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Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song

Beth A. Hahn[1,2,3,*] **and Emily D. Silverman**[1]

[1]*School of Natural Resources and Environment,* [2]*Museum of Zoology, and* [3]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA*
**Author for correspondence* (bahahn@umich.edu).

For migratory songbirds nesting in northern temperate forests, a short breeding season demands that males rapidly establish territories. Because critical insect and vegetation resources are unavailable during spring arrival, we suggest that conspecifics serve as settlement cues for males new to a local population. To test conspecific attraction, we conducted playback experiments with American redstarts *Setophaga ruticilla*. Experimental results demonstrate that song playbacks strongly attract conspecifics, recruiting an average of 4.2 additional males per plot; adult males new to our sites increased, while yearling males failed to respond. Yearlings arrived 6 to 10 days later than adults, raising the possibility that yearlings responded to songs of early arriving adults rather than to playbacks. Our work indicates that conspecific attraction is an important mechanism for breeding habitat selection in an established population of a migratory forest songbird, but the effect is moderated by age, reproductive experience and arrival timing.

Keywords: conspecific attraction; public information; territoriality

1. INTRODUCTION

The selection of suitable breeding habitat is essential to the reproductive success of most animals. Proposed cues for breeding territory selection by birds include habitat characteristics and individual experience: animals may sample food or vegetation, or they may return to the site of their birth or previous reproductive success (Greenwood & Harvey 1982; Steele 1992; Payne & Payne 1993). Social cues may also influence habitat selection: mechanisms include assessing conspecific reproductive success and settling near heterospecifics (Danchin *et al.* 1998; Mönkkönen *et al.* 1999; Nocera *et al.* 2006). Settling near conspecifics, conspecific attraction, is another social mechanism that may explain habitat selection (Stamps 1988; Smith & Peacock 1990; Danchin *et al.* 2004). Conspecific attraction could be particularly important to long-distance migratory birds if conspecifics reduce dispersal and settlement costs by signalling appropriate habitat. Conspecific attraction has been confirmed in many colonial birds (Danchin *et al.* 1998; Brown *et al.* 2000), as well as cavity-nesting territorial species (Alatalo *et al.* 1982; Muller *et al.* 1997; Doligez *et al.* 1999). Recent experiments indicate that open-nesting black-capped vireos *Vireo atricapilla* use conspecific cues when establishing territories in unoccupied habitat (Ward & Schlossberg 2004). To date, however, no study has experimentally tested conspecific attraction as a mechanism for breeding habitat selection in an established population of open-nesting, territorial birds that includes large numbers of returning breeders.

Migratory songbirds breeding in northern forests provide an ideal model for testing conspecific attraction. American redstarts *Setophaga ruticilla* are long-distance migrants that breed in second-growth deciduous forests of North America (Sherry & Holmes 1997). After migrating to northern forests in spring, redstarts select territories and acquire mates during a limited breeding season. The short season constrains habitat selection, requiring that males establish territories weeks before the appearance of vegetation and insect resources essential to reproduction. As a consequence, migrants may use early arriving males as a guide to settlement. Although song is a behavioural mechanism that excludes conspecifics from the territory of the singer (reviewed by Falls 1992), song may also function to recruit conspecifics.

The strength of conspecific attraction should vary with age and reproductive experience. Passerine males typically return to territories or habitat patches where they have nested successfully during preceding summers. In contrast, previously unsuccessful adults and inexperienced yearlings may rely on conspecific males as a cue when selecting habitat rather than evaluating multiple habitat patches. Throughout the redstart breeding range (Sherry & Holmes 1997), including the Upper Peninsula of Michigan (Smith & Moore 2005), adult males return first, followed by yearlings, a pattern supporting the possibility that naive breeders use conspecific cues.

We experimentally tested conspecific attraction by measuring territory establishment in response to song playbacks. We investigated whether male redstarts select habitat in response to song and whether their response differed by age and reproductive experience; we predicted that naive yearlings would respond most strongly, while returning adults would ignore conspecifics.

2. MATERIAL AND METHODS

From 2003–2005, we studied colour-marked American redstarts breeding in the Hiawatha National Forest of Michigan (46°40′ N, 84°94′ W). In 2003, we assessed forest characteristics and redstart abundances before establishing six 90 000 m^2 plots in areas with low redstart densities (5–8 males per plot) and six 90 000 m^2 plots in areas with high redstart densities (16–17 males per plot), within a landscape of contiguous redstart nesting habitat. Plots were located at least 500 m apart to avoid overlapping territories, which averaged 46 m in diameter, regardless of density (J. E. Law & E. D. Silverman 2005, unpublished work).

We broadcast song playbacks at the start of two breeding seasons: in 2004, three randomly selected plots from each 2003 density level received song and the remaining plots served as controls; in 2005, treatments were reversed. Redstart songs were played during spring arrival (0500–1430 during May), when males establish territories; playbacks began 12–18 days before the first male was observed. Redstart song was played continuously from the centre of the plot, using an amplified speaker (Saul Mineroff Electronics AFS Speaker) and compact disc player (Sony D-EJ001) mounted on a tree 2 m above the ground. Using a sound meter,

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Table 1. Mean number of redstart males ± standard error (*n*) by treatment, density and year; *n*, number of plots.

		density				year					
		low		high		2004		2005		total	
all males	control	7.0 ± 0.5	(6)	16.0 ± 0.9	(6)	12.2 ± 2.3	(6)	10.8 ± 1.9	(6)	11.5 ± 1.4	(12)
	playback	11.8 ± 0.8	(6)	19.5 ± 1.0	(6)	16.7 ± 2.0	(6)	14.7 ± 1.7	(6)	15.7 ± 1.3	(12)
	total	9.4 ± 0.8	(12)	17.8 ± 0.8	(12)	14.4 ± 1.6	(12)	12.8 ± 1.3	(12)	13.6 ± 1.0	(24)
yearlings	control	1.0 ± 0.0	(6)	6.0 ± 1.3	(6)	3.2 ± 1.4	(6)	3.8 ± 1.5	(6)	3.5 ± 1.0	(12)
	playback	3.0 ± 1.2	(6)	4.5 ± 0.6	(6)	3.0 ± 1.0	(6)	4.5 ± 0.8	(6)	3.8 ± 0.7	(12)
	total	2.0 ± 0.6	(12)	5.3 ± 0.7	(12)	3.1 ± 0.8	(12)	4.2 ± 0.8	(12)	3.6 ± 0.6	(24)

playback amplitude was standardized to peak at 90 dB at 1 m from the speaker. At this volume, playbacks were clearly audible 100 m away. Playback discs included 68 min of redstart songs recorded in 2003 interspersed with 12 min of silence. Redstarts sing both serial and repeat song types, in accented and unaccented modes (Sherry & Holmes 1997). Playback discs represented all combinations by age (yearling or adult), type and mode. Six unique discs were rotated daily to prevent habituation and to avoid confounding effects from any particular song(s); each plot was exposed to songs from 75 individuals (Kroodsma 1989).

We visited each plot from 0600–1500 four times weekly throughout the breeding season. We walked transects to record arrival date, location, identity and age of redstart males. Males were aged by plumage characteristics; delayed plumage maturation in redstarts simplified the distinction between yearling and adult males. New males were captured and uniquely marked with colour bands. To avoid detection biases, we alternated observers among transects and time of day for plot visits.

We tested for a playback effect on the numbers of territorial and yearling males using a fixed-factor ANOVA for a two-treatment, two-period crossover (Milliken & Johnson 1996); to improve normality and homoscedascity we applied square-root transformations. We analysed the effect of 2003 density levels (low, high), treatment (control, playback), treatment sequence (control–playback, playback–control) and the four possible interactions (density × treatment, density × sequence, treatment × sequence, density × treatment × sequence).

In this design, the treatment × sequence interaction incorporates both the residual effect of previous season playbacks (carry-over) and the difference between years (year effect). Because only 2004 playback plots should exhibit carry-over in 2005, we can estimate these two effects. The difference between mean redstart density on the playback plots in 2005 and 2004 ($\bar{x}_{\text{playback},2005} - \bar{x}_{\text{playback},2004} = \Delta\bar{x}_{\text{playback}}$) estimates the year effect, because playback plots in both 2004 and 2005 have not previously received playbacks. The carry-over is the difference between mean redstart density for the 2005 control plots, which are subject to residual playback effects, and the mean for the 2004 control plots ($\bar{x}_{\text{control},2005} - \bar{x}_{\text{control},2004} = \Delta\bar{x}_{\text{control}}$), less the year effect ($\Delta\bar{x}_{\text{control}} - \Delta\bar{x}_{\text{playback}}$). We also calculated the expected carry-over as the 2004 playback effect ($\bar{x}_{\text{playback},2004} - \bar{x}_{\text{control},2004}$) multiplied by the 2005 return rate, the percentage of all territorial males from 2004 that returned in 2005. Comparing observed and expected carry-over effects indicates whether additional birds attracted by 2004 playbacks are more, less or equally likely to return in 2005 as redstarts breeding on 2004 controls.

To estimate the playback response of adult males new to our plots in 2005, we conducted a *post hoc* analysis of the square-root transformed data using a fixed-factor ANOVA with density and treatment as factors. We also analysed arrival dates: we compared the time of arrival for individual yearling and adult males using a two-way ANOVA with plot as a random factor and age (yearling and adult for 2004; yearling, new adult and returning adult for 2005) as a fixed factor; *post hoc* comparisons were conducted with the Tukey HSD test.

3. RESULTS

More redstart males were attracted to playback relative to control plots ($F_{1,8} = 106$, $p < 0.0001$; table 1, figure 1*a*): playbacks resulted in a mean increase of 4.2 males per plot. Fewer redstarts occupied low-density plots than high-density plots in both years ($F_{1,8} = 83$, $p < 0.0001$; table 1, figure 1*a*). The number of males showed a significant density × treatment interaction ($F_{1,8} = 10$, $p = 0.01$); on average, playbacks recruited 1.3 more males to low-density plots than high. Redstart males also demonstrated a significant treatment × sequence interaction ($F_{1,8} = 13$, $p = 0.006$). We estimated that there were 2.0 ± 1.3 fewer birds in 2005 ($\Delta\bar{x}_{\text{playback}} \pm$ s.e.; table 1). The difference between 2005 and 2004 control plots was −1.4 ± 1.4 birds ($\Delta\bar{x}_{\text{control}} \pm$ s.e.; table 1), resulting in an observed carry-over of 0.6 ± 2.1 ($\Delta\bar{x}_{\text{control}} - \Delta\bar{x}_{\text{playback}}$; table 1). The expected carry-over was 1.3 birds, based on a 2004 playback effect of 4.5 birds and a 2005 return

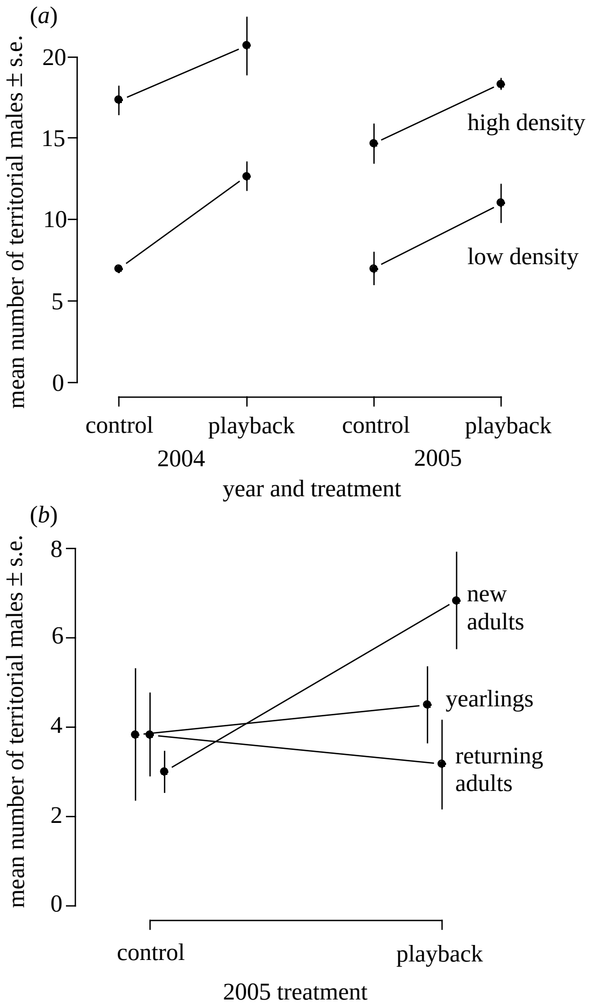

Figure 1. Settlement response to song playback experiments. (*a*) Mean number of redstart males ± standard error ($n = 6$ plots) by treatment, year and density. (*b*) Mean number of territorial redstart males ± standard error ($n = 12$ plots) in 2005 by age class and treatment.

rate of 28%, indicating that in 2005, fewer redstarts returned to 2004 playback plots than expected based on the 2005 return rate.

Over both years, there were significantly more yearlings on high-density than low-density plots ($F_{1,8}=20$, $p=0.002$; table 1), but yearlings failed to respond to song playbacks relative to controls ($F_{1,8}=0.3$, $p=0.6$; table 1). Yearling numbers were smallest on low-density control plots, while comparison of the four density×treatment means for yearlings revealed significant differences only between low-density controls and the high-density plots (table 1).

In 2005, playback plots recruited an average of 3.8 more new adult males than controls ($F_{1,8}=18$, $p=0.003$; figure 1*b*). Adult males arrived significantly earlier than yearlings in 2004 ($F_{1,83}=84$, $p<0.001$); on average, yearlings arrived 10 days after adult males. Arrival dates of yearling, new adult and returning adult males also differed in 2005 ($F_{2,117}=35$, $p<0.0001$). Yearlings arrived significantly later than both returning ($q_{117,3}=11$, $p<0.0001$) and new adult males ($q_{117,3}=10$, $p<0.0001$); on average, yearlings arrived 6 days after adults.

4. DISCUSSION

We found compelling evidence that conspecific attraction influences breeding habitat selection by American redstarts. Our study is the first to demonstrate conspecific attraction in an established population of an open-nesting territorial songbird.

The settlement response to conspecific song was strong, but varied with population density, age and reproductive experience. For all redstart males over both years, playback response was most pronounced on low-density plots. Playbacks appear to prompt settlement most where they produce the largest relative increase in conspecific song and where available space for settlement is greatest. Playbacks resulted in higher redstart densities, but these elevated densities still fell within observed ranges from 2003 regional surveys (B. A. Hahn 2003, unpublished work). Although the playbacks' artificial social cues resulted in some carry-over from 2004 (i.e. more birds returned to 2004 playback plots in 2005), this effect was dampened by lower than expected site fidelity to these plots and fewer overall redstarts in 2005.

Yearlings failed to respond to playbacks, but were found in greater numbers on plots with high redstart densities. Yearlings breeding on our sites arrived 6 to 10 days later than adult males, supporting the possibility that yearlings might settle in response to natural conspecific song: since we used only one speaker per plot, playbacks might be swamped by the singing of males already settled when yearlings arrive. While our prediction that yearlings would establish territories near playbacks was not supported, song may nonetheless be an important cue for breeding habitat selection by naive birds and time of arrival may moderate the conspecific cue.

Our results add to evidence demonstrating that conspecific attraction is an important mechanism for breeding habitat selection by many avian species with differing life histories and social behaviours. Conspecific song has previously been demonstrated to attract territorial black-capped vireos to unpopulated areas (Ward & Schlossberg 2004); we found a strong effect of conspecific song in a well-established population, in areas of high and low densities and in the presence of returning redstarts. Conspecific attraction appears to be an important mechanism for habitat selection by adults choosing new territories, despite their experience with habitat, reproductive and social cues from previous summers. This mechanism may also be affected by time of arrival: the influence of the conspecific song cue should increase as birds arrive, even as the available space for territories decreases. Such a tradeoff may help to explain the later arrival of yearling males, who lack breeding experience and may rely more on conspecific cues when establishing territories. We suggest that a better understanding of how migratory songbirds balance arrival timing and social facilitation will help to explain patterns of territory selection among different age groups.

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