

Conspecific cues and breeding habitat selection in an endangered woodland warbler

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Summary

1. Research on habitat selection has focused on the role of vegetative and geologic characteristics or antagonistic behavioural interactions.
2. Conspecifics can confer information about habitat quality and provide positive density-dependent effects, suggesting habitat selection in response to the presence of conspecifics can be an adaptive strategy.
3. We conducted a manipulative field experiment investigating use of conspecific location cues for habitat selection and consequent reproductive outcomes for the endangered golden-cheeked warbler (*Setophaga chrysoparia*). We investigated the response in woodlands across a range of habitat canopy cover conditions typically considered suitable to unsuitable and using vocal cues presented during two time periods: pre-settlement and post-breeding.
4. Warblers showed a strong response to both pre-settlement and post-breeding conspecific cues. Territory density was greater than four times higher in treatment sample units than controls. The magnitude of response was higher for cues presented during the pre-settlement period. Positive response to conspecific cues was consistent even in previously unoccupied areas with low canopy cover typically considered unsuitable, resulting in aggregations of warblers in areas generally not considered potential habitat.
5. Pairing and reproductive success of males was not correlated with canopy cover, as commonly thought. Pairing success and fledging success increased with increasing territory density suggesting that conspecific density may be more important for habitat selection decisions than the canopy cover conditions typically thought to be most important. These results suggest the range of habitat within which birds can perform successfully may be greater than is typically observed.
6. Our results suggest the territory selection process may not be substantially influenced by competition in some systems. Settlement in response to conspecific cues produced aggregations within larger areas of similar vegetative characteristics. Understanding what cues drive habitat selection decisions and whether these cues are correlated with habitat quality is critical for conserving fitness-enhancing habitats, avoiding creation of ecological traps, generating accurate predictions of species distributions and understanding how occupancy relates to habitat suitability.

Key-words: conspecific attraction, density dependence, golden-cheeked warbler, public information, social information

Introduction

Most research on habitat selection has focused on the role of vegetative, geologic and geomorphic habitat characteristics (Kendeigh 1945; Rosenzweig 1991). Where behavioural interactions are considered negative, density dependence and competition have been the emphasis (Fretwell & Lucas 1970), although some researchers have questioned the emphasis on competition (Darling 1952; Connell 1983;

Brawn, Boecklen & Balda 1987; Dodds 1997). Bird song is typically considered a behaviour used for competitive exclusion or mate attraction (Falls 1992), but song can also function as an inadvertent source of information for habitat selection that can attract conspecific males (Doligez *et al.* 2004; Araújo & Guisan 2006; Hahn & Silverman 2006). Social information is used for habitat selection decisions in several taxa (Stamps 1988; Donahue 2006). Auditory, visual or chemical cues from conspecifics or heterospecifics can provide public information (Danchin *et al.* 2004) about local habitat quality, with varying reliability (Van Horne 1983;

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Clark & Mangel 1984; Valone 1989). Migratory birds often select a breeding site with incomplete information (Arlt & Part 2007; Seppanen *et al.* 2007) about relevant habitat conditions, such as predators or food resources, because of temporal and perceptual constraints (Hilden 1965; Orians & Wittenberger 1991; Dall *et al.* 2005). Presence of conspecifics may be an efficient surrogate or indicator of habitat quality, which may be reliable often enough to be an adaptive strategy over time (Forbes & Kaiser 1994; Danchin, Heg & Doligez 2001). However, although to our knowledge this has not been explicitly investigated, conspecific vocalizations may serve as a location cue (Danchin *et al.* 2004) by which species can form aggregations that confer positive density-dependent benefits (Allee 1927; Courchamp, Clutton-Brock & Grenfell 1999; Stephens, Sutherland & Freckleton 1999), independent of conferring any public information about habitat conditions.

Conspecific cues detected during different temporal periods may play different roles. For migratory songbirds, conspecific cues early in the breeding period may serve as inadvertent public information not as basic location cues (Danchin *et al.* 2004). Presence of conspecifics in early breeding may serve as an indicator that an area of habitat has suitable quality, particularly in species in which older males arrive to breeding grounds first and frequently show site fidelity where previously successful (Nocera, Forbes & Giraldeau 2006), if habitat quality across the site is spatially autocorrelated such that male presence in one territory plausibly indicates quality in nearby areas. For many bird species, however, reproductive success at some sites is low, and site fidelity is regular or frequent even among unsuccessful males (Campomizzi *et al.* 2012), making these early breeding season conspecific cues a potentially unreliable indicator of habitat quality (Bollinger & Gavin 1989; Pulliam & Danielson 1991; Sedgwick 2004).

Birds can also prospect neighbouring territories late or post-breeding for conspecific cue for use in selection decisions in the subsequent year (Doligez, Danchin & Clobert 2002; Betts *et al.* 2008). Post-breeding cues may serve as public information that is more indicative of habitat quality because it provides direct information about conspecific performance (e.g. territorial males, pairs, number of fledglings) and thus habitat quality of an area, than mere presence of conspecifics during early breeding. Sampling performance of multiple conspecific individuals in an area may provide a way to gain a more precise estimate of habitat quality in an area than the performance of an individual if habitat quality is spatially and temporally autocorrelated (Hoover 2003). However, if habitat quality varies substantially between years, post-breeding cues may not reliably indicate expected habitat quality in the subsequent year. It is less likely that post-breeding cues serve as location cues by which species can form beneficial aggregations, because the presence of the cue is temporally offset from the time when a settlement decision is made in the subsequent year.

Research has largely assumed conspecific cues are used as public information (*sensu* Danchin *et al.* 2004), interpreted

by individuals as an indicator of habitat quality. However, if conspecific cues are frequently unreliable indicators of habitat quality, we might not expect that these cues are primarily interpreted and used by individuals as an indicator of habitat quality. Rather, these cues may serve as location cues in some cases, by which attraction to conspecific cues can serve as a means to recruit conspecifics to an area to increase densities and to form aggregations that confer positive density-dependent benefits including predator dilution, increased vigilance and increased mating opportunities (Courchamp, Clutton-Brock & Grenfell 1999; Forsman, Seppanen & Monkkonen 2002; Kokko & Rankin 2006; Gaston *et al.* 2010). Although work on pre-settlement and post-breeding conspecific cue use has increased in recent years, research has often been limited by small sample size, lack of randomization and potential confounding variables such as differences in size of sample patches (Ward & Schlossberg 2004; Hahn & Silverman 2006), limiting our ability to make inferences and draw conclusions about the dynamics of this behaviour. Investigating the relative influence of conspecific cues in the context of other habitat cues (e.g. vegetation structure, species composition) and the reproductive consequences of selection decisions influenced by conspecific cues can provide insight into the potential drivers of this behaviour (Hilden 1965; Arlt & Part 2007). Additionally, understanding the role of inadvertent social cues can provide insight into potential consequences of anthropogenic changes in habitat conditions that, for example, render once-reliable cues misleading (Schlaepfer, Runge & Sherman 2002). Recent research has demonstrated response to conspecific cues during the post-breeding period across a gradient of habitat conditions thought to be associated with habitat quality (Betts *et al.* 2008). However, to our knowledge, published research to date has not addressed the influence of pre-settlement conspecific cues across a range of habitat conditions including habitat considered unsuitable or unoccupied, compared response to pre-settlement and post-breeding cues or assessed the reproductive outcomes of individuals responding to pre-settlement or post-breeding conspecific cues across a range of habitat conditions.

We conducted two replicated, randomized, manipulative field experiments in 2008–2010 to: (i) investigate the use and relative influence of conspecific location cues by the golden-cheeked warbler (*Setophaga chrysoparia*, hereafter, warbler) across a range of habitat vegetation conditions, (ii) examine mating and reproductive outcomes related to apparent use of conspecific cues for settlement decisions and (iii) compare the influence of cues presented during warbler arrival and settlement to those presented during the post-breeding period.

Materials and methods

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. Most land in the study region is privately owned, with *c.* 88% of land used for

farming or ranching (U. S. Census Bureau 2005). Sample units were located in woodland and mixed woodland–shrubland on sites previously surveyed for warbler occupancy in 2005–2008 (Collier *et al.* 2010) where vegetation includes pasture, grassland, mixed woodland–shrubland and mature oak–juniper woodland (*Quercus* spp. – *Juniperus ashei*).

OBJECTIVES: EXPERIMENT 1 – USE OF PRE-SETTLEMENT CONSPECIFIC CUES ACROSS RANGE OF HABITAT

In 2008 and 2009, we investigated the relative influence of conspecific cues across a range of habitat vegetation characteristics by determining whether warblers will settle in response to conspecific vocalizations in a range of canopy cover considered optimal to poor habitat based on current accepted habitat management guidelines (see below; Campbell 1996; Texas Parks Wildlife Department 2003) and whether reproductive outcomes vary as result of consequent territory density and with canopy cover. We tested whether: (1a) density of warbler territories was greater in the treated sample unit than control unit of each pair of units, (1b) difference in territory density between treatment and control decreased with decreasing per cent canopy cover, (1c) per cent of territories successfully paired was positively correlated with territory density and (1d) per cent of territories successfully fledging ≥ 1 young was positively correlated with territory density.

OBJECTIVES: EXPERIMENT 2 – USE OF POST-BREEDING CONSPECIFIC CUES ACROSS RANGE OF HABITAT

We conducted a manipulative experiment to determine whether warblers use conspecific cues (i.e. conspecific song and fledgling calls) gathered during post-breeding prospecting of other conspecific 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 Wildlife Department 2003). We tested whether (2a) density of warbler territories was greater in the treated sample unit than control unit of each pair of sample units, (2b) difference in territory density between treatment and control decreased with decreasing per cent woodland canopy cover and (2c) difference in territory density between treatment and control was greater in response to the pre-settlement conspecific cue treatment than for the post-breeding conspecific cue treatment.

EXPERIMENTAL TREATMENT: BROADCAST OF VOCALIZATIONS

We used broadcast of conspecific vocalizations for both experiments. Three broadcast systems were placed in trees or tall shrubs 20–30 m apart to simulate multiple territorial conspecific individuals in the centre of the treatment sample unit area (described below). Broadcast systems consisted of a 36 cm \times 24 cm \times 16 cm lidded plastic box, with openings for sound to broadcast, containing a power source; timer; compact disc (CD) player; amplified speaker; and power converters, adapters, and jumper wires (Farrell & Campomizzi 2011) and 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.

Golden-cheeked warbler vocalizations have not been well studied, but unpublished data to date indicate that song characteristics

appear consistent across the species breeding range of 35 counties in central Texas (M. L. Morrison unpublished data). Additionally, recent research suggests warbler occurrence is widely spread across the range (Collier *et al.* 2012) and that populations are panmictic, not spatially, genetically structured (Lindsay *et al.* 2008). Thus, there was no evidence that songs recorded at multiple sites across the range would be sufficiently variable to confound the intended purpose of the recordings, to represent conspecifics. We produced audio CDs using audio files publically available on the Internet, as well as our own recordings, and mixed using audio editing software (Audacity® Version 1.2.6, <http://audacity.sourceforge.net>, accessed 1 Feb 2008).

Vocalizations were broadcast from 06.00 to 11.00 daily during the experimental period: 2 weeks prior to expected bird arrival and for 4 weeks following arrival of the first male warblers for the pre-settlement Experiment 1. For the post-breeding Experiment 2, we conducted playback starting at observation of first warbler fledglings in the study area, 15 May to 8 August 2009, when most warblers left study sites (S. L. Farrell & A. J. Campomizzi, personal observation) for the post-breeding cue experiment; response data for Experiment 2 were collected in 2010. Warblers use two primary song types: the A song comprises most of the singing during settlement, territory establishment and pairing, with a shift to the B song once nesting is underway (Bolsinger 2000). Late in the season, as territorial boundaries begin to break down and the post-breeding period begins, singing shifts to a mixture of A and B songs. Our song playbacks were designed to replicate the song characteristics of the time during which they were played. Our pre-settlement treatment was comprised of c. 85% A songs, 10% B songs, 5% call notes. Our post-breeding playbacks contained a larger proportion of B songs, with c. 45% of each song type along with 10% calls to represent the more frequent calling that occurs as adults and fledglings communicate through call notes.

In 2008, we observed warblers regularly counter-singing with simulated song broadcasts, indicating that warblers perceived the simulated song as another male conspecific. Control sites did not have broadcast systems. Broadcast of non-conspecific song or other sounds was not used as a control, to avoid potential confounding effects of response to heterospecific songs or anthropogenic sounds (Monkkonen, Helle & Soppela 1990; Nocera, Forbes & Giraldeau 2006). Thus, absence of experimental sound was the best choice for the control, and we assumed presence of a small, transparent plastic box in a tree did not influence warbler behaviour.

SITE SELECTION

Research on golden-cheeked warbler occurrence suggests that canopy cover is the most common, effective predictor of occurrence (DeBoer & Diamond 2006; Collier *et al.* 2010, 2012). Current guidelines suggest 30–50% canopy cover is suboptimal habitat unlikely to be occupied and > 50–100% canopy cover is likely to be occupied. Additional work in the study region suggests probability of occupancy approaches 1 in > 70% canopy cover, but is lower for areas with c. 50–70% canopy (Texas Parks Wildlife Department 2003; De Boer & Diamond 2006; M. L. Morrison unpublished data). We identified woodland in the study region using 2008 National Agriculture Imagery Program (NAIP) imagery of the area from the United States Department of Agriculture (USDA). We ran an unsupervised classification using Spatial Analyst in ArcMap™ to identify woodland areas with 30–50%, > 50–70% and > 70% canopy cover. Woodland patches can vary in size and relative deciduous–juniper (*Juniperus ashei*) composition. To standardize, we thus limited sites to ≥ 8 ha, to include patches large enough to exceed minimum patch sizes for occurrence and potential pairing and fledging and large

enough to contain at least four warbler territories (Ladd & Gass 1999; Butcher *et al.* 2010), to enable any experimental effect to be detectable. We excluded monotypic stands and selected patches with at least 10% deciduous or juniper component to meet current criteria for suitability for warblers (Texas Parks Wildlife Department 2003). We excluded sites to which we were unable to gain permission to access the land parcel.

For the pre-settlement Experiment 1 in 2008, we selected from patches of oak–juniper woodland known to be occupied by warblers based on pre-treatment data collected in previous years (M. L. Morrison unpublished data; Butcher *et al.* 2010), with >70% canopy cover. For the pre-settlement Experiment 1 in 2009, we selected from areas known to be unoccupied by warblers in previous years or with unknown status, with 30–50% and >50–70% canopy cover, that were within *c.* 300–500 m of known occupied areas.

For the post-breeding Experiment 2 in 2009–2010 (i.e. treatment in 2009 and data collection in 2010), we selected from areas of 30–50% and >50–70% canopy cover known to be unoccupied by warblers in previous years (M. L. Morrison unpublished data; Butcher *et al.* 2010) adjacent (i.e. within 300–500 m) to known occupied woodland areas. We did not include the >70% canopy cover sites in Experiment 2 because we only included sites that were previously unoccupied; most mixed woodlands with >70% canopy cover in this region are occupied by warblers. We used the 300–500 m distance from previously occupied patches to ensure that experimental sites were plausibly within detection distance, through movement and auditory detection, for warblers in adjacent occupied areas (Naguib 1996; Forman 2000). There is no published research on warbler post-breeding behaviour, but information available to date suggests warblers do not cover large distances from their breeding site, most often moving around within their breeding patch with some movement to adjacent areas of open woodland or shrubland prior to migration (M. L. Morrison unpublished data).

Canopy cover categories based on remote imagery classification were used for sampling design, to ensure a distribution of sample units across the desired range of canopy cover. Following bird response data collection, we collected on-the-ground estimates of per cent canopy cover over 2 m in height using point sampling on a 20 m × 20 m point grid. Current research suggests on-the-ground, point-based estimates of canopy cover tend to be 5–10% lower than the remote imagery-derived estimates, potentially because available imagery does not allow for distinction in plant height and thus includes woody cover that is not at canopy height in the total cover estimate (M. L. Morrison unpublished data). All ground-based estimates were within the categories we assigned for use in the sampling design using the remote imagery classification ±5%, and thus, we used these continuous ground-based estimates for subsequent analyses.

Among sites that met the aforementioned criteria, we systematically paired sites by identifying the nearest adjacent site with canopy cover within 10%. For the pre-settlement Experiment 1, we randomly selected five pairs of sites with >70% canopy cover in 2008, and randomly selected five pairs of sites with >50–70% and six with 30–50% cover in 2009. For the post-breeding Experiment 2, we randomly selected six pairs with 30–50% cover and six with 50–70% in 2009–2010. We did not include sites in Experiment 2 with >70% canopy cover because this experiment targeted only previously unoccupied sites, and most sites with >70% canopy cover have a high probability of occupancy by warblers. No sample units were used in more than 1 year. Sample units were comprised of a 250-m-radius circle, which encompassed the approximate distance at which sound from the broadcast treatment units was to be audible and elicit

response (Naguib 1996; Forman 2000). We confirmed that while some minor variation existed due in part to some variation in vegetation cover characteristics, sound attenuated at or near 250 m, by listening for broadcast sound every 50 m at each of the treatment sample units. All sample units were at least 500 m apart, beyond the distance expected for sound to attenuate, so individuals in the area of one sample unit (i.e. treatment or control) were not exposed to the audio treatment from the nearest experimental treatment unit. We randomly assigned treatment to one of each pair of sample units.

RESPONSE VARIABLES

We measured the response variables territory density, pairing success and fledging success within each 250-m-radius sample unit in 2008 and 2009 for Experiment 1 and measured only territory density for Experiment 2 in 2010. We conducted territory spot-mapping (Shankar Raman 2003; Probst *et al.* 2005) in each sample unit ≥1 time per week from the time of the first male warbler arrival in the study region to 8 weeks after, *c.* 15 March–15 May. We 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 three visits to the territory using minimum convex polygons to delineate territory polygons using Hawth's Tools (Beyer 2004) in ArcMap™. We 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. We surveyed one time per week for 1 h in each territory using a modified Vickery method (Vickery, Hunter & Wells 1992) to determine pairing status and whether fledglings were present; this approach has been demonstrated to be a reliable indicator of reproductive success (Christoferson & Morrison 2001) and is the accepted and commonly used method for the golden-cheeked warbler because nests are particularly difficult and highly time-consuming to find and fledglings and family groups are vocal and highly detectable (Butcher *et al.* 2010; Lackey *et al.* 2011; Marshall 2011). We considered a territory productive if ≥1 dependent fledgling was detected in the territory with one or both of the adults. We combined 2008 and 2009 data for analysis because preliminary analysis showed the direction and magnitude of effect was similar between years (Fig. 1). Although the behavioural response to

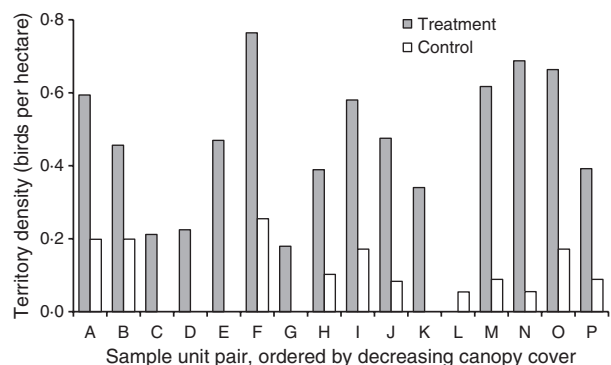


Fig. 1. Territory density of golden-cheeked warblers in 16 pairs of experimental conspecific vocalization treatment and control sample units, plotted by increasing canopy cover of oak–juniper woodland from 30 to 70% in patches in east-central Texas.

conspecific cues may vary among years and changing conditions, we were primarily interested in the behaviour in general across variations in time and space.

ANALYSIS

We were unable to find any literature or generate any reasoning based on theory indicating a difference in territory density that would result in biologically relevant implications. Thus, we considered a difference of one territory per 250-m-radius sample unit between treatment and control (i.e. a difference in density of 0.05 territories per ha) as an *a priori* effect size we were willing to accept, given some sites would have few territories. We used two-tailed, paired-sample Wilcoxon sign rank tests (Zar 1999:538–539) to test for difference in the territory density between paired control and treatment locations. We used a Spearman's rank correlation (Zar 1999:395–398) to test whether pairing and fledging success increased with increasing territory density and whether pairing and fledging success were correlated with canopy cover in Experiment 1. We used scatter plots to explore any relationship between the magnitude of difference in territory density between treatment and control units decreased with decreasing canopy cover. We conducted a Mann–Whitney *U*-test (Mann & Whitney 1947) to test for difference between response to pre-settlement and post-breeding treatments; for this test, we only included sample unit pairs from Experiment 1 in 2009, because they represented the same canopy cover categories as for Experiment 2.

All tests were 2-tailed. We set $\alpha = 0.05$ for all tests except for tests of hypothesis 1c and 1d for which we used a Bonferroni adjusted $\alpha = 0.025$ to adjust for multiple comparisons. We did not use multivariate modelling or model selection approaches because we were specifically interested in testing the effect of the experimental treatment and implemented the pairwise, randomized experimental design blocked to account for the role of canopy cover (Burnham & Anderson 2002). All analyses were conducted using SPSS (SPSS for Windows, Version 15.0.0; SPSS Inc. 2006, Chicago, IL, USA) and R statistical software (R Development Core Team, R Version 2.11.1. 2010; R Foundation for Statistical Computing, Vienna, Austria).

Results

EXPERIMENT 1: USE OF PRE-SETTLEMENT CONSPECIFIC CUES ACROSS RANGE OF HABITAT

Territory density was higher in the treatment unit in 15 of the 16 pairs of sample units. Territory density was on average greater than four times higher in treatment units than controls in each pair (Fig. 1; mean treatment density = 0.44, SE = 0.05 territories per ha; mean control density = 0.09, SE = 0.02 territories per ha; mean difference between treatment and control for each pair = 0.35, SE = 0.04; paired-samples Wilcoxon sign rank two-tailed test, d.f. = 16, $Z = -3.464$, $P = 0.001$). Territory density was not significantly correlated with canopy cover (two-tailed Spearman's $\rho = 0.130$, $P = 0.48$, $N = 32$). The magnitude of difference in territory density between treatment and control units did not show a significant relationship with canopy cover (Fig. 2; two-tailed Spearman's $\rho = -0.355$, $P = 0.18$, $N = 16$).

Pairing success of males showed evidence of positive, although not statistically significant, trend with increasing

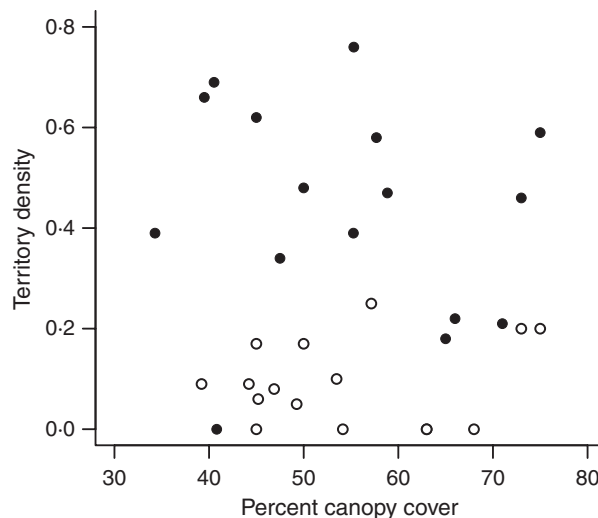


Fig. 2. Territory density of golden-cheeked warblers in 16 pairs of experimental conspecific vocalization treatment and control sample units. Closed circles represent density in treatment sample units; open circles represent control sample units.

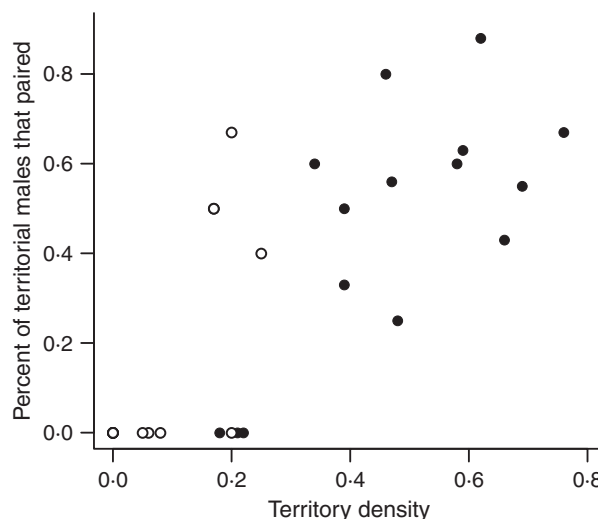


Fig. 3. Proportion of territorial male golden-cheeked warblers that successfully formed pairs plotted against territory density in 16 pairs of experimental conspecific vocalization treatment and control sample units. Closed circles represent density in treatment sample units; open circles represent control sample units.

territory density (Fig. 3; two-tailed Spearman's $\rho = 0.245$, $P = 0.23$, $N = 26$), with a potential threshold around 0.02 territories per hectare. The six sample units that had no territorial males, and thus no pairs, were excluded from the aforementioned test. Fledging success of paired males did not show evidence of a relationship with territory density (two-tailed Spearman's $\rho = 0.215$, $P = 0.38$, $N = 19$). The seven sample units where no males paired, and thus no fledging could be expected, were excluded from the aforementioned test. Neither pairing success of males nor fledging success of pairs was significantly correlated with

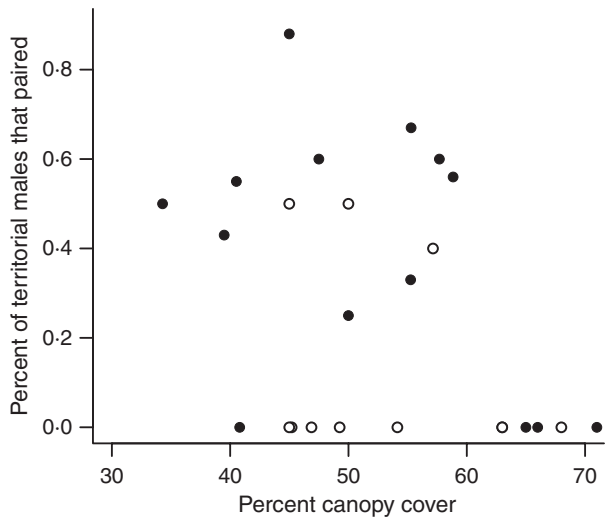


Fig. 4. Proportion of territorial male golden-cheeked warblers that successfully formed pairs plotted against canopy cover in 16 pairs of experimental conspecific vocalization treatment and control sample units. Closed circles represent density in treatment sample units; open circles represent control sample units.

canopy cover (Fig. 4; pairing success: two-tailed Spearman's $\rho = -0.111$, $P = 0.59$, $N = 26$; fledging success: two-tailed Spearman's $\rho = 0.047$, $P = 0.82$, $N = 19$).

EXPERIMENT 2: USE OF POST-BREEDING CONSPECIFIC CUES ACROSS RANGE OF HABITAT

Density of warbler territories was greater in treatment sample units for eight of 11 pairs of sample units in the post-breeding cue experiment, with two of the remaining three pairs of units having no territories in treatment and control units. Territory density was three times higher in treatment units than controls (Fig. 5; mean treatment density = 0.21, SE = 0.06 territories per ha; mean control density = 0.06, SE = 0.02 territories per ha; mean difference between treatment and

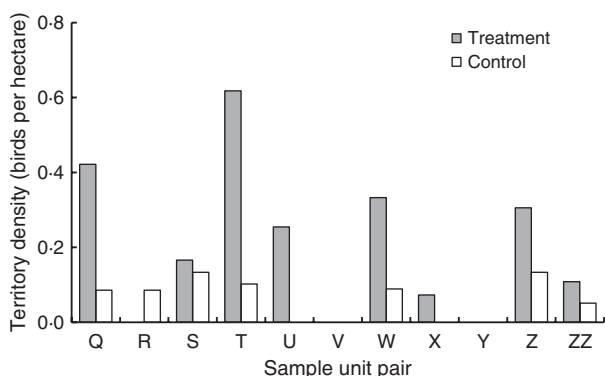


Fig. 5. Territory density of golden-cheeked warblers in 11 pairs of post-breeding experimental conspecific vocalization treatment and control sample units across a range of canopy cover of oak-juniper woodland patches in east-central Texas in 2010.

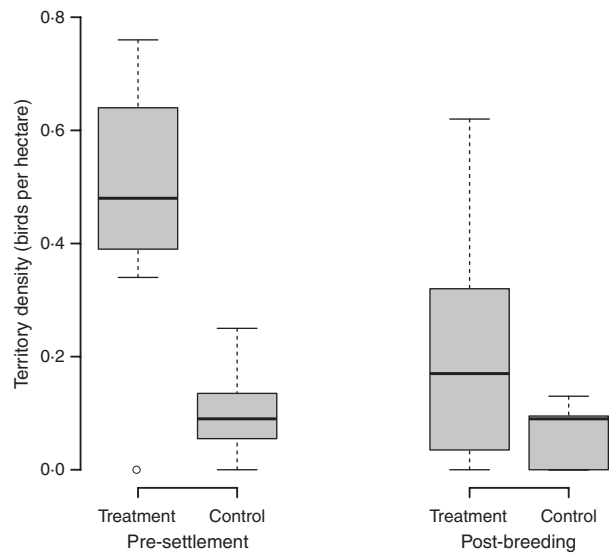


Fig. 6. Box plot of territory density of golden-cheeked warblers for previously unoccupied treatment and control unit pairs for pre-settlement and post-breeding conspecific vocalization experiments across a range of canopy cover in oak-juniper woodland patches in east-central Texas in 2008 to 2010.

control for each pair = 0.15, SE = 0.05; paired-samples Wilcoxon sign rank two-tailed test, d.f. = 11, $Z = -2.192$, $P = 0.03$). Direction and magnitude of response to treatment 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. 6; Mann-Whitney U two-tailed test, d.f. = 11, $Z = -2.660$, $P = 0.008$).

Discussion

Territory density on average was 4 times greater in response to treatment, across a range of canopy cover, the most conspicuous and oft cited habitat correlate for the species. Warblers respond to conspecific cues in areas considered unsuitable, even when high canopy cover areas were available nearby, suggesting these cues can be highly influential on settlement decisions (Jones 2001; Dall *et al.* 2005). We hypothesized this direction of effect, but the magnitude of effect was greater than we expected, given effects reported in similar studies (Ahlering, Johnson & Faaborg 2006; Hahn & Silverman 2006) and densities commonly reported for golden-cheeked warblers (M. L. Morrison unpublished data; Butcher *et al.* 2010; Collier *et al.* 2010). The treatment simulated multiple territorial individuals singing consistently in a small area, early in the breeding season, which may explain the large effect; additionally, as males selected territories in treatment units, a positive feedback loop may have developed as more singing males increased the strength of the social cue signal.

Magnitude of response did not decrease with decreasing canopy cover as we had expected. Nocera, Forbes & Giraldeau (2006) found most male bobolinks (*Dolichonyx oryzivorus*) settling in unsuitable habitat in response to post-breeding conspecific cues left the sites after several weeks, but researchers used an intermittent, rather than consistent, conspecific location cue treatment, which may explain this difference. Warblers that settled in low canopy cover sites might be expected to perform poorly, responding to an experimentally created ecological trap where the simulated inadvertent cue from conspecifics was unreliable and led to a choice of poor habitat (Hilden 1965; Clark & Mangel 1984; Danchin, Heg & Doligez 2001). However, birds induced to settle in low canopy areas performed as well as those in higher canopy in pairing and fledging success.

Theory focused on competitive interactions would predict warblers to select habitat sequentially, filling the best available habitat until competitive exclusion reduces access to resources such that an individual should select the next best area (Fretwell & Lucas 1970). But our results suggest that the territory selection process may not be substantially influenced by competition within the range of density and resources conditions we observed and that suitable areas may remain unoccupied or sparsely occupied, while adjacent areas are densely filled in response to conspecific location cues (Campomizzi *et al.* 2008). We found some evidence that pairing success increased with increasing conspecific territory density, supporting the hypothesis that conspecific song may be a signal not only for competitive exclusion (Falls 1992) but also for recruiting conspecifics to form aggregations that enhance fitness (Dodds 1997; Araújo & Guisan 2006; Hahn & Silverman 2006). Some have suggested this may represent a 'hidden lek' phenomenon (Wagner 1998), although there is no information regarding rates of extra-pair copulations for this species. However, high-density concentrations of males may simply provide a highly detectable signal for females seeking potential mates and information indicating high-quality habitat areas for use in female selection. Once males were paired, we did not observe a positive relationship between fledging success and territory density. Factors affecting fledging success such as nest predation may not be strongly affected by conspecific density in our study system.

Magnitude of response to the post-breeding conspecific cue treatment was lower than for the pre-settlement treatment. Nocera, Forbes & Giraldeau (2006) found settlement responses were greater for treatment during late breeding and post-breeding; our treatment was longer and more consistent and thus likely had different information content for the receiver of the cue. Post-breeding location cues are theorized to provide more reliable information about habitat quality than the presence of conspecifics at the start of a breeding season (Bollinger & Gavin 1989; Danchin, Boulinier & Massot 1998; Doligez *et al.* 2004; Nocera, Forbes & Giraldeau 2006). The post-breeding cue may be as influential as the pre-breeding cue, but loss of individuals that detected post-breeding cues because of over-winter mortality could decrease the potential set of responders in the

subsequent year. Alternately, if habitat quality varies substantially between years, presence of conspecifics at the end of one breeding year may not be a good indicator of the expected quality in the following year, thus pre-settlement cues may be more influential as a more reliable indicator of habitat quality in the year it is detected. Also, the timing of pre-settlement cues makes it more likely that they can be used as location cues facilitating formation of fitness-enhancing conspecific aggregations, rather than, or in addition to, use as public information potentially indicative of habitat quality. Future research comparing the relative influence of pre- and post-breeding conspecific location cues in systems with consistent and variable conditions among years can investigate this hypothesis. Lastly, if conspecific cues are primarily used for the purposes of establishing conspecific aggregations rather than for information about habitat quality, pre-settlement cues would be the most salient signals to use for forming aggregations.

Current research and management paradigms assume that because warbler occupancy is often associated with increasing canopy cover, warblers select for higher canopy cover, and these areas confer higher reproductive success or other fitness benefits (Texas Parks and Wildlife 2003; De Boer & Diamond 2006), but our results suggest this assumption may be inappropriate. Warblers may occur in high canopy cover areas because of factors such as tradition resulting from their evolutionary history (Hilden 1965; Nocera, Forbes & Giraldeau 2006), perceptual constraints or site tenacity. Reports from long-term banding and nest monitoring for warblers on Fort Hood, Texas, indicate that site fidelity reported for warblers is *c.* 35–50% (Peak & Thomas 2010). Thus, the remaining 50% of warblers make novel site selection decisions in any given year. Our results suggest the range of habitat they can select and reproduce successfully in may be greater than what is typically occupied in this region. Occupied areas may not represent the full range of useable habitat and, consequently, occupancy should not be taken to imply preference or indicate habitat quality. Our results suggest simulated conspecific cues have potential use as tools for establishing or re-establishing occupancy in restored habitats. Additionally, manipulating the locations and densities of individuals within suitable habitat may also be possible and provide approaches to minimize direct impacts to individuals where habitat manipulation, such as clearing of woodland for roadways or transmission lines, is required (Ahlering & Faaborg 2006; Hahn & Silverman 2007).

Incorporating knowledge of aggregative habitat selection behaviour and the consequent impact on species distributions is essential for creating more accurate spatially explicit predictive occupancy models and accurately determining when low or no occupancy is the result of habitat unsuitability or simply because of clustered distribution patterns (Lichstein *et al.* 2002; Campomizzi *et al.* 2008). Additionally, changes in habitat because of anthropogenic or other causes can lead to habitat conditions within which birds cannot perform well. If birds are unable to detect deleterious changes and make habitat selection decisions accordingly, attraction

to conspecific cues can lead to occupancy of non-adaptive habitat. Understanding how anthropogenic changes may affect habitat quality and how such changes can cause disjunction between cues used for selection and characteristics that affect fitness is critical for avoiding creation of ecological traps.

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