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Habitat features and long-distance dispersal modify the use of social information by a long-distance migratory bird

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Summary

1. The processes by which individuals select breeding sites have important consequences for individual fitness as well as population- and community-dynamics. Although there is increasing evidence that many animal species use information acquired from conspecifics to assess the suitability of potential breeding sites, little is known about how the use of this social information is modified by biotic and abiotic conditions.

2. We used an automated playback experiment to simulate two types of social information, post-breeding public information and pre-breeding location cues, to determine the relative importance of these cues for breeding site selection by a migratory songbird, the American redstart (*Setophaga ruticilla*). In addition, we used stable hydrogen isotopes to determine the dispersal status of individuals that responded to our experimental treatments and quantify whether long-distance dispersers use different social cues to select breeding sites compared to philopatric individuals.

3. We found that points that received pre-breeding location cue treatments were significantly more likely to be settled by redstarts than control points that received no playback. However, we found no evidence the redstarts used post-breeding public information gathered during one season to select breeding sites the following year. Breeding site habitat structure was also a strong predictor of settlement probability, indicating that redstarts modified the use of social information based on habitat cues. Furthermore, stable hydrogen isotope signatures from individuals that responded to location cue treatments suggest that long-distance dispersers may rely more heavily on these cues than local recruits.

4. Collectively, these results indicate that redstarts use multiple sources of information to select breeding sites, which could buffer individuals from selecting suboptimal sites when they breed in unfamiliar locations or when habitat quality becomes decoupled from social cues.

Key-words: conspecific attraction, deuterium, habitat selection, location cues, public information, *Setophaga ruticilla*, social information

Introduction

The ability to locate and select high-quality breeding sites is a key behavioural process that links individual fitness to population- and community-level dynamics, including population regulation (Fretwell & Lucas 1970; Pulliam 1988), community assembly (Fletcher 2008; Betts, Nocera & Hadley 2010) and maintaining biological diversity (Ward & Schlossberg 2004). Understanding the cues that individuals use to assess and select breeding sites is thus a central question in ecology, evolution and conservation (Morris 2003; Danchin *et al.* 2004; Ahlering & Faaborg 2006). In recent decades, empirical research has demonstrated that information acquired from conspecifics, termed *social information*, is widely used by many species to assess the quality of potential breeding sites (Reed *et al.* 1999; Valone 2007). Compared to other sources of information (e.g. habitat features or previous reproductive success), social information is relatively efficient to collect, can provide information about habitat quality even when

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the features that influence fitness are not apparent, and is available to most individuals regardless of age or reproductive experience (Szymkowiak 2013). However, not all types of social information are equally reliable and understanding when and under what conditions individuals use different types of social information remains poorly understood (Doligez *et al.* 2003; Danchin *et al.* 2004; Stamps & Krishnan 2005).

Social information is generally divided into two categories: information about the presence/absence of conspecifics, termed *location cues*, and information about the reproductive performance of conspecifics, termed *public information* (Danchin *et al.* 2004). When the quality of breeding sites is predictable across years, both cues can provide information about the location of suitable breeding sites. However, while the presence of breeding individuals is generally associated with suitable habitat, location cues do not provide direct information about the relative quality of different sites, and under certain circumstances, it is possible for location cues to become uncoupled from habitat quality (i.e. ecological traps, Schlaepfer, Runge & Sherman 2002). In contrast, because public information is based directly on conspecific performance, it is generally a highly reliable cue for assessing breeding site quality. For this reason, public information should be favoured over location cues in stable environments (Doligez *et al.* 2003). Despite this prediction, empirical studies have demonstrated that location cues are widely used by many species (e.g. Serrano *et al.* 2004; Ahlering, Johnson & Faaborg 2006; Szostek, Schaub & Becker 2014). Explaining the coexistence of these two strategies is an important step to developing a general theory of breeding site selection (Szymkowiak 2013).

Several hypotheses may explain why individuals use location cues even when public information provides more reliable information about breeding site quality. First, when all individuals in a population breed synchronously, young individuals do not have the opportunity to gather public information (Nocera, Forbes & Giraldeau 2006) and may be forced to rely on location cues (Doligez *et al.* 2004). Secondly, dispersers forfeit any previously acquired public information when they move to new locations, and therefore, immigrants may be more reliant on location cues than philopatric individuals (Szostek, Schaub & Becker 2014). Although interspecific comparisons of social information use provide some empirical support for both hypotheses (Reed *et al.* 1999; Stamps & Krishnan 2005), the dynamics of populations are ultimately influenced by intraspecific variation in habitat selection behaviour (Kristan 2003). Therefore, linking individual behaviour to population dynamics requires understanding the causes of intraspecific variation in breeding site selection. Few studies, however, have simultaneously quantified the relative importance of public information and location cues for individuals within the same population (but see Doligez *et al.* 2004; Nocera, Forbes & Giraldeau 2006).

In this study, we simulated post-breeding public information and pre-breeding location cues to experimentally test the relative importance of each cue for breeding site selection in a migratory songbird, the American redstart (*Setophaga ruticilla*). This experimental simulation allowed us to test the following predictions:

1. Redstarts use both pre-breeding location cues and post-breeding public information to select breeding sites: Several studies have documented the use of pre-breeding location cues by American redstarts (Hahn & Silverman 2006; Fletcher 2007), and therefore, we predicted that this would be an important source of social information for birds in our population. The use of post-breeding public information by redstarts has not been studied, but Betts *et al.* (2008) experimentally demonstrated that individuals of the closely related black-throated blue warbler (*Setophaga caerulescens*) monitor the reproductive performance of conspecifics and use this information to select breeding sites the following year. Given the close phylogenetic relationship between these two species (Lovette *et al.* 2010) and the similarity of their breeding habitat, we predicted that redstarts would also use post-breeding public information to select breeding sites.
2. Pre-breeding location cues are a more important source of information than post-breeding public information: Black-throated blue warblers often produce two broods per season, and this asynchrony provides individuals from early broods the opportunity to gather public information from the territories of successful second broods (Betts *et al.* 2008). In contrast, because redstarts are obligate single brooders (Sherry & Holmes 1997), their short, synchronous breeding season may prevent newly fledged redstarts from gathering public information (Nocera, Forbes & Giraldeau 2006). Therefore, we predicted that post-breeding public information would be a less important source of social information than pre-breeding location cues for redstarts.
3. The use of social information differs between adults and yearlings due to asynchronous opportunities to collect public information: Although newly fledged redstarts may not have the opportunity to collect public information, many yearling males in our population remain unmated throughout the breeding season (C. Rushing pers. obs.) and these individuals provide a potential pool of prospectors that could gather and use post-breeding public information when they return as adults the following year (Doligez *et al.* 2004). Therefore, we predicted that adults would be more likely than yearlings to settle in response to post-breeding public information treatments, whereas pre-breeding location cues would be more important for yearlings attempting to breed for the first time.
4. Long-distance dispersal modifies the use of social information cues: Because dispersing individuals

cannot rely on post-breeding public information gathered the previous year, we predicted that immigrants would be more likely to use pre-breeding location cues than philopatric individuals.

Materials and methods

STUDY SPECIES AND EXPERIMENTAL DESIGN

American redstarts are long-distance neotropical migratory songbirds that breed throughout North America and winter in the Caribbean and Latin America (Sherry & Holmes 1997). Since 2009, we have studied a large population of redstarts breeding at the Patuxent Research Refuge in Laurel, Maryland, USA (39° 04’N, 76° 47’W). The 250-ha study area consists primarily of beech-dominated bottomland forests adjacent to the Patuxent River.

To test our predictions, we simulated both post-breeding public information and pre-breeding location cues at points located within the larger population of redstarts at our study site. The basic experimental design consisted of simulating post-breeding public information cues during the fledging period of one breeding season (to simulate successful territories) and then simulating pre-breeding location cues at a different set of locations during the arrival period the following year (to simulate the presence of territorial males). During the second year of the experiment, all points were monitored to determine the number of redstarts holding territories in the vicinity of each point. We repeated this design twice, with the first round initiated during the 2011 fledging period and completed during the 2012 arrival period (hereafter referred to as the 2012 round) and the second initiated in 2012 and completed in 2013 (hereafter referred to as the 2013 round).

In 2011 and then again in 2012, we selected points for our experiment and randomly assigned each point to one of three treatments: post-breeding public information (n = 20), pre-breeding location cues (n = 20) or control (n = 30). To minimize the influence of habitat structure or previous experience, we selected points that were similar in general habitat structure (e.g. forested) and we used point counts and territory surveys to ensure that all sites were ≥150m from existing redstart territories in the years of the experiment, though we were unable to determine whether sites had been occupied by redstarts in previous years. Additionally, all points were separated by >250 m. Playback treatments were not audible at distances greater than 100, so 250 m was adequate to ensure independence of experimental treatments.

For both the post-breeding public information and pre-breeding location cue treatments, playback was broadcast using a portable CD player (Supersonic SC251) housed in a waterproof box and connected to two speakers (Dual LU43PW) mounted 2 m above the ground, 20 m apart and facing in opposite directions. An automated timer (Borg General TA5027) turned on the playback each morning at 0500 and broadcast the treatment until 1400. Each song track was separated by 15 of silence and was alternated between the two speakers every 5 min to minimize habituation. Post-breeding public information treatments were broadcast during the local redstart fledging period (June 1-August 1) and consisted of locally recorded male and female redstarts vocalizing while feeding young and fledgling begging calls. Pre-breeding location cue treatments were broadcast during the arrival period at our study site (April 10-May 15) and consisted of locally recorded territorial male songs. In 2013, one pre-breeding location cue station failed and was removed from analysis, resulting in a total of 19 replications for this treatment. Because both anthropogenic and heterospecific cues can influence settlement patterns of birds, we chose not to apply any playback at control points (Betts *et al.* 2008).

To determine whether redstarts collect post-breeding public information by observing the reproductive performance of conspecifics (i.e. prospecting), we conducted 10-min point counts once per week during the public information treatment period at all post-breeding public information and control points. All point counts were conducted between 0600 and 1000 on days without rain or wind. After a 2-min settling period, any redstart seen or heard within 50 m of point during the 10-min point count was considered a prospector and we used a logistic regression to compare the number of prospectors at public information and control point. During the post-breeding period, the age and sex of redstarts with female-like plumage cannot be reliably determined (Pyle, Howell & Ruck 1997), so we did not record the age or sex of prospectors unless they were adult males.

During the 2012 and 2013 arrival periods, all treatment and control points were surveyed daily to record the presence of male redstarts. Any male that was observed within 75 m of a point on >3 consecutive days and responded aggressively to conspecific song was considered to be settled at that point.

MEASURING HABITAT STRUCTURE

Although treatment and control points were visually inspected to ensure similar habitat structure, fine-scale differences in habitat features could still have influenced settlement decisions. To control for the influence of habitat structure, we quantified vegetation features within a 5-m-radius circle centred on each point and within three more circles located 25 m from the centre at 0, 120 and 240° (Tarof, Ratcliffe & Grubb 2004). Within each circle, we measured five habitat features: the number of saplings [<3 cm diameter at breast height (DBH)], the number of trees (>3 cm DBH), the number of beech trees, the percentage shrub cover and the percentage canopy cover. For each tree, DBH was measured 2 m above the ground using a diameter tape. We chose to record the number of beech trees because this is the preferred nesting tree for redstarts at our study site (C. Rushing unpublished data) and therefore may influence settlement decisions. Shrub cover was visually estimated as the percentage of the ground covered in shrubs and was recorded on a scale of 1–4 (1 = 0–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%). To estimate percentage canopy cover, we photographed the canopy directly above each circle using a Nikon Coolpix 990 digital camera fitted with a Nikon LC-ER1 8 mm 180° fisheye converter and vertically mounted on a tripod. We then used Gap Light Analyzer 2·0 (Frazer, Canham & Lertzman 1999) to quantify the percentage canopy cover within each photograph. In addition to these five habitat features, we also estimated the mean tree basal area and the total basal area (TBA) within each circle. We calculated tree basal area as $0{\cdot}005454xDBH^2$ (James & Shugart 1970). To estimate TBA, we converted the tree basal areas to basal area/acre ($0ot00007854x$tree basal area) and then summed these measures for all trees within the circle (James & Shugart 1970).

For each habitat feature, measurements were averaged across the four circles to derive a single estimate for the entire point. A multivariate ANOVA indicated that the mean scores of the seven habitat variables did not systematically differ among the three treatments ($F_{14,122} = 1{\cdot}22, P = 0{\cdot}27$). To reduce the number of dimensions used to measure habitat structure, we then used a princile component analysis (PCA) to collapse our original seven variables into a smaller number of orthogonal predictors. The first two principle components described over half of the variation in habitat structure (see Supporting Information, Table S1), and we included these scores in our analysis of settlement at playback points (see below).

INFERRING DISPERSAL STATUS

To test our prediction about the influence of long-distance dispersal on the use of social information, we attempted to capture all males that responded to our experimental treatments and used stable hydrogen isotopes to determine the dispersal status of each individual. All individuals were captured in mist nets using decoys and playback of conspecific song. After capture, each individual was classified as either a yearling (1 year old) or an adult (>1 year old) following Pyle, Howell & Ruck (1997), fitted with an aluminium USFWS leg band and a unique combination of plastic colour bands, weighed to the nearest 0·1 g, measured for body size (bill length, bill width, bill depth, tarsus length and unflattened wing chord) to the nearest 0·5 mm and released.

During banding, we also collected one tail feather (R3) for stable hydrogen isotope analysis. Stable hydrogen isotopes in feather samples ($\delta^2 H_f$) vary geographically (Chamberlain *et al.* 1997; Hobson & Wassenaar 1997) and can be used to infer long-distance movements in birds (Wunder, 2010, 2012). Because redstarts grow tail feathers at their breeding location prior to fall migration, $\delta^2 H_f$ values from redstarts that bred at our study site in 2011 and 2012 and were recaptured in 2012 and 2013 provided the expected $\delta^2 H_f$ distributions for birds originating at our study site during the years of our experiment. We then used these distributions to probabilistically determine dispersal status of individuals captured at playback stations, with each individual classified as local or an immigrant based on a predefined threshold of correctly classifying local individuals (Van Wilgenburg *et al.* 2012). To determine whether our results were sensitive to the threshold used to classify dispersal status, we carried out our analyses using three progressively stringent thresholds (4 : 1 odds, 9 : 1 odds, 19 : 1 odds). See Appendix S2 for more details about stable isotope analysis and inferring dispersal status.

In addition to the individuals that responded to our experimental treatments, we also collected isotope data from 97 unbanded male redstarts (2012: $n = 62$, 2013: $n = 35$) in the general population at our study site. These data served as a baseline for comparing immigration patterns in our treatment groups.

ANALYSIS

Do social information and habitat structure influence settlement decisions?

To determine whether playback treatments and habitat characteristics influenced settlement decisions of redstarts, we tested whether the probability that sites settled by redstarts differed between treatments using a logistic regression model, which we refer to as the *settlement* model. Because we predicted *a priori* that settlement patterns would differ for adults and yearlings, we fit separate settlement models for each age class. For each age class, we modelled whether or not each site i was occupied by ≥1 redstart (denoted C_i) as a Bernoulli trial as follows:

$$C_i \sim \mathrm{Bernoulli}(\psi_i) \qquad \text{eqn 1}$$

$$\begin{aligned} logit(\psi_i) = \alpha + \beta_1 \mathrm{Trt}_i + \beta_2 \mathrm{Year}_i + \beta_3 \mathrm{PC1}_i + \beta_4 \mathrm{PC2}_i \\ + \beta_5 \mathrm{PC1}_i * \mathrm{Trt}_i + \beta_6 \mathrm{PC2}_i * \mathrm{Trt}_i + \beta_7 \mathrm{Year}_t * \mathrm{Trt}_i, \end{aligned} \qquad \text{eqn 2}$$

where ψ_i is the probability of settlement at site i, α is the baseline settlement probability at control sites, Trt_i is a dummy variables indicating whether site i received location cue treatment or post-breeding public information treatment, Year_i is a dummy variable indicating whether the treatment was applied in the second year of the experiment, and $\mathrm{PC1}_i$ and $\mathrm{PC2}_i$ are the first two habitat scores for site i. To test our predictions about the factors that influence breeding site selection of redstarts, we dropped each of the predictors from two and then tested the fit of the reduced model using a likelihood ratio test (LRT). For predictors that were included in significant interaction terms, main effects were tested by dropping both the main effect and interactions.

Does long-distance dispersal modify the use of social information?

Given the small sample size of our experiment, we used a simple Bayesian binomial model (Kéry 2010) to test whether individuals that settled at playback sites were more or less likely to be immigrants than individuals from the general population. We modelled dispersal by independently fitting binomial models for each of the treatment types and for the population as a whole. For each model, the parameter of interest was the probability that an immigrant settled a site. We also derived the posterior distribution for differences between the dispersal probability of each treatment and for the general population (denoted p_{diff}). For example, a positive p_{diff} indicated that individuals responding to playback were more likely to be immigrants than individuals from the general population and a negative value indicates that playback individuals were less likely to be immigrants. We evaluated the degree of overlap in 95% credible intervals for the estimates of p_{diff} to identify significant differences in immigration probability.

We estimated posterior probability distributions with MCMC algorithms in JAGS 3.4.0 (Plummer 2003) via the R2jags package (Su & Yajima 2014) in R v3.0.2 (R Core Team 2013). We used uninformative priors for all parameters: Normal (0, 100) for regression parameters in the settlement model and Uniform (0, 1) for parameters in the immigration model. Three chains were computed for each parameter, and we stored 25 000 samples from each chain after discarding the first 10 000 iterations as burn-in. Convergence of the chains was assured by visual inspection of trace plots and by Gelman diagnostics (Brooks & Gelman 1998). To assess model fit, we used posterior predictive checking (Kruschke 2010). For each model, we used draws from the posterior distribution of each parameter to simulate a data set of the same size as the observed data. We then plotted the simulated data against the observed data to graphically inspect the fit of each model (Appendix S3).

Results

THE USE OF SOCIAL INFORMATION BY AMERICAN REDSTARTS

Over the course of our experiment, 52·6% (10/19) of the sites receiving pre-breeding location cue treatments were settled by at least one adult redstart, compared to 10% (3/30) of the control sites and 0% (0/20) of the post-breeding public information sites. Model selection results indicated that adult settlement probability was positively influenced by location cue treatments and negatively influenced by habitat PC1 (Table 1). We found no evidence that year or habitat PC2 influenced settlement probability (Table 1) nor did we find evidence of an interaction between treatment and habitat (PC1: χ^2 = 2·2, d.f. = 2, P = 0·33; PC2: χ^2 = 0·05, d.f. = 2, P = 0·98). Therefore, our conclusions about adult settlement are based on the top model containing treatment effects and the main effect of habitat PC1. After controlling for the influence of habitat, the adult *settlement* model indicated that the probability of settlement at sites that received the pre-breeding location cue treatment was ~8× higher than at control sites (Table 2; Fig. 1). Model coefficients associated with the post-breeding public information treatment were not estimable because all sites that received this treatment were unoccupied by adults. Therefore, contrary to our prediction, we conclude that adults redstarts did not respond to these post-breeding public information treatments.

The top adult model also indicated that settlement probability was negatively associated with the habitat features associated with habitat PC1 (Table 2; Fig. 2). Factor loadings indicate that habitat PC1 was positively correlated with the number of trees and negatively correlated with shrub cover (Table S1), indicating that adult redstarts were more likely to settle at sites with few trees, and to a lesser extent high shrub cover. Although we did not find statistical evidence that treatment response of adults varied as a function of habitat, inspection of the treatment-specific habitat effects suggests that the strength of the habitat PC1 effect did differ among the three treatment levels but that we did not have sufficient power to detect this interaction (Fig. 2). Thus, it appears that habitat PC1 had a strong influence on which pre-breeding location cue sites were settled but only a weak influence at control sites and no influence at post-breeding public information sites. Furthermore, this result suggests that the settlement probability of adults at pre-breeding location cue sites was only higher than at control sites when these treatments were conducted at sites with low habitat PC1 scores.

For yearlings, 47·4% (9/19) of the sites receiving pre-breeding location cue treatments were settled by at least one adult redstart, compared to 10% (3/30) of the control sites and 20% (4/20) of the post-breeding public information sites. Model selection results indicated that yearling settlement probability was positively influenced by location cue treatments and negatively influenced by habitat PC2 (Table 1). We found no evidence that year or habitat PC1 influenced settlement probability (Table 1) nor did we find evidence of an interaction between treatment and habitat (PC1: χ^2 = 0·82, d.f. = 2, P = 0·66; PC2: χ^2 = 3·48, d.f. = 2, P = 0·18). Therefore, our conclusions

Table 1. Factors influencing breeding site selection by American redstarts. Coefficient estimates (β) SE are from the settlement models for yearlings and adults. Because no adult males settled at points receiving the public information treatment, the public information coefficient was not estimable in the adult settlement model. χ^2, d.f. and P values for each predictor refer to the likelihood ratio test (LRT) used to compare the model without that predictor to the full model. The treatment predictor and year predictor treat control points and the year 2012 as dummy variables, respectively. Interaction terms from the full model that were not significant were dropped and are not displayed here. Bold values indicate predictor variables that were significant at the 0·05 level

Predictor	β	SE	χ^2	d.f.	P
Yearlings					
Intercept	−2·63	0·81	–	–	–
Treatment					
Public information	**0·38**	**0·91**	**11·4**	**2**	**0·003**
Location cues	**2·39**	**0·87**			
Year	−0·65	0·68	0·97	1	0·32
Habitat PC1	−0·26	0·23	1·35	1	0·24
Habitat PC2	**−0·65**	**0·29**	**5·87**	**1**	**0·02**
Adults					
Intercept	−3·24	1·07	–	–	–
Treatment					
Public information	–	–	**2·62**	**2**	<0·001
Location cues	**3·17**	**1·04**			
Year	−1·03	0·91	1·35	1	0·25
Habitat PC1	**−0·75**	**0·33**	**7·53**	**1**	**0·006**
Habitat PC2	−0·58	0·35	2·94	1	0·08

Table 2. Estimated odds ratios and 95% confidence intervals (CI) for parameters included in the top settlement models for yearlings and adults. For playback treatments, the odds ratio is the relative probability of settlement at sites receiving that treatment compared to the probability of settlement at control sites, after controlling for habitat features. Because no adult males settled at points receiving the public information treatment, the public information odds ratio was not estimable. For habitat effects, the odds ratio is the change in settlement probability associated with one unit change in the habitat score

Predictor	Odds ratio (e^{β})	2.5% CI	97.5% CI
Yearlings			
Control	–	–	–
Public information	1·19	0·23	6·93
Location cues	8·64	1·93	50·99
Habitat PC2	0·52	0·28	0·90
Adults			
Control	–	–	–
Public information	–	–	–
Location cues	11·51	3·12	10·56
Habitat PC1	0·55	0·28	0·91

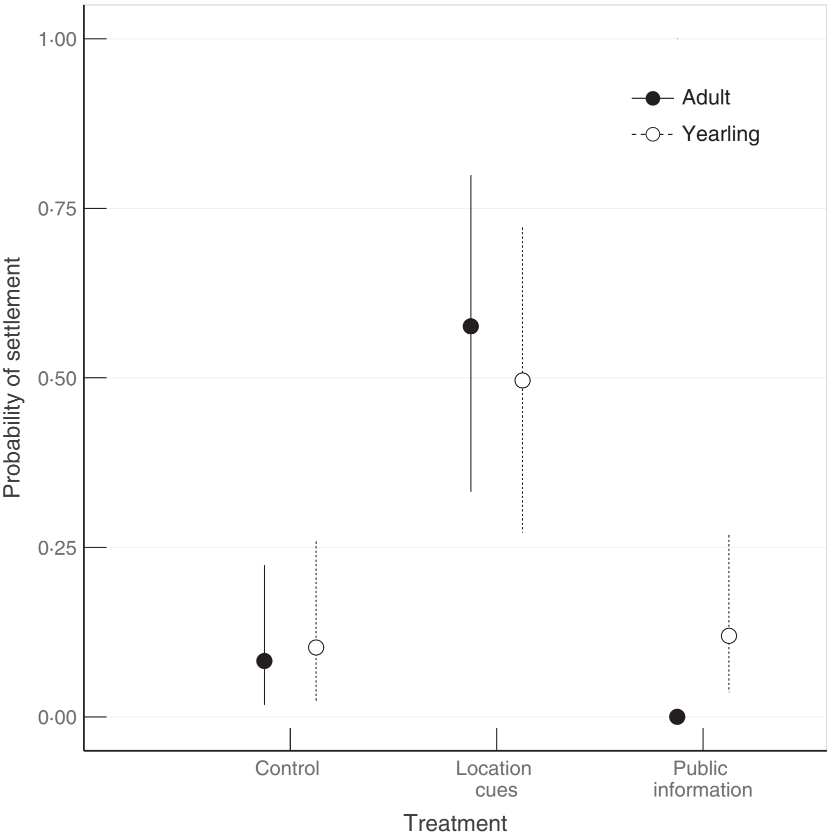

Fig. 1. Response of American redstarts to experimental playback treatments. Points show the predicted probability of settlement from the top *settlement* models for each age class, after controlling for the influence of habitat features. Error bars indicate the 95% confidence interval (CI) for each parameter. Model results indicate that, for both adults and yearlings, the probability of settlement at location cue points was significantly higher than at post-breeding public information or control points.

about yearling settlement are based on the top model containing treatment effects and the main effect of habitat PC2. After controlling for the influence of habitat, the yearling *settlement* model indicated that the probability of settlement at sites that received the pre-breeding location cue treatment was ∼8× higher than at control sites (Table 2; Fig. 1). In contrast, the settlement model indicated the post-breeding public information treatment did not increase the odds of settlement compared to control sites (Table 2; Fig. 1).

As for adults, the top yearling model indicated that settlement probability was influenced by habitat features. However, unlike adults, yearling settlement was negatively associated with the habitat PC2 rather than PC1 (Table 1; Fig. 3). Habitat PC2 was positively correlated with the number of saplings and negatively correlated with mean tree basal area and percentage canopy cover (Table S1), indicating that yearlings chose sites that had higher tree basal area, and to a lesser extent higher percentage canopy cover and fewer saplings. Also as for adults, we did not find statistical evidence that treatment response of yearlings varied as a function of habitat but inspection of the treatment-specific habitat effects suggests that the strength of the habitat PC2 effect did differ among the three treatment levels (Fig. 3). In particular, it appears that that the influence of habitat PC2 on yearling settlement was stronger at sites that received playback treatments than at control points. Thus, although the settlement probability was always higher at location cue treatment sites than at public information treatment sites or control sites, this effect declined as habitat PC2 score increased. Furthermore, these results suggest that yearlings may have responded positively to post-breeding public information treatments, but only at sites with low habitat PC2 score. Unfortunately, although some of these sites were settled by yearlings, we were not able to conclusively attribute this response to our playback treatments.

EVIDENCE OF PROSPECTING

Over both years of the experiment, only two redstarts were recorded at post-breeding public information points during the playback period. The number of prospectors recorded at post-breeding public information points did not differ from the number recorded at control points ($n = 1$, $z = 0{\cdot}566$, d.f. = 1, $P = 0{\cdot}57$). Together with the settlement data, these results provide additional evidence that redstarts did not respond to our post-breeding public information treatments.

THE INFLUENCE OF LONG-DISTANCE DISPERSAL ON THE USE OF SOCIAL INFORMATION

Because we did not see a response to the post-breeding public information treatment, we restricted our analysis of long-distance dispersal to individuals that settled in response to pre-breeding location cues. The age ratio of yearlings to adults in the experimental group (1·5 year-

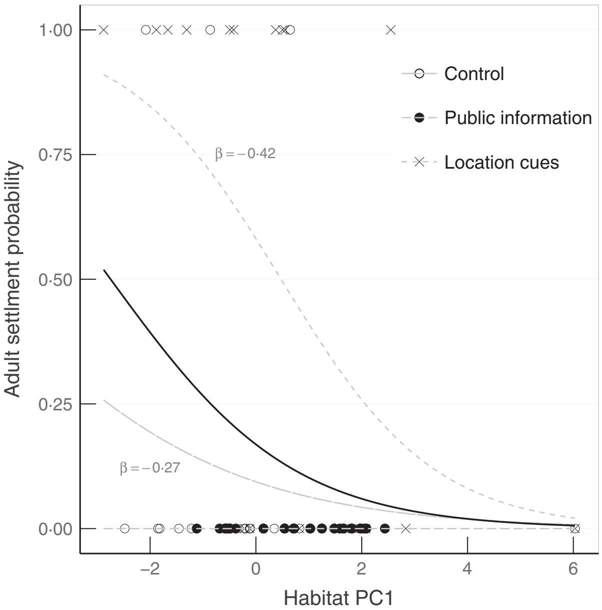

Fig. 2. Influence of habitat PC1 on the settlement probability of adult American redstarts. The solid line shows the estimated settlement probability from the top adult settlement model as a function of habitat PC1 for all points, independent of playback treatment. Dashed lines, and the associated slope coefficients, show the estimated effect of habitat PC1 for each treatment separately. Points show the observed settlement patterns within each treatment. Habitat PC1 was positively correlated with the number of trees and negatively correlated with shrub cover (Table S1), indicating that adult redstarts were more likely to settle at sites with few trees, and to a lesser extent high shrub cover. Although we did not find statistical support for a habitat × treatment interaction in the top model, treatment-specific habitat effects suggest that the effect of habitat PC1 may have been stronger at location cue treatments than at control sites or public information treatments.

lings/adult) was similar to the age ratio of individuals sampled from the general population (1·42 yearlings/adult), allowing us to directly compare immigration rates without correcting for potential age-related biases. When immigrants were classified using a 4 : 1 odds ratio, the immigration rate for individuals that were captured at pre-breeding location cue points ($n = 15$) was significantly higher than the immigration rate in the general population ($n = 97$; $p_{\text{diff}} = 0{\cdot}22$, 95% CI = 0·007:0·46; Fig. 4). However, the immigration rates did not differ when dispersal status was classified using the more stringent 9 : 1 odds ratio ($p_{\text{diff}} = 0{\cdot}055$, 95% CI = −0·10 : 0·27) or the 19 : 1 odds ratio ($p_{\text{diff}} = -0{\cdot}02$, 95% CI = −0·12 : 0·13).

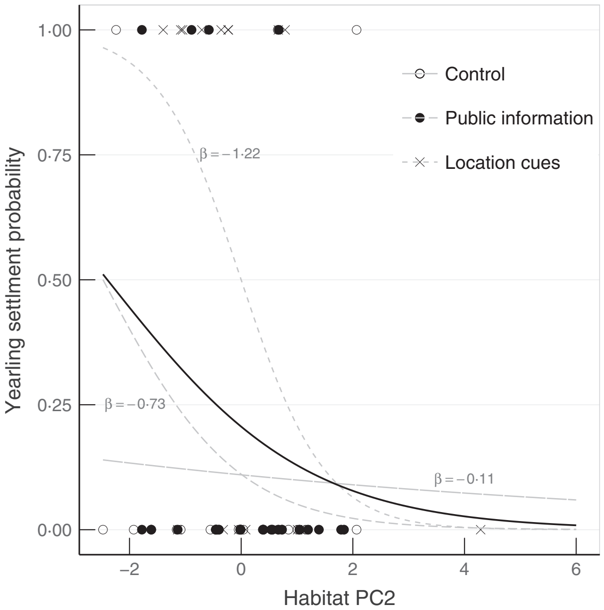

Fig. 3. Influence of habitat PC2 on the settlement probability of yearling American redstarts. The solid line shows the estimated settlement probability from the top yearling settlement model as a function of habitat PC2 for all points, independent of playback treatment. Dashed lines, and the associated slope coefficients, show the estimated effect of habitat PC2 for each treatment separately. Points show the observed settlement patterns within each treatment. Habitat PC2 was positively correlated with the number of saplings and negatively correlated with mean tree basal area and percentage canopy cover, indicating that yearlings responded more strongly to location cue treatments at sites that had higher tree basal area, and to a lesser extent higher percentage canopy cover and fewer saplings. Although we did not find statistical support for a habitat × treatment interaction in the top model, treatment-specific habitat effects suggest that the effect of habitat PC2 may have been stronger at playback sites than at control sites.

Discussion

At the beginning of the breeding season, male migratory birds are under severe time constraints to locate suitable habitat and establish territories. These tasks are made more challenging because the features that influence fitness (e.g. vegetation features, resource abundance, predation) are often not apparent at the time when settlement decisions are made. Under these circumstances, both pre-breeding location cues and post-breeding public information may provide reliable information for quickly locating suitable breeding sites but little is known about the relative importance of these cues in wild populations.

Our experimental simulation of pre-breeding location cues demonstrated that although both adult and yearling American redstarts use these cues to select breeding sites, the use of this information is modified by specific habitat features. For yearlings, response to location cues was strongest at sites with a high number of saplings and a low mean tree basal area. In contrast, settlement probability of yearlings at location cue sites did not differ from control sites in other habitat types. Likewise, adults responded strongly to location cue treatments at sites with more trees and lower shrub cover but settlement probability did not differ from control points in other habitat types. Unfortunately, we did have the necessary data to link these habitat features to reproductive performance so it remains unclear why the age classes used different habitat cues. However, it is worth noting that both the number and the size of trees are readily apparent at the

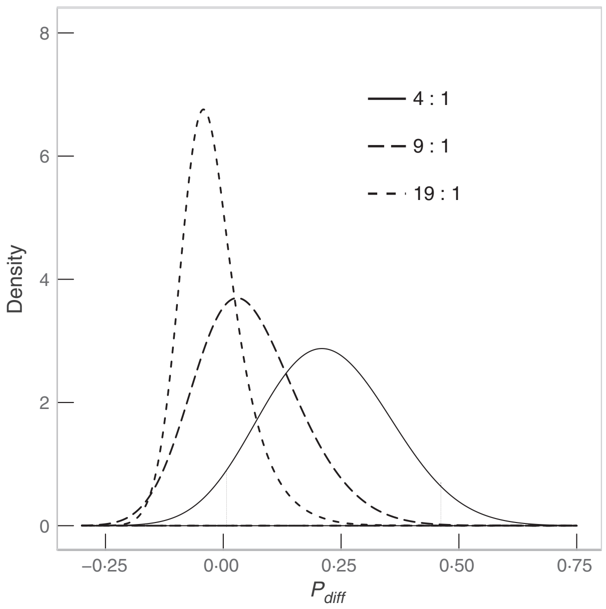

Fig. 4. Posterior distributions for difference in the immigration rate (p_{diff}) between individuals that settled in response to location cue treatments and individuals from the general population. When immigrants were classified using the 4 : 1 odds ratio, individuals that settled in response to experimental pre-breeding location cues were more likely to be immigrants than individuals in the general population and the 95% credible interval (CI), indicated by the vertical dotted lines, did not contain zero. However, immigration rates did not differ under the 9 : 1 odds ratio or the 19 : 1 odds ratio. The 95% CIs for the 9 : 1 and 19 : 1 odds ratio are not shown to reduce clutter.

beginning of the breeding season. If these features are indicative of habitat quality, using these habitat cues to modify the use of social information could provide an efficient and reliable method for selecting high-quality breeding sites. In particular, location cues could provide a rapid assessment of potential breeding locations (Stamps 1988). However, because these cues can become uncoupled from underlying habitat quality (i.e. ecological traps; Schlaepfer, Runge & Sherman 2002), modifying the use of this location cues based on easily assessed habitat features could provide a safeguard against settling in low-quality habitat (Szymkowiak 2013).

This strategy may be particularly important for individuals attempting to breed for the first time or in unfamiliar locations due to the lack of public information available to these individuals, a hypothesis which we were able to test using of stable hydrogen isotopes. When dispersal status was classified using a 4 : 1 odds ratio, our data indicate that the individuals that responded to pre-breeding location cue treatments were more likely to be immigrants than individuals from the general population. Furthermore, the immigration rate of the experimental group (35·3%) was high compared to immigration rates reported for other songbirds (e.g. Hansson *et al.* 2002; Abadi *et al.* 2010), including estimates based on hydrogen isotopes (Studds *et al.* 2012; Van Wilgenburg *et al.* 2012), suggesting that this group was disproportionately composed of long-distance dispersers. However, when dispersal status was classified using the more conservative 9 : 1 and 19 : 1 odds ratios, the immigration rate did not differ between pre-breeding location cue treatments and the general population. Thus, although our data provide some evidence that immigrants were more likely to use pre-breeding location cues, we were not able to conclusively accept or reject our prediction about the role of dispersal.

The inconclusive results of our dispersal analysis are likely related to several limitations of our methods that have made it difficult for us to detect an effect of dispersal on the use of social information. First, the geographic resolution of stable isotopes is low, and therefore, many of the individuals that were classified as local may have been short-distance dispersers that were using pre-breeding location cues. Secondly, although stringent thresholds (e.g. 9 : 1 and 19 : 1) make it less likely that local individuals will be misclassified as dispersers, increasing the threshold also makes the groups appear more similar, since a larger proportion of individuals in both groups will be classified as local. As a result, even if the immigration rates in the experimental group and general population differed, the more stringent thresholds may have falsely indicated that the two groups were similar. Finally, the general population almost certainly contained individuals that used location cues to select breeding sites, adding to the difficultly of detecting differences from our experimental group. Ideally, the birds that responded to our location cue treatments would be compared to a true control group made up of individuals that used a different strategy for selecting breeding sites. Unfortunately, too few redstarts settled at our control or post-breeding public information points to make such a comparison. Given the large difference observed under the 4 : 1 odds ratio, and the limitations associated with the more stringent thresholds, we suggest that our data provide at least moderate support for the prediction that long-distance dispersers rely on pre-breeding locations cues to select breeding sites to a larger extent than philopatric individuals.

The positive response that we observed in yearlings towards pre-breeding location cues contrasts with earlier research on redstarts, which found that adults, but not yearlings, responded to this source of social information (Hahn & Silverman 2006). However, in that study, playback was broadcast on plots already occupied by redstarts, whereas we purposefully placed our experimental treatments in locations that were uninhabited by redstarts. Yearling redstarts generally begin to arrive on the breeding around 7–10 days after adults (Hahn & Silverman 2006, C.S.R. Rushing *et al.* unpublished data) and are generally subordinate to adults when selecting breeding sites (Sherry & Holmes 1997). Therefore, the presence of early arriving adults on the plots used by Hahn & Silverman (2006) may have prevented yearlings from settling in response to their playback treatments. If competition for territories is responsible for the differences between our results and those of Hahn & Silverman (2006), than we would predict that sites in our experiment that were occupied by adults would be less likely to be occupied by yearlings. However, we found no relationship between adult occupancy and yearling occupancy ($\chi^2 = 2{\cdot}197$, d.f. = 1, $P = 0{\cdot}14$), suggesting that yearlings neither avoided nor were attracted to sites occupied by adults. This result may indicate that competition does not explain the discrepancy between our results and those of Hahn & Silverman (2006). On the contrary, our experimental design may have limited the severity of competition by purposefully selecting sites that were unoccupied by redstarts and thus reducing breeding densities. Given the age-specific influence of habitat cues observed in our experiment, it is also possible that the discrepancy observed between the two studies could have resulted from differences in the habitat types included in the experiments.

In contrast to the strong response to our location cue treatments, we found little evidence that redstarts use post-breeding public information to select breeding sites. No redstarts were observed prospecting at our public information treatments and, contrary to our prediction, no adult redstarts settled in response to public information treatments. Intriguingly, the response of yearlings to public information treatments appeared to increase in the same habitat types where we saw the strongest response to location cue treatments (Fig. 3), suggesting that some yearlings may have used post-breeding cues in preferred habitat types. Unfortunately, the large uncertainty in these responses did not allow us to conclusively determine whether settlement probability at these sites differed from settlement probability at control points with similar habitat features. Thus, although we were unable conclude that yearlings responded to our public information treatments, it is possible that subsequent experiments carried out in specific habitat types could find a response to these cues.

Several hypotheses could potentially explain the lack of response to our public information treatments. First, our treatments relied solely on auditory cues and the absence of visual cues (e.g. fledglings) could have kept redstarts from responding to our simulated cues. However, Betts *et al.* (2008) found that the closely related Black-throated Blue warbler responded equally to public information treatments with auditory cues only and to treatments with both auditory and visual cues. Because post-breeding song and fledgling begging calls are easily accessed by prospectors and are reliable indicators of reproductive performance, Betts *et al.* (2008) concluded that auditory cues alone are a sufficient source of public information for songbirds. Thus, the absence of visual cues is unlikely to explain the lack of response to our public information cues, though additional experiments are necessary to conclusively rule out this hypothesis.

A second explanation for the lack of response to public information treatments is that the single synchronous brood produced by redstarts limits the availability of post-breeding social information compared to species that have multiple broods per season. To date, most research on the use of public information has been carried out on colonial species (e.g. Aparicio, Bonal & Munoz 2007; Boulinier *et al.* 2008; Calabuig *et al.* 2008) or on species that breed asynchronously or produce multiple broods each year (e.g. Nocera, Forbes & Giraldeau 2006; Parejo *et al.* 2007; Betts *et al.* 2008). In contrast, relatively few experiments have tested whether public information is used in non-colonial, single-brooding species. Our results are in line with the those of Nocera, Forbes & Giraldeau (2006), who found that location cues were the primary source of social information for yearling bobolinks (*Dolichonyx oryzivorus*), another songbird with a short, synchronous breeding period. Thus, breeding synchrony and the number of broods produced within a breeding season may be important drivers of social information use, though additional experiments are needed to determine the generality of these conclusions.

Although the synchronous breeding season of redstarts may limit the availability of social information for young redstarts, 40–60% of yearling males in our population do not acquire a mate (C. Rushing, pers. obs.) and public information from the territories of successful adults should be available to these individuals (Doligez *et al.* 2004). The lack of response to post-breeding public information treatments by these individuals was particularly surprising given that the use of public information by non-breeding adults has been documented in a number of other migratory songbirds (Boulinier & Danchin 1997; Reed *et al.* 1999). The fact that they do not use this reliable source of information therefore appears to conflict with conventional research on the use of social information by migratory birds and suggests that breeding synchrony alone may not be sufficient to explain interspecific variation in the use of social information. Therefore, a third hypothesis for the lack of public information use by redstarts is that if selection favours a location/habitat cue strategy for first-time breeders and long-distance dispersers, there may be little need to develop an alternative public information-based strategy for future breeding attempts, particularly if individuals can supplement social information with personal information gained through reproductive experience. Unfortunately, it remains unknown whether this joint location/habitat cue strategy represents a viable alternative to the use of public information, largely because few studies have simultaneously compared the use of location cues and public information within the same species (Doligez *et al.* 2004; Nocera, Forbes & Giraldeau 2006) or directly tested how the use of social information is modified by biotic and abiotic conditions (Fletcher 2007; Betts *et al.* 2008). Furthermore, because many studies that fail to document behavioural responses to experimental treatments go unpublished (M. Betts, pers. comm.), generating and testing hypotheses about interspecific variation in the use of social information are difficult at present. Publication of negative results is critical to fully assessing when and why species use different types of social information, and we encourage researchers and publishers to make these results available.

Advancing this subject through experimental and comparative studies that explore the relationship between social information use, life-history traits and habitat quality is critical to predicting the vulnerability of species to changes caused by anthropogenic activities. Given that post-breeding public information is generally a reliable indication of breeding site quality, conventional wisdom holds that species that rely on public information should be less vulnerable to non-ideal habitat selection than species that rely on location cues (Doligez *et al.* 2003). Ironically, however, precisely because public information is reliable, species that rely heavily on public information may use these cues at the expense of directly assessing habitat features. Indeed, several studies on breeding site selection in migratory birds have found that experimental simulation of social information during the post-breeding period can trump habitat cues, leading individuals to settle in suboptimal habitat (Nocera, Forbes & Giraldeau 2006; Betts *et al.* 2008). For this reason, species that rely heavily on public information may be particularly vulnerable when anthropogenic activities make environmental conditions less predictable. In contrast, because the presence of conspecifics can more easily become decoupled from habitat quality (Schlaepfer, Runge & Sherman 2002), species that rely heavily on location cues may retain the ability to directly assess habitat quality as a safeguard against selecting unsuitable breeding sites (Szymkowiak 2013). If true, these species may be more resilient in the face of changing conditions than species that rely on public information.

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Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.sf103 (Rushing *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Results of habitat principle component analysis.

Appendix S2. Additional information about stable isotope analysis and dispersal status determination.

Appendix S3. Posterior predictive checks for the settlement and dispersal models.

Appendix S4. R code used for analysis of playback and dispersal models.