing density of conspecifics should be considered a potentially positive component of habitat quality (Dodds 1988, Bertness and Callaway 1994). As in many songbirds, female warblers arrive to breeding grounds after males have arrived and at least started to select territories. I often observed females moving through habitat patches in groups, and high density concentrations of territorial males may not only provide a strong signal for females in search of potential mates but high density areas may also provide information indicating high quality habitat areas for use in female selection. My experiment may have generated stronger than expected aggregation effects, but previous research has suggested that warblers typically show signs of aggregating (Campomizzi et al. 2008) within suitable habitat and potentially across suboptimal habitat areas. This may suggest that aggregations are a desirable or adaptive distribution pattern for warblers, for increased pairing success and perhaps for other potential components of fitness that I did not quantify in this study.

Information gathered through prospecting is theorized to provide more reliable information about the reproductive quality or potential of the habitat than the mere presence of conspecifics at the start of a breeding season (Danchin et al. 1988, Bollinger and Gavin 1989, Doliguez 2004, Nocera et al. 2006). My results showed a response to post-breeding conspecifics cue treatment, but the magnitude of the response was significantly lower than for the pre-settlement treatment. Nocera et al (2006) found settlement responses were greater in response to treatment during the later part of the breeding season or post-breeding period. As I stated previously, my treatment was longer-term and more consistent that that used by Nocera et al. (2006) for both pre-settlement and post-breeding treatments, and thus it likely had a different meaning to receivers of the signal. This difference may be due to several factors. First, some individuals who detected post-breeding treatment cues may have experienced over-winter mortality, thus decreasing the potential pool of responders. Thus, the influence of the post-breeding signal may be as great as the pre-breeding signal, but a loss of potential response is incurred because fewer birds who detected the cue are available in the subsequent year to select territories in response to the cue. Further research considering loss of potential response due to overwinter mortality may help to accurately interpret the relative strength of the response to the 2 cues. Second, the pre-settlement cue may be more heavily used because it is a more reliable indicator of habitat quality in the year it is detected. If habitat quality in this system varies widely between years, the presence of conspecifics at the end of one breeding year may not relate closely to the expected quality of that site in the following year. Future research comparing the relative influence of pre and post-breeding conspecifics location cues in systems that vary widely and those that are relatively consistent among years can provide information about whether inter-annual variation in habitat quality explains this difference in response to the 2 cues. Lastly, if use of conspecifics cues is not primarily for information content about habitat quality, but for the purposes of establishing conspecific aggregations, pre-settlement cue in the same breeding year would be the most salient signals to use for forming aggregations and conversely, post-breeding cues would be relatively less relevant or useful for this application.

Previous research and management paradigms suggest that occupancy by warblers is higher with increasing canopy cover in the study region and have assumed that warblers select for higher canopy cover that must confer fitness benefits, and is thus higher quality habitat (Texas Parks and Wildlife 2003, DeBoer and Diamond 2006). However, our data suggests that apparent selection for relatively high canopy cover may instead be a vestige of the evolutionary history of the warblers and their woodland habitat (Hilden 1965) or tradition in habitat selection (Nocera et al 2006). For warblers and perhaps other species, the range of habitat within which they can successfully perform may be greater than is typically predicted based on occupancy, and occupancy should not be taken to necessarily imply preference or quality as defined by high reproductive success, survival, or other potential components of fitness (Klassen 2011). Particularly for species of concern, this experimental approach may provide a means for exploring arrange of potential habitat within which a species may be able to successfully reproduce, providing additional area to the known potential habitat and providing additional options for conservation and management. However, changes in habitat due to anthropogenic or other causes can lead to habitat conditions within which birds cannot perform well. In cases where information or cues about these changes is not readily detectable during habitat selection, such as the introduction of a significant predator that is not active or detectable during bird settlement, attraction to conspecifics can lead to continued or even increasing occupancy of non-adaptive habitat, or an ecological trap. Understanding how anthropogenic changes in habitat may affect habitat quality and how these changes may create a disjunction between cues used for selection and characteristics that affect survival, mating success, reproductive success, and ultimately fitness, particularly for species that show site fidelity and conspecifics attraction, is critical for avoiding creation of ecological traps.

Additionally, my results suggest that the dynamic process of territory selection may not be substantially influenced by competition, that suitable areas may be left unoccupied or sparsely occupied while immediately adjacent areas, in some cases areas typically less likely to be selected or those considered less suitable, are densely filled in response to conspecifics location cues (Campomizzi et al. 2008). Those sites in experiments 2 and 3 which were previously known to be unoccupied were typically considered unoccupied due to suboptimal or poor habitat quality on the basis of low woodland canopy cover. Incorporating knowledge of positive, aggregative habitat selection behavior and the resulting distributions is essential for creating more accurate spatially-explicit predictive occupancy models and understanding species distributions and occupancy patterns, to accurately determine when unoccupied areas are unsuitable or unoccupied simply due to clustered distribution patterns.

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