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Original Article

Experimentally provided conspecific cues boost bird territory density but not breeding performance

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Decision-making during different life-history stages requires information, which is obtained through own or others' experience and interaction with the environment. In birds, song is important for territory defense and mate attraction. Although song has evolved to purposely convey information, it can be inadvertently exploited by conspecifics. Experiments attempting to attract focal species by playing back their song are numerous, yet the consequences for reproductive performance remain little understood. In 2013 and 2014, settlement, reproduction, and extrapair paternity of *Phylloscopus sibilatrix* were assessed in a randomized experiment. We hypothesized that territory number, reproductive performance, and extrapair paternity would be higher on song plots (wood warbler song playbacks during prebreeding periods) than on control plots (no wood warbler song playback). On song plots, 3 times more territories were established, settlement occurred faster, and maximum plot occupancy was higher compared with control plots. Pairing rate, daily nest survival rate, mean clutch size, mean number of nestlings and fledglings, rates of extrapair young, nest abandonment, and nest predation did not differ between treatments, but fledging success was lower on song plots compared with control plots. This study shows the important role social cues can play for territory selection of birds, but also exemplifies the necessity for postattraction evaluation of reproduction to rule out negative effects of artificial attraction. Decreased fledging success on song plots and ambiguity about consequences of artificial attraction for distribution and settling dynamics of the species give reason to further evaluate whether acoustic attraction represents a suitable method for songbird conservation.

Key words: brood reduction, conspecific acoustic cues, extrapair parentage, field experiment, passerine, reproductive performance, song playback, territory density, wood warbler.

INTRODUCTION

In several animal taxa, decision-making is key in habitat selection, mate choice, foraging, and predation avoidance (Danchin et al. 2004). Decision-making relies on information, which can be obtained from direct interactions with one's physical environment (e.g., Arnott and Elwood 2007) or from own previous reproductive performance (e.g., Citta and Lindberg 2007), both of which is referred to as personal information. On the other hand, information can be obtained from con- or heterospecifics (Danchin et al. 2004), termed social information. Social information often stems from purposely conveyed information through olfactory, visual, or acoustic cues to achieve various tasks. However, every action or activity may inadvertently convey information, which can be based

on the performance (public information, Valone 2007), or on the presence or abundance (conspecific and/or heterospecific attraction via location cues, Ahlering et al. 2010).

The use of inadvertent social information appears to be widespread across plant and animal taxa. Examples include tobacco plants (*Nicotiana attenuata*) increasing chemical defense when growing near artificially clipped sagebrush (*Artemisia tridentata*) (Karban and Maron 2002), American toads (*Bufo americanus*) and cope's gray tree frog (*Hyla chrysoscellis*) using chorus sounds to join breeding aggregations (Swanson et al. 2007), nine-spined sticklebacks (*Pungitius pungitius*) using foraging activity and success of conspecifics to evaluate foraging patch quality (Coolen et al. 2003; van Bergen et al. 2004), and female mice (*Mus musculus*) choosing mates diffusing odor of other estrous females (Kavaliers et al. 2014). Inadvertent social information is also well documented in birds in regard to foraging site location (Bijleveld et al. 2015), mate choice (Gros-Louis et al.

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2003), or territory selection (Parejo et al. 2007) and often results in individuals settling near conspecifics (Muller et al. 1997). The latter, referred to as conspecific attraction hypothesis (Stamps 1988), predicts that individuals are attracted to and settle near conspecifics based on information gathered from conspecifics either in previous years or right before settlement (Ahlering et al. 2010). Conspecific attraction, tested with experimental manipulation, has been found in many bird species, including species belonging to the orders Passeriformes, Ciconiiformes, Procellariiformes, Pelecaniformes, and Charadriiformes (reviewed in Ahlering et al. 2010). Attraction experiments have utilized visual and acoustic cues to achieve colony relocation, site recolonization, or boosting reproduction. Conspecific attraction can be so strong that birds even settle in seemingly unsuitable habitat (Nocera et al. 2006; Betts et al. 2008; Fletcher 2009). In passerines, conspecific attraction has mostly been tested using acoustic cues, as territory defense and mate attraction are achieved via song or calls. Some species rely on acoustic cues to monitor the presence of conspecifics principally during the prebreeding, territory settlement period, either to assess territory quality (the best territories available being colonized first; e.g., Tschumi et al. 2014) or to identify sites with increased opportunities for promiscuity (see the social mate choice hypothesis by Allee 1958). Acoustic cues can also be used for the assessment of territory quality after the breeding season: postbreeding song may provide information not only about habitat quality but also about reproductive success (Betts et al. 2008). However, the use of postbreeding song as a proxy of future habitat quality holds only if site quality is correlated across years.

From one of the earliest playback experiments attracting common terns (*Sterna hirundo*) and Arctic terns (*Sterna paradisaea*) to previously abandoned habitat (Kress, 1983) to attracting multiple species at once in more recent time (DeJong et al. 2015), numerous studies in the last decades have successfully used song playback to attract focal species. Despite the relatively large number of studies using playback experiments to investigate conspecific attraction, little is known about the fitness consequences of such artificial attraction for individuals or populations (reviewed by Ahlering et al. 2010). Monitoring fitness consequences can be time consuming and logistically difficult, it is however important to detect possible negative consequences of playback experiments, such as the creation of ecological traps (Battin 2004). Ignorance about fitness consequences of playback experiments also hinders assessment of whether artificial conspecific attraction with acoustic methods provides a suitable tool for species conservation.

We conducted a 2-year field experiment that aimed at testing the conspecific attraction hypothesis and assessing potential fitness consequences of artificial attraction in the wood warbler (*Phylloscopus sibilatrix*). We evaluated whether wood warblers settled in response to the simulated presence of conspecifics. More specifically, we compared the settling behavior of the study species on plots with experimental playback of wood warbler song (song plots) with control plots without song. We expected more males setting up territories on song plots compared with control plots. To assess fitness consequences of the experiment, we evaluated reproductive performance in terms of clutch size, number of fledglings, fledging success, and daily nest survival rate on song plots compared with control plots. We expected larger clutches, more fledglings, and higher daily nest survival rate on song plots compared with control plots.

We also evaluated 2 a posteriori hypotheses concerning territory clustering of the wood warbler (Herremans 1993): the social mate choice hypothesis and the hidden lek hypothesis. The social mate choice hypothesis predicts that clustered settlement may, at least in some breeding systems, offer an increased chance of successfully

finding mates (social mate choice hypothesis (Allee 1958) reviewed in Tarof et al. 2004). We therefore expected that pairing rates on song plots were higher than on control plots. The hidden lek hypothesis predicts that females and males seek out aggregations to increase the chance for extra pair copulations (Wagner 1998). Hidden leks share in fact the most important resource typically encountered in the normal leks of promiscuous species: mating partners. Extrajoint copulations regularly occur even in socially monogamous species, because males and females can gain various direct and indirect benefits (reviewed in Griffith et al. 2002). Thus, if territory clustering is driven by opportunities for extrajoint copulations, we expected 1) a higher number of nests with extrajoint young (EPY) and 2) a higher share of EPY on song plots than on control plots.

METHODS

Study sites and species

The study took place in the Jura Mountains of North Switzerland. The experiment was conducted in 2 study sites, as no single study site contained forest tracts with suitable wood warbler habitat large enough to accommodate the entire experiment. The 2 sites chosen (Blauen, canton of Basel-Landschaft [BL], N 47° 27.6' E 7° 31.7', 672 m asl and Erschwil, canton of Solothurn [SO], N 47° 22.7' E 7° 33.3', 704 m asl) had hosted over the 3 years preceding the experiment a sufficiently large number of wood warbler territories, but differed in size and in availability of suitable habitat, resulting in an uneven distribution of experimental plots between sites (22 and 7 plots in Blauen and Erschwil, respectively). The 2 sites chosen were part of an ongoing study initiated in 2010 addressing settlement behavior, habitat selection, and reproductive performance of the wood warbler in 16 study sites (Grendelmeier et al. 2015; Pasinelli et al. 2016). Using territories previously occupied by wood warblers allowed us to conduct the experiment in habitat suitable in terms of structure and to some degree rodent abundance, which both influence territory choice. Rodent abundance has repeatedly been shown to negatively correlate with wood warbler numbers (Wesołowski et al. 2009) or settlement probability (Pasinelli et al. 2016), though the underlying mechanisms remain unclear. The 2 study sites, in which the experiment took place, were located on slopes exposed to the south (Blauen) and south-west (Erschwil), respectively, and consisted of mixed-deciduous forest stands dominated by European beech (*Fagus sylvatica*), with other deciduous and coniferous tree species interspersed. Stands predominantly consisted of old polewood and young timber with a relatively closed canopy and a sparse shrub layer, if at all present (Huber et al. 2016). As part of our ongoing studies on wood warblers, we also worked in 4 additional study sites that did not receive any experimental treatment. These unmanipulated study sites were used for comparative purposes to evaluate annual variation in general breeding conditions (see General field methods): Lauwil (BL; N 47° 22.5' E 7° 39.7'), Montsevelier (Jura; N 47° 22.1' E 7° 29.5'), Kleinlützel (SO; N 47° 26.3' E 7° 25.9'), and Scheltenpass (SO; N 47° 20.8' E 7° 37.1'). The wood warbler has suffered long-term declines in many EU countries (Vickery et al. 2014). It is classified as vulnerable on Switzerland's red list (Keller et al. 2010b) and is considered a priority species for the Swiss recovery program for breeding birds (Keller et al. 2010a). This insectivorous and nomadic forest-interior passerine exhibits very little breeding site fidelity (ring return percentages reviewed in Wesołowski et al. 2009), resulting in high interannual turnover of individuals and in strong annual fluctuations of local population size. The wood warbler is a trans-Saharan migrant

(Hobson et al. 2014) that occupies breeding sites in Europe between the end of April and September (Glutz von Blotzheim et al. 1991).

General field methods

To map singing males, pairs, and nests, each study site was visited twice a week from 1 April 2013 to 31 March 2014, respectively, until the last young had fledged in July. On finding a nest, one trail camera (Reconyx PC900 HyperFire Professional High Output Covert; Reconyx, Inc., Holmen, WI) was installed, pointing directly at the nest entrance at a distance of 1–2 m. Trail cameras allowed to simultaneously monitor many nests, while keeping researcher disturbance at a minimum (Ibanez-Alamo et al. 2012), to survey activity of adults and (old) nestlings, to identify nest predators, and to determine the exact date of nest predation or fledging of nestlings. Nest status (i.e., still nesting or empty) was determined at each visit and nestlings were aged with pictures of reference nestlings from nests where exact hatching dates were known. With weekly nest checks, it was possible to visit each nest at least twice during each phase. During egg-laying, we could determine the exact date the first egg was laid, because the laying interval is 1 day. Visiting the nest immediately after hatching allowed us to determine the exact hatching date by aging nestlings through pictures as described above or sometimes witnessing hatching. Visiting nests when nestlings were 6 to 7 days old and again at around the age of 10 days allowed us to determine the number of lost nestlings and how many young would fledge. We worked with the assumption that all nestlings seen during the second nestling stage visit would survive till fledging, unless predated, which would be captured by cameras. Date of fledging could be inferred via picture analysis. Once a nest was inactive (successful or unsuccessful), we measured vegetation parameters and rodent occurrence (details given in [Supplementary Table S1](#)). We used the same field methods to map and monitor bird nests in the 4 additional, but unmanipulated study sites mentioned above.

To evaluate whether breeding conditions were generally good or bad during the period of the experiment in 2013 and 2014, respectively, we compared mean reproductive performance (number of eggs, nestlings, and fledglings) of nests in unmanipulated study sites (i.e., receiving no experimental treatment) in 2013 and 2014, respectively, with nests in the same 4 study sites in 2010–2012. We also compared reproductive performance of nests on control plots in experimental study sites of 2013 and 2014, respectively, with reproductive performance of nests in the same 2 areas before the experiment in 2010–2012.

Treatments, vocalizations, and playback schedules

Each of the 29 experimental plots was 5 ha in size, roughly equaling a circle with radius of 125 m, which would allow wood warblers to settle within the experimental plot (territory size spans 0.12–3 ha or circles of 20–100 m radius, Glutz von Blotzheim et al. 1991). To each experimental plot, 1 of 3 treatments (wood warbler song, noise control, and silent control, see below) was randomly assigned and switched between the 2 years of the experiment. Switching the assignment of song and control plots between 2013 and 2014 further ensured that experimental results arose from the treatment and not from confounding factors such as habitat. Interannual carryover effects from the experimental treatment very likely played a minimal role, if at all, as our study species exhibits very low breeding site fidelity. In 2013, 15 and 14 experimental plots served as song and control plots, respectively, with the opposite distribution in 2014.

On each song plot, 2 playback stations broadcasting vertically up were set up 50 m from the plot center, that is, 100 m apart from each other on an east-west alignment. To simulate movement of a singing male, song playback alternated between the 2 stations. While station 1 played back a 6-min file where the first 3 min contained song and the remaining 3 min complete silence, station 2 played back a 6-min file with 3 min of silence first and then 3 min of song. To avoid pseudoreplication, we broadcast a unique wood warbler song per song plot. In the 3 years preceding the experiment, singing males had been recorded in different locations in northern Switzerland during settlement with Sennheiser ME-66 microphones and Olympus LS-10 and Marantz PMD670 digital recorders (.wav format, sampling frequency: 44.1 kHz, resolution: 16 bit). For the experiment, recordings from 15 different males were selected and edited by muting passages without wood warbler song. The recordings were then run through a high pass filter with threshold of 1 kHz to remove low-frequency background noise from passages with wood warbler song. All editing of recordings was done with sound-editing software Audacity® 2.0.6. Wood warbler song mimicking the natural song rate of around 5 strophes per minute (Glutz von Blotzheim et al. 1991; Bijlsma 2016) was broadcast from 15 April to 7 June in 2013 and from 14 April to 6 June in 2014. This 8-week interval roughly corresponds to the main settlement period of the wood warbler in our study sites (Glutz von Blotzheim et al. 1991) and hence to the prebreeding period. We focused on prebreeding singing activity for 2 reasons. First, song activity of the wood warbler sharply drops after pairing, never returning to prebreeding levels later on (Trees 1996, personal communication). Second, habitat quality of breeding grounds varies between years due to intermittent resource pulses triggered by seed masts in the mixed-deciduous forests inhabited by the wood warbler. Autumn seed masts initiate a cascade of responses, including outbreaks of ground-dwelling rodents (*Apodemus* and *Myodes* spp.), thereby decreasing habitat quality for wood warblers (Wesolowski et al. 2009). As a result, postbreeding acoustic cues to assess future territory quality cannot apply in this case.

Intentionally broadcast sound itself and/or unintentional background or loudspeaker noise may attract or deter birds from the experimental plots. To test for this possible loudspeaker effect, we divided the 14 control plots into 7 silent controls with loudspeaker dummies and 7 noise controls in 2013. Due to the aforementioned unbalanced sample of experimental plots, we had 7 silent controls and 8 noise controls in 2014. We played back calls of the common wood pigeon (*Columba palumbus*), a species commonly occurring in our study forests. We used pigeon recordings from <http://www.xeno-canto.org> (last accessed 1 March 2013) and used an identical editing procedure as for wood warbler recordings. Pigeon calls were broadcast at similar rates to wood warblers song (around 5 strophes/min), which is higher than natural pigeon call rates with around 3 call strophes per minute (calculated based on song recordings from <http://www.xeno-canto.org>).

Playback stations consisted of one audio player (MusicWalker 4GB from Intenso capable of playing uncompressed .wav files), 2 Maxxtro 2.0 stereo speakers with built-in amplifier (frequency range 20–20000 Hz), one 12V timer switch from GEV (Gutkes Elektro Vertriebs GmbH, Hannover, Germany), and 1 lead-acid battery (12V 18Ah, FG21803 from FIAMM). Player, timer, and battery were placed in a small plastic box (casing) to protect from the elements, whereas speakers were covered with kitchen saran wrap. We used the same equipment and broadcast schedule on noise control

plots as on song plots, but only the casing and loudspeaker dummies on silent control plots. Equipment on song and control plots was checked twice a week.

Responses measured

The measured response was the number of wood warbler territories in song and control plots (i.e., the 5-ha circles), respectively, in the same breeding season the experiment took place. Following standardized methods for the Swiss common breeding bird survey “Monitoring Häufige Brutvögel MHB” (Schmid et al. 2001), a territory was defined to occur if either 1) a nest was found, 2) a pair was seen at least once, or 3) a singing male was heard on at least 3 visits (about 2 weeks) in the same vicinity. Color-ringing as many individuals as possible also allowed us to detect movements within study areas (no between-study area movements detected). Reproductive performance was evaluated with 4 components of reproduction: clutch size (number of eggs of a completed clutch), number of nestlings (number of young that successfully hatched), number of fledglings (young that left the nest), and daily nest survival rate (*dnsr* hereafter). To assess reproductive performance in greater detail, we also calculated hatching rate (proportion of eggs that successfully hatched), nestling success (proportion of hatchlings that fledged), fledging success (proportion of eggs that produced a fledgling), nest predation (proportion of predated nests), and nest abandonment (proportion of abandoned nests).

DNA sampling

To evaluate the hidden lek hypothesis, we investigated patterns of extrapair parentage (EPP) of wood warblers that settled and bred on song and control plots in 2014. All birds that could be caught for ringing in 2014 were also sampled for DNA (on song plots: 12 males, 9 females, 37 young; on control plots: 4 males, 3 females, 17 young). To test the utility of conserved avian microsatellite markers for use with the wood warbler (see below for more details), the first 10 individuals (all males) captured were sampled for blood by puncturing the brachial vein and collecting a drop of blood with Whatman® grade 4 filter paper. For all subsequently captured individuals ($n_{\text{males}} = 6$, $n_{\text{females}} = 12$, $n_{\text{nestlings}} = 54$ from 10 nests), we used the buccal swab method (Handel et al. 2006; Yannic et al. 2011), as it is less invasive than blood sampling. Buccal swab samples yield less DNA than blood samples, but quantities are sufficient for molecular sexing and genotyping (Handel et al. 2006; Yannic et al. 2011). For an extended analyses of EPP in wood warblers (presented elsewhere), additional individuals ($n_{\text{males}} = 24$, $n_{\text{females}} = 32$, $n_{\text{nestlings}} = 151$ from 29 nests) from the 4 unmanipulated study sites were sampled and used here for the allele frequency analysis (Table 1). Samples were stored in 96% ethanol and kept at 5 °C. Capturing and ringing were done with permits from the Federal Office of Environment (FOEN), Switzerland, taking blood samples and buccal swabs with permission for animal experimentation from the Cantonal Veterinary Office, Basel-Landschaft (permission number BL468).

DNA extraction from buccal swabs and blood samples was performed with the DNeasy Blood and Tissue kit, Qiagen. Tests of markers' polymorphism, multiplex development, genotyping, and molecular sexing were done by Ecogenics GmbH, Schlieren, Switzerland. We tested for utility of 24 microsatellite markers in the set of Conserved Avian Microsatellites described by Dawson et al. (2013) and of markers TG02-088 und TG04-012 (Dawson et al. 2010) in 15 samples of wood warbler. For this, the procedure originally described by Schuelke (2000) using the fluorophore-labeled

universal M13 primer was followed. Products were analyzed on an ABI3730 sequencer using an internal size standard. Based on the level of polymorphism and the band patterns in the wood warbler, we chose 13 markers for the subsequent genotyping of the samples in 3 multiplex-polymerase chain reactions (PCRs) (Table 1) using HotStarTaq Master Mix, Qiagen, and the following cycling protocol: 35 cycles at 94 °C for 30s, 56 °C for 90s, and 72 °C for 60s; before the first cycle, a prolonged denaturation step (95 °C for 15 min) was included and the last cycle was followed by a 30-min extension at 72 °C. Sex was determined by PCR with the primers P2/P8 and visualization of the products in agarose gel (Griffiths et al. 1998).

Statistical analyses

As occupancy rate did not differ between silent and noise control plots (Fisher's Exact test, $P = 0.999$), the responses measured on the 2 control plot types were pooled in all subsequent analyses. Even though experimental plots were set up in areas with wood warbler territories in previous years, we tested whether habitat varied between treatment types. We used multivariate analysis of variance with the 3 dependent variables rodent occurrence, number of trees, and number of grass tussocks (see Supplementary Table S1 for more details) and 1 independent variable treatment type (2 levels: wood warbler song plots vs. control plots). We ran separate analyses for both years (2013 and 2014), due to possible variation in rodent occurrence between the years. As none of the 3 dependent variables differed significantly between song and control plots (Supplementary Table S2), none were included in subsequent analyses.

We analyzed settlement, clutch size, number of nestlings, number of fledglings of successful nests, and *dnsr* in relation to treatment type with generalized linear mixed effects models (GLMMs, package lme4, Bates and Maechler 2010) and likelihood ratio tests in R (R Development Core Team 2008). For the analysis of settlement, we modeled the number of territories per plot as dependent variable in relation to treatment (wood warbler song playback or control) and year (2013 or 2014) as independent variables (fixed effects), assuming a Poisson distribution of errors and a log link. We included “study site” as random effect to account for the data dependency arising from using multiple experimental plots close to each other in each of the 2 study sites. A second random effect of “plot.id” nested within “study site” was used to account for using the same plot in 2 separate years. Assuming a Poisson distribution with log link, we repeated the same analysis for the dependent variables clutch size, number of nestlings, and number of fledglings, respectively. Additionally, we included laying date (number of days since the first egg of the first clutch per season of both study areas was laid) as fixed effect to account for the known seasonal decrease in clutch size and number of fledglings (Grendelmeier et al. 2015). For the analysis of *dnsr*, each exposure day constituted 1 line of data, which was coded and modeled as a binomial dependent variable indicating success (= 1) or failure (= 0) per nest and day. We modeled *dnsr* in relation to treatment, year, and nest age (Grendelmeier et al. 2015) as fixed effects, and “study site” and “nest ID” as random effects assuming a binomial error distribution and a logit link. The random effect “nest ID” was included to account for multiple lines of data for each nest.

For each analysis described above, we first evaluated whether there was a significant interaction between treatment type and year, comparing a model with both main effects plus their interaction to a model without interaction. We continued to evaluate the significance of treatment type by comparing the full model and a reduced

Table 1
Summary statistics for 13 microsatellites analyzed for wood warblers in 2014

Marker	Multiplex assay	Primer sequence 5'-3'	BP size	No. of alleles	No. of typed adults	Hobs	Hexp	PIC	NE-1P	NE-2P	NE-PP	HW	F(null)
cam-06	M1	GTGATGGTCCAGGTCCTTGC CAAGAGGAACAGATGAGGGTGC	273-303	11	75	0.520	0.673	0.634	0.728	0.547	0.347	*	0.1416
cam-10	M1	TATCCMGAGAAATGGGCATC KGCCTCATTGTCAATGCTG	194-196	2	84	0.464	0.502	0.375	0.875	0.813	0.719	NS	0.0364
cam-18	M1	TAAAGAAGTTTACACCCAGCG GCTAAATAACAGAGCCAGGAAG	337-343	4	82	0.329	0.375	0.329	0.93	0.82	0.705	ND	0.0606
cam-24	M1	CCCAGTTCAGTCTTCAGAGC TGGAGTATTTGGGATTTGAG	129-147	9	84	0.679	0.681	0.62	0.737	0.574	0.394	NS	-0.0116
cam-23	M2	CTCCACTTAGCTTTGAAATGCCAC CCAAAGRAGTGCCCTAGATGTC	138-156	9	84	0.679	0.834	0.811	0.5	0.329	0.149	NS	0.0983
cam-07	M2	AAATGATGAGRGTGGGTGAG CCATTTCCAAAGWGATTTGC	230-234	5	84	0.417	0.456	0.409	0.893	0.758	0.613	NS	0.0337
cam-12	M2	TGGCARTAAWTCAGAGATTACC CTGRCATTTGTCTTAAAGGGTGC	344-358	12	61	0.230	0.668	0.636	0.722	0.536	0.324	***	0.5036
cam-15	M2	SGACGACTCCITTAITTTCCC TTCGTGACTTCGYCAGGTAACAC	267-293	14	81	0.753	0.831	0.805	0.509	0.338	0.16	NS	0.0449
TG04-012	M2	TGAATTTAGATCCTCTGTCTAGTGTGC TTACATGTTTACGGTATTTCTCTGG	131-137	7	82	0.220	0.576	0.535	0.817	0.648	0.462	***	0.4480
cam-19	M3	TCTTGGAGGCAGATARGAAGTG GAGCAAGCAAAGATCACAAAGC	241-252	10	84	0.702	0.755	0.711	0.647	0.471	0.285	NS	0.0345
cam-02	M3	GAATTAAGAYAGCAGATGCAGG AGCTGATGAAATCAGAAATGCAG	378-401	16	81	0.765	0.84	0.817	0.483	0.316	0.138	NS	0.0442
cam-03	M3	ATTAGCATAGCTCAGCAATGGCC CGAGCATTCAMCCTGTCAATC	148-174	14	78	0.859	0.885	0.868	0.39	0.241	0.088	ND	0.0115
cam-01	M3	AAAGGCCAAAGRCCAGTAATG CTCTCATCCACCCTGTATAGC	300-313	6	83	0.59	0.649	0.574	0.785	0.637	0.481	NS	0.0472

Marker names correspond to Dawson et al. (2010) and (2013).

Loci with significant deviation from HW and a high frequency of null alleles (cam-06, cam-12, TG04-012) were excluded from subsequent analysis. Hobs, observed heterozygosity; Hexp, expected heterozygosity; PIC, polymorphic information content; NE-1P, average nonexclusion probability for one candidate parent; NE-2P, average nonexclusion probability for 1 candidate parent given the genotype of a known parent of the opposite sex; NE-PP, average nonexclusion probability for a candidate parent pair; HW, significance of deviation from Hardy-Weinberg equilibrium (NS, not significant, *significant at the 5% level, **significant at the 1% level, ***significant at the 0.1% level, ND, the test could not be performed due to too few individuals); F(null), estimated null allele frequency for each locus.

model missing treatment type with likelihood ratio tests. For the analyses of clutch size, number of nestlings, number of fledglings, and *dnst*, we also evaluated the significance of laying date by comparing the full model with a reduced model missing laying date. *Dnst* per treatment type and the corresponding standard errors were calculated according to Mayfield (1961) and Johnson (1979). To obtain *dnst*, we divided “number of lost nests” by “total exposure days” (of all nests) and subtracted the result from 1. Standard errors were then calculated with the following formula:

$$\sqrt{\frac{(\text{Total exposure days} - \text{Number of lost nests}) \times \text{Number of lost nests}}{(\text{Total exposure days})^3}}$$

(Johnson, 1979).

To assess the social mate choice hypothesis, we compared pairing rates between song and control plots with a Fisher’s Exact test in R (R Development Core Team 2008). We also used Fisher’s Exact tests to assess hatching rate, nestling success, fledging success, nest predation, and nest abandonment.

Lastly, to evaluate EPP, we used parental genotypes from 6 study sites. First, we tested the assumption of a homogenous population using Arlequin (Excoffier and Lischer, 2010), which was met. We proceeded by determining expected and observed heterozygosity, and deviations from Hardy–Weinberg equilibrium using Cervus 3.0.7 (Kalinowski et al. 2007) and subsequently had to omit 3 of 13 microsatellite loci due to high null allele frequencies (Table 1). Parent–offspring relationships were analyzed using Wang’s (2004) maximum likelihood method implemented in Colony 2.0.5.6., allowing for a 0.01 error rate. All offspring are simultaneously partitioned into paternal and maternal family clusters, to which candidate parents are assigned at 95% confidence intervals (CIs). For missing parent data, Colony will reconstruct parental genotypes and give an index to each missing parent ID. We conducted 4 iterations (chosen arbitrarily) of the analysis and qualitatively compared the 4 resulting outputs to assess whether the program converged for our data and whether we had sufficient marker information to reliably infer the genetic structure (Colony User’s Guide under FAQ 7.2). The 4 iterations had varying “random number seeds,” but the following and consistent input settings: “update allele frequency,” “inbreeding absent,” “polygamy,” “no clones,” “10 runs,” “very long run,” “full-likelihood,” and “very high precision.”

Ethics statement

All procedures were performed according to the laws of Switzerland and rules of the Swiss Ornithological Institute and approved by the Federal Office for the Environment FOEN (reference F044-0799) and the Cantonal Office for forest (reference 410 [rodent captures]; BL468/25097 [DNA sampling of birds]).

RESULTS

Settlement response to playback

In 2013, song plot occupancy (percentage of occupied song plots out of all song plots) amounted to 7% after the first week, compared with 0% control plot occupancy (percentage of occupied control plots out of all control plots). In 2014, song plot occupancy amounted to 57% one week after the experiment had started compared with 7% control plot occupancy in the same week. Peak occupancy for song plots occurred 5 weeks after the onset of the experiment in both years and amounted to 73% and 71% in 2013 and 2014, respectively. Occupancy rate of control plots never exceeded 36% in either year (Figure 1).

For the analysis of settlement, there was no significant difference for models with and without the interaction between treatment and year (likelihood ratio test, $\chi^2 = 0.042$, $df = 1$, $P = 0.838$). At the end of the experiment (both years pooled), we recorded 1.2 ± 0.3 territories (mean \pm SE, $n_{\text{territories}} = 40$) on song plots compared with 0.4 ± 0.14 territories ($n_{\text{territories}} = 12$) on control plots (likelihood ratio test, $\chi^2 = 13.682$, $df = 1$, $P < 0.001$; Figure 2). Number of territories on song and control plots ranged from 0 to 4 and from 0 to 1, respectively. In total, 23 (2013) and 29 (2014) males set up territories on experimental plots. On song plots, 17 males found a mate and 23 males remained unpaired. On control plots, 4 males found a mate and 8 males remained unpaired. There was no significant difference in the number of paired and unpaired males on song and control plots (Fisher’s Exact test, $P = 0.741$).

Reproductive performance

From a total of 22 nests, 21 could be used for the analyses of clutch size, number of nestlings, and *dnst*, respectively, and 14 for the analysis of number of fledglings. One nest had to be omitted from all analyses due to incomplete data.

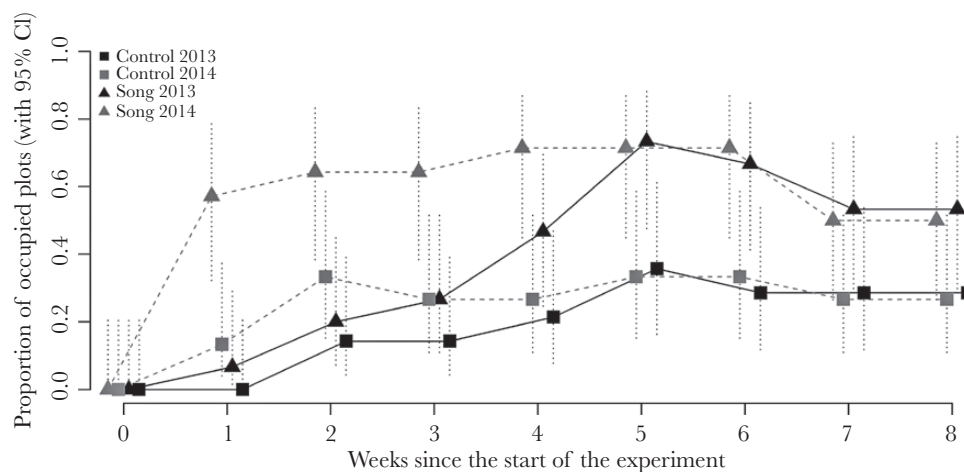


Figure 1

Proportion of study plots occupied by wood warblers after the start of the experiment with respect to treatment type (triangles: song plots; squares: control plots; black: 2013; gray: 2014). A plot was considered as occupied if at least 1 territory had been established. $N = 29$ plots.

We found 14 nests on song plots and 7 nests on control plots, meaning that 3 females moved to adjacent control plots (>50 m of movement between 2 successive mappings) to build their nests, after pairing on song plots (based on observation in 2 cases and coloring identification in 1 case). *Dnsr* over an average nesting period of 31 days was negatively related to nest age (Figure 3), but did not differ for nests on song plots (mean ± SE: 0.984 ± 0.007, *n* = 14) and control plots (0.988 ± 0.009, *n* = 7) (likelihood ratio test, $\chi^2 = 0.596$, *df* = 1, *P* = 0.44). Furthermore, there was no interaction between year and treatment type (likelihood ratio test, $\chi^2 = 0.643$, *df* = 1, *P* = 0.423).

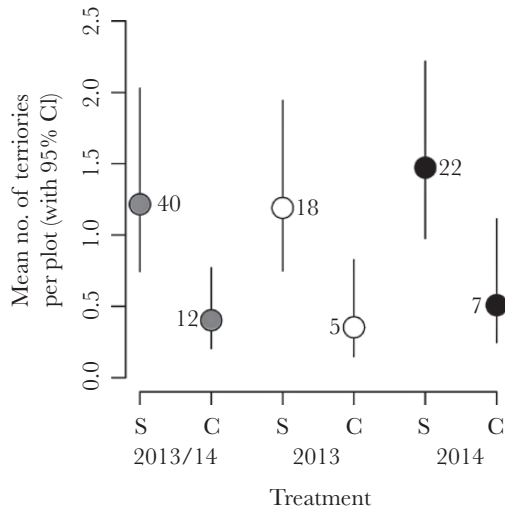


Figure 2 Mean (with 95% CI) number of territories observed on song plots (S) and control (C) plots for both years together (gray) and separate for 2013 (white) and 2014 (black). Values next to circles indicate the territory sample size the model and graph are based on.

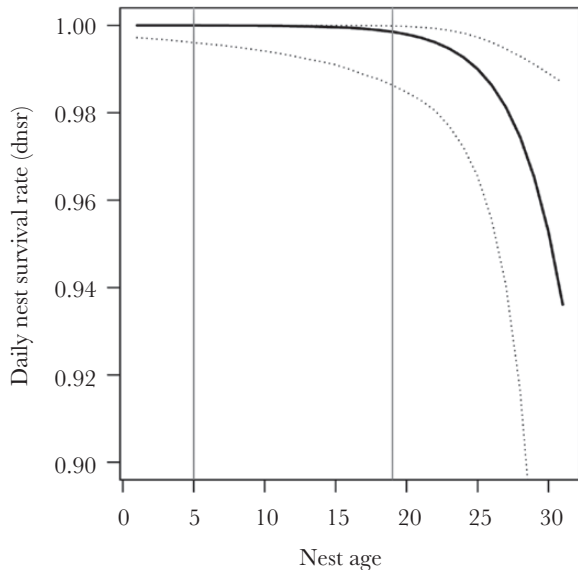


Figure 3 Daily nest survival rate in relation to nest age (in days). Plot shows fitted values (solid lines) and 95% CIs (dashed lines) based on a model combining 21 nests on song and control plots of 2013 and 2014. Vertical gray lines at nest age 5 and 19 depict end of egg-laying and incubation, respectively, based on average egg laying, incubation, and rearing durations in our study.

Treatment type also had no significant influence on average clutch size (likelihood ratio test, $\chi^2 = 0.046$, *df* = 1, *P* = 0.831; Figure 4), average number of nestlings (likelihood ratio test, $\chi^2 = 0.005$, *df* = 1, *P* = 0.947; Figure 4), or average number of fledglings of successful broods (likelihood ratio test, $\chi^2 = 0.02$, *df* = 1, *P* = 0.885; Figure 4). The date a clutch was initiated (i.e., first egg being laid) had no significant effect on average clutch size (likelihood ratio test, $\chi^2 = 0.17$, *df* = 1, *P* = 0.677, *n* = 21), average number of nestlings (likelihood ratio test, $\chi^2 = 1.153$, *df* = 1, *P* = 0.253, *n* = 21), average number of fledglings (likelihood ratio test, $\chi^2 = 0.38$, *df* = 1, *P* = 0.538, *n* = 14), or *dnsr* (likelihood ratio test, $\chi^2 = 0.082$, *df* = 1, *P* = 0.775, *n* = 21). There was no significant difference for models with and without the interaction between treatment and year for the analysis of clutch size (likelihood ratio test, $\chi^2 = 0.123$, *df* = 1, *P* = 0.726), average number of nestlings (likelihood ratio test, $\chi^2 = 0.654$, *df* = 1, *P* = 0.419), or average number of fledglings (likelihood ratio test, $\chi^2 = 0.054$, *df* = 1, *P* = 0.816).

The total number of eggs produced on song and control plots were 90 and 43, respectively (likelihood ratio test, $\chi^2 = 7.86$, *df* = 1, *P* = 0.005; Figure 5). The total number of fledglings produced on song and control plots were 43 and 29, respectively (likelihood ratio test, $\chi^2 = 1.01$, *df* = 1, *P* = 0.315; Figure 5). Considering all nests, with 90 eggs from 14 nests on song plots and 43 eggs from 7 nests on control plots, a significant difference between song and control plots was found for fledging success (song: 48% vs. control: 67%, Fisher’s Exact test, *P* = 0.041), but not for hatching rate (song: 82% vs. control: 93%, Fisher’s Exact test, *P* = 0.117) or nestling success (song: 58% vs. control: 73%, Fisher’s Exact test, *P* = 0.157). Omitting predated nests from the analysis, but retaining abandoned nests, with 71 eggs in 11 nests on song plots and 31 eggs in 5 nests on control plots, hatching rate (song: 80% vs. control: 97%; Fisher’s Exact test, *P* = 0.034), nestling success (song: 75% vs. control: 97%; Fisher’s Exact test, *P* = 0.015), and fledging success (song: 61% vs. control: 94%; Fisher’s Exact test, *P* = 0.001) were all lower on song plots compared with control plots. Finally, neither nest predation (Fisher’s Exact test, *P* = 0.999) nor nest abandonment (Fisher’s Exact test, *P* = 0.521) differed between song and control plots, though nest abandonment occurred only on song plots (3 of 14 nests).

General breeding conditions in 2013/2014 appeared to have been better than in 2010–2012. We found increased clutch sizes and number of nestlings in unmanipulated study sites in 2013/2014 compared with the same sites in 2010–2012, and number of fledglings tended to differ (Figure 6, compare categories “others”). Clutch sizes, number of nestlings, and number of fledglings also tended to be higher on control plots of the 2 manipulated study sites in 2013/2014 than in the same sites of 2010–2012, though 95% CIs are large due to small sample size.

Extrapair parentage

All loci were polymorphic (number of alleles 2–16) and observed heterozygosity ranged from 0.220 to 0.859 per locus (Table 1). The 4 iterations conducted in Colony to determine output accuracy produced identical family clusters. Based on the best (maximum likelihood) configuration under the full likelihood model, Colony detected EPY in 1 out of 7 nests on song plots and in 1 out of 3 nests on control plots, respectively. Two of the 6 nestlings in the nest with EPY on song plots were from another male than the social-pair male. In the control plot nest with EPY, 1 of 6 nestlings was sired by a male other than the social-pair male. No evidence for extrapair maternity was found.

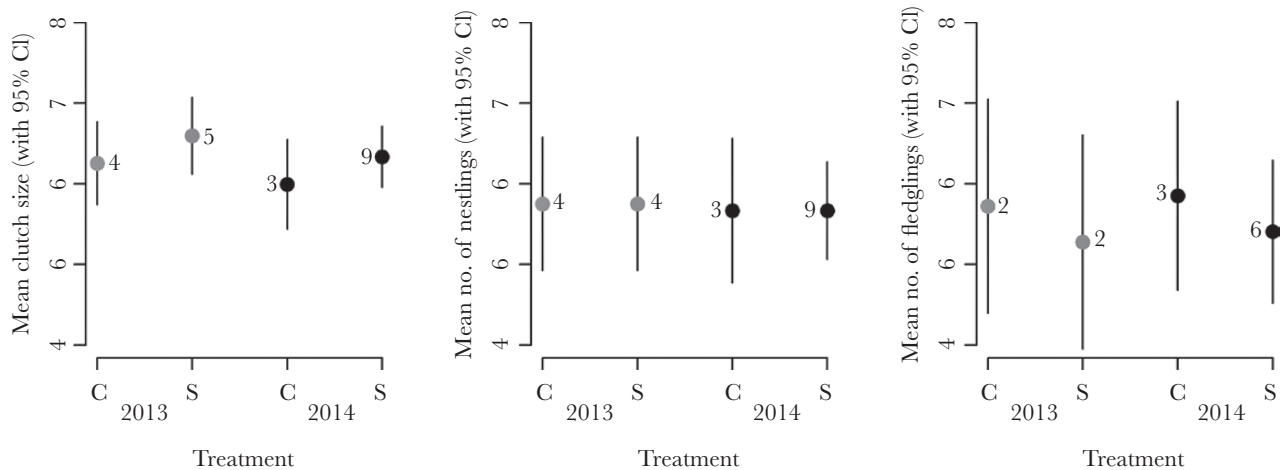


Figure 4

Mean (with 95% CI) clutch size ($n = 21$ nests), mean number of nestlings ($n = 20$ nests), and fledglings ($n = 13$ nests) on song plots (S) and control plots (C) for 2013 (gray) and 2014 (black). Values next to circles represent the nest sample size the model and graph are based on.

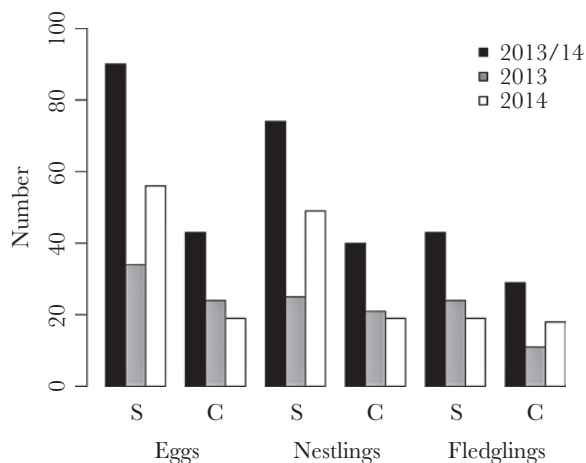


Figure 5

Number of eggs (based on 21 nests), nestlings (20 nests), and fledglings (13 nests) on song plots (S) and control (C) plots in 2013 (gray bars), in 2014 (white bars), and summed up for both years (black bars).

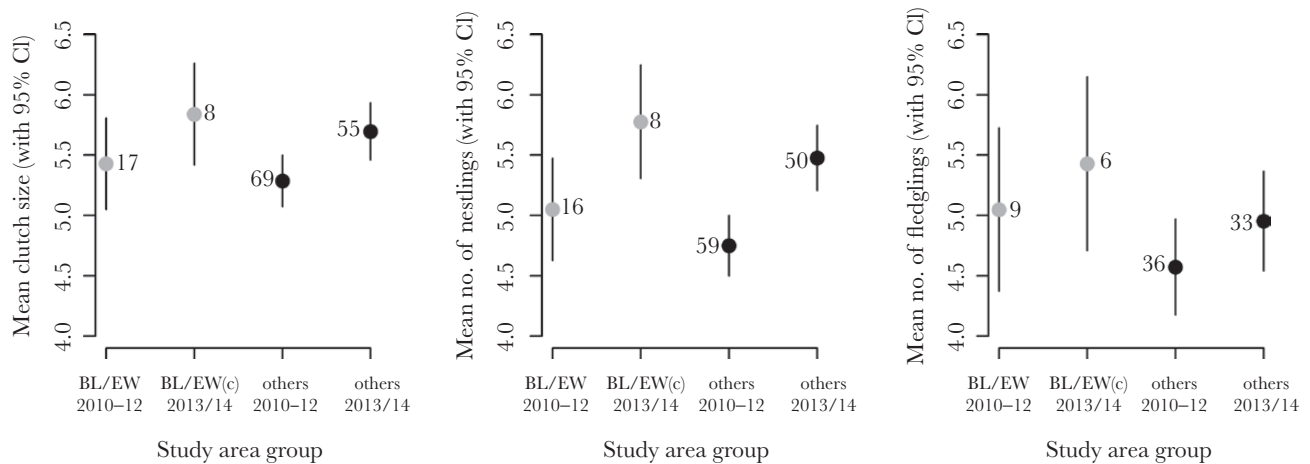
DISCUSSION

In both years, settlement probability was higher on song plots compared with control plots. Song plots were occupied faster than control plots, which was especially evident in 2014. There was no difference in pairing rates between treatment types. Though overall more eggs were produced on song plots than on control plots, mean clutch size, mean and absolute number of fledglings, as well as mean *dnst* did not differ between treatment types. Fledging success was lower on song plots than on control plots. Furthermore, we found evidence for EPP, but not maternity, in wood warblers breeding in Switzerland.

Our results support the first expectation of the conspecific attraction hypothesis because plots with experimental playback of wood warbler song had more than 3 times as many territories compared with control plots without wood warbler song playback. In addition, song plots were settled faster than control plots. The presence of conspecifics appears thus to be an important component for the settlement of wood warblers. These findings are in line with results reported in most playback experiments carried out over

the past 4 decades in the context of artificial conspecific attraction (20 out of 24 studies reviewed by Ahlering et al. 2010 resulting in attraction of the focal species). In at least 14 additional studies since 2010, artificial attraction resulted in higher territory density on song plots compared with control plots in 7 studies (Harrison et al. 2009; Ward et al. 2011; Farrell et al. 2012; Virzi et al. 2012; Andrews et al. 2015; DeJong et al. 2015; Szymkowiak et al. 2016;) and increased prospecting, but not breeder recruitment, in 5 studies (White 2008; Bradley et al. 2011; Major and Jones 2011; Buxton and Jones, 2012; Finity and Nocera 2012; Quilodran et al. 2014). In 2 studies, no difference in territory density between treatment types could be observed (Cornell and Donovan 2010; Bayard and Elphick 2012). Of the studies reviewed by Ahlering et al. (2010) and the 14 studies mentioned above, which provide evidence for artificial attraction, 4 used postbreeding period cues, whereas 30 used prebreeding period cues as in the present work.

Information about reproductive performance after artificial attraction is crucial for the potential applicability of the method in species conservation, especially given the inherent risk of creating ecological traps. In the 34 studies mentioned above, reproduction could be observed and was reported in 12 of the studies employing artificial (visual and/or acoustic) attraction methods, of which 5 concerned songbirds. The only study where nest success was higher on song plots than on control plots concerned the black-capped vireo (*Vireo atricapilla*) (Ward and Schlossberg 2004). However, nest success was only higher on song plots than on control plots if the brood-parasitizing brown-headed cowbird (*Molothrus ater*) was managed (Ward and Schlossberg 2004). In the remaining 4 studies on songbirds, nest success did not vary between treatments (Fletcher 2009; Harrison et al. 2009; Bayard and Elphick 2012; Farrell et al. 2012). The 6 studies reporting reproductive consequences after artificial attraction and conducted on species other than songbirds generally found nesting near attractants (sound decoys, bird replica decoys, and/or mirrors) to be higher than in areas without attractants (Kress 1983; Kotliar and Burger 1984; Kress and Nettleship 1988; Crouch et al. 2002; Parker et al. 2007; Ward et al. 2011). In summary, reproductive performance was observed and reported in only about a third of the mentioned studies using artificial attractants, with 2 general results depending on experimental design and goal: 1) Translocation or recolonization projects using artificial attractants to manipulate nonpasserine birds often reported a

**Figure 6**

Mean (with 95% CI) clutch size, number of nestlings, and fledglings with respect to experimental manipulation and time period. Each panel is divided into 4 categories: 1) the 2 study sites Blauen and Erschwil when they were unmanipulated in 2010–2012 (labeled as “BL/EW 2010–12”), 2) the 2 study sites Blauen and Erschwil when they received experimental manipulation in 2013/14 (data from control plots only, labeled as “BL/EW(c) 2013/14”), 3) the 4 unmanipulated study sites Kleinlützel, Lauwil, Montsevelier, and Scheltenpass in 2010–2012 (labeled as “others 2010–12”), and 4) the 4 unmanipulated study sites Kleinlützel, Lauwil, Montsevelier, and Scheltenpass in 2013/2014 (labeled as “others 2013/14”). Values next to circles represent the nest sample size the model and graph are based on.

positive effect on reproduction and 2) studies testing the conspecific attraction hypothesis on passerine birds generally found little evidence for varying reproductive performance between treatment plots. Likewise, we found little support for our second expectation of the conspecific attraction hypothesis that reproductive performance would be generally better on song plots compared with control plots after artificial conspecific attraction. In our study, more eggs were laid on song plots compared with control plots due to more nests on song plots. We did however not detect any difference in mean clutch size, total and mean number of nestlings, total and mean number of fledglings, or *dnst* between treatment types. Even though increased territory density on song plots apparently resulted in a higher cumulative breeding output, the difference of 43 fledglings on song plots compared with 29 fledglings on control plots was statistically not significant. However, fledging success (proportion of eggs that produced a fledgling) was lower on song plots than on control plots. When nest predation was accounted for, the difference of lost young between song and control plots became even larger, suggesting that reasons other than nest predation, which did not differ between treatments, might have affected breeding performance, such as density dependence and/or quality of attracted individuals. Density-dependent regulation has been shown to impact incubation and rearing (e.g., Hixon and Johnson 2001), negatively affecting hatching rate, nestling success, and fledging rate. Density-dependent reproduction has previously been found, for example in great tits (*Parus major*; Both 1998) or Seychelles warblers (*Acrocephalus sechellensis*; Brouwer et al. 2009). The artificially created high density of territories and nests in our study might have surpassed the local carrying capacity, possibly compromising the success of any single nest (e.g., via food competition [e.g., Forero et al. 2002] or interference competition [e.g., Krüger 2004] under high density). That the density in our song plots (maximum of 8 territories per 10 ha) and control plots (maximum of 2 territories per 10 ha) remained below that reported in most other wood warbler studies (up to 15.3 breeding pairs per 10 ha; Glutz von Blotzheim et al. 1991) does not weaken the hypothesis of negative density dependence for 2 reasons: 1) We do not know local carrying

capacity in our study system and 2) comparing density across studies is difficult, as density typically varies with habitat quality (Van Horne 1983). Whether density-dependent regulation occurred in our study remains speculative. It could be argued that if song playback is used to establish a population in a new breeding area, the role of mechanisms such as density-dependent regulation might be less important than in suitable and regularly occupied habitats. However, although this may be true for many species, in the case of wood warblers, with their fairly unique nomadic behavior, we argue that any site is perceived as new site, as individuals, at least individuals migrating through Switzerland, have most likely never seen this site before.

Complementary to possible density-dependent regulation, quality of attracted individuals may also play a role in reproductive performance. It is hypothesized that generally older individuals have higher reproductive success than younger individuals (reviewed in Forslund and Part 1995) and that mainly young, inexperienced individuals use public information (Nordell and Valone 1998) and respond to conspecific cues, including artificially provided ones (Nocera et al. 2006). Considering both hypotheses, individuals breeding in aggregations could be a mix of high-quality old individuals arriving early and poor quality inexperienced individuals being attracted and arriving later, resulting in decreased average reproductive performance across the aggregation. We have no data on age and very limited data on body condition of wood warblers during the period of the experiment, making it impossible to assess individual quality.

Quality may also play a role from the perspective of attracted individuals. Wood warblers appear to be attracted to conspecifics differentially depending on the quality of conspecifics (Szymkowiak et al. 2016). In their study, more territories were established on song plots with playback of poor quality males (mean song rate of 2 strophes/min) compared with song plots with playback of good quality males (mean song rate of 6 strophes/min) or control plots with no wood warbler song. However, theory predicts that settlement decisions of good quality individuals, with experience and success, should be copied and not decisions of low quality

individuals (Laland 2004). Szymkowiak et al. (2016) proposed that the observed pattern of settling near poor quality individuals was a tradeoff between information quality and competition. In the Polish study, wood warblers apparently actively avoided settling near good quality conspecifics. In our study, however, wood warblers settled on plots with simulated good quality individuals (with 5 strophes/min) more frequently than on control plots, indicating that benefits of conspecific attraction outweighed potential drawbacks of intraspecific competition or that individuals ignored drawbacks of intraspecific competition. The latter may subsequently have led to the patterns observed in this study, with decreased fledging success in nests on song plots with territory aggregations.

The observed clustering of territories did apparently not result in increased reproductive output as discussed above. Territory clustering also did not increase the chance of finding a mate, as pairing rates on song and control plots did not differ. Hence, we found no evidence to support the social mate choice hypothesis in our experimental system. Of the 34 experimental attraction studies mentioned above, only 1 reported differential pairing rates between treatments, with higher pairing rates on song than on control plots (Farrell et al. 2012). In 10 further studies, pairing was observed, but no additional details regarding pairing rates were reported (Kress, 1983; Kotliar and Burger 1984; Kress and Nettleship 1988; Crouch et al. 2002; Ward and Schlossberg 2004; Nocera et al. 2006; Parker et al. 2007; Betts et al. 2008; Fletcher 2009; Harrison et al. 2009).

Even with no apparent direct benefit, clustering may facilitate promiscuity thereby increasing the chance of individuals to pass on genes to the next generation, essentially via extrapair copulation. Although work carried out in central Sweden on wood and willow warblers (*Phylloscopus trochilus*) concluded that extrapair copulations are rather uncommon in these 2 species (Gyllenstein et al. 1990), a recent study in Russia provided evidence for frequent extrapair offspring in wood warblers: from 12 out of 23 wood warbler nests, 38 out of 130 young were not related to their social father (Moskalenko et al. 2014). In our study, we found EPY in 1 of 7 nests on song plots and in 1 of 3 nests on control plots, with young from 2 fathers in each case. The low rates of EPY could be an artifact of the relatively low wood warbler abundance in 2014 (when DNA samples were taken) compared with other years and precludes a robust test of the hidden lek hypothesis. What factors underlie territory clustering, experimentally induced in this study and previously reported in observational studies (Herremans 1993; Wesolowski et al. 2009), remain to be assessed in the wood warbler and in other species (Fletcher and Miller 2006).

The conspecific attraction hypothesis has received much attention and experimental testing, particularly in North American ecosystems and species. However, despite its apparent importance, conspecific attraction is often overlooked in studies investigating settlement behavior. We experimentally demonstrated that social information, more specifically conspecific attraction, plays an important role in the settlement process of a forest species found throughout Europe. From a metapopulation point of view, it remains to be studied whether artificial attraction presents an opportunity for individuals to reproduce, which would have otherwise not done so, or whether artificial attraction merely causes a redistribution of the population. Should the latter be the case, then this method mainly serves the purpose of attracting individuals to areas desired from a human perspective, but may not be important for conservation purposes or support of the global population of the species. Although individual reproductive performance in artificially created territory clusters after experimental attraction was

altered, mean reproductive output was comparable with control plots. Although our results on fledgling production indicate that our experiment did not create an ecological trap, lower fledging success on song plots gives reason to further evaluate the usefulness of this method for conservation purposes. Neither this study nor other studies on passerines assessing consequences for reproduction after attraction treatment found strong evidence for increased reproductive performance on song plots compared with control plots (except in 1 case where additional management was required). These results further urge the need for more studies looking at distribution, settling dynamics, and fitness consequences of the focal species with and without artificial attraction, as well as the reasons for territory clustering. Although this study exemplifies how important social cues can be in territory selection of birds, it also shows how crucial it is to evaluate reproductive performance during and after experimental treatments.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Grendelmeier et al. (2016).

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