

# Species interactions and population density mediate the use of social cues for habitat selection

ROBERT J. FLETCHER, JR

Avian Science Center, Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

## Summary

1. The perspective that populations and communities are structured by antagonistic interactions among individuals has dominated much of ecology. Yet how animals use social information to guide decisions, such as habitat selection, may be influenced by both positive and negative interactions among individuals. Recent theory also suggests that the way animals use social information may be substantially influenced by population density, which alters the potential costs and benefits of such behaviours.

2. I manipulated cues of two competitors, the dominant least flycatcher *Empidonax minimus* (Baird & Baird) and the subordinate American redstart *Setophaga ruticilla* (Linnaeus), to assess the use of conspecific and heterospecific cues during habitat selection, and if population density influences these strategies. The experiment consisted of surveying birds during a pre-treatment year, which allows for the control and testing the effect of baseline densities, and a treatment year, in which treatments were applied just prior to settlement. Treatments included broadcasting songs of flycatchers and redstarts, and were compared with controls.

3. When controlling for pre-treatment densities, bird densities, and to a lesser extent arrival dates, during the treatment year suggested that flycatchers were attracted to both conspecific and heterospecific cues during settlement. Furthermore, attraction was strongest for flycatchers in plots with moderate pre-treatment densities. American redstarts were rare in the study area but showed apparent attraction to conspecifics and avoidance of heterospecifics.

4. These results provide experimental evidence for the use of multiple social cues in habitat selection and suggest that heterospecific attraction may operate under broader contexts than originally envisioned. In such instances, nontarget effects can potentially occur when manipulating social cues to elicit settlement in conservation strategies. The impact of population density on the use of social cues shown here can also influence our understanding of metapopulation dynamics by causing complex threshold effects on the likelihood of rescue, which may influence metapopulation stability and the likelihood of local extinction.

*Key-words:* competition, conspecific attraction, facilitation, heterospecific attraction, inadvertent social information.

*Journal of Animal Ecology* (2007) **76**, 598–606  
doi: 10.1111/j.1365-2656.2007.01230.x

## Introduction

The view that communities are structured by antagonistic interactions among individuals, such as competition and predation, has dominated perspectives in ecology

(Bruno, Stachowicz & Bertness 2003). This perspective is exemplified in empirical and theoretical investigations of habitat selection by animals (Fretwell & Lucas 1970; Rosenzweig 1981; Danielson & Gaines 1987; Pallini, Janssen & Sabelis 1997; Martin & Martin 2001; Morris 2003; Nilsson 2006). In habitat selection theory, individuals are often assumed to behave ideally, selecting available habitat where fitness is highest, and fitness is often assumed to decline with increasing population density (Fretwell & Lucas 1970; Rosenzweig 1981; Morris

2003). Density dependence results from competition for limiting resources or increased risk of predation, such that individuals should avoid others to an extent that limits negative interactions among individuals requiring similar resources or sharing predators (Danielson & Gaines 1987; Martin & Martin 2001; Nilsson 2006). Consequently, most theory predicts that conspecific and heterospecific avoidance should be important behaviours influencing habitat selection strategies (i.e. the 'avoidance' hypothesis; Stamps 1991).

Recent behavioural evidence suggests, however, that the location or presence of others, social cues hereafter (Dall *et al.* 2005; 'location cues' of Danchin *et al.* 2004), can positively influence the likelihood of settlement (e.g. Muller 1998; Ward & Schlossberg 2004; Donahue 2006), which in turn may increase reproductive performance and community diversity (Forsman, Seppanen & Mönkkönen 2002; Thomson, Forsman & Mönkkönen 2003). These behaviours have been coined conspecific and heterospecific attraction (Stamps 1988; Mönkkönen, Helle & Soppela 1990). The conspecific and heterospecific attraction hypotheses challenge assumptions of most habitat selection theory, by suggesting a prominent role for positive density dependence, and metapopulation theory, by reducing colonization and increasing rescue effects (Ray, Gilpin & Smith 1991; Greene & Stamps 2001; Reed & Levine 2005). Furthermore, if animals use conspecific and/or heterospecific attraction, such behaviours may help explain animal sensitivity to habitat fragmentation and suggest the potential for novel alternatives to conservation (Reed & Dobson 1993; Ward & Schlossberg 2004; Ahlering & Faaborg 2006; Fletcher 2006). Understanding how social cues influence habitat selection will thus be critical for refining habitat selection theory and conserving populations in changing landscapes.

A potential complication for interpreting the role of social cues in habitat selection is that the costs and benefits may vary with population density. Recent theoretical modelling suggests that conspecific and heterospecific attraction may be most beneficial at moderate population densities, such that the strength of attraction should have a unimodal relationship with density (Mönkkönen *et al.* 1999; Fletcher 2006). This relationship is predicted because at low densities cues are often unavailable to guide habitat selection and the potential for Allee effects exists, whereas at high densities competition may outweigh any benefits from using attraction. Yet, the only field experiment to date conducted at an appropriate spatial scale spanning a range of population densities only addressed heterospecifics and found that heterospecific attraction showed linear increases with density (Thomson *et al.* 2003). These paradoxical results highlight that the potential effects of population density need to be further tested and applied to both conspecifics and heterospecifics. Such knowledge will be important for interpreting the generality of attraction (Fletcher 2006), the influence of attraction

on population dynamics (Stephens & Sutherland 1999), and understanding how individual interactions influence coexistence across large spatial scales (Mönkkönen, Forsman & Thomson 2004).

I report on a large-scale experiment that tests both for the use conspecific and heterospecific cues in habitat selection decisions and provides a crucial test of ecological theory regarding how population density influences the likelihood of using social cues. For this experiment, I focused on two migratory songbirds that are interspecific competitors, the dominant least flycatcher *Empidonax minimus* (Baird & Baird) and the subordinate American redstart *Setophaga ruticilla* (Linnaeus). Because of their competitive interactions (Sherry & Holmes 1988; Martin *et al.* 1996) and their intraspecific clustered dispersions (Sherry & Holmes 1985; Lemon, Perreault & Lozano 1996), both attraction and avoidance could be operating in their habitat selection strategies. I predicted that both species would show conspecific attraction and heterospecific avoidance during habitat selection, but that heterospecific avoidance should be more pronounced for the subordinate species. Furthermore, I predicted that attraction would be strongest at moderate densities (Forsman *et al.* 2002; Fletcher 2006).

## Methods

### FOCAL SPECIES AND STUDY AREA

Least flycatchers are competitors with American redstarts, where behavioural and removal experiments provide unequivocal evidence for flycatchers being competitively dominant over the smaller redstart (Sherry & Holmes 1988; Martin *et al.* 1996). Both species are good candidates for investigating conspecific attraction because both cluster in space on the breeding grounds (Sherry & Holmes 1985; Lemon *et al.* 1996) and frequently engage in extra-pair copulations (Sherry & Holmes 1997; Tarof *et al.* 2005), which is one potential selective pressure for conspecific attraction in territorial species (Wagner 1998; Fletcher & Miller 2006). Both species are migratory and spend relatively little time on the breeding grounds throughout much of their breeding range (Briskie 1994; Sherry & Holmes 1997); short breeding seasons may promote using social cues to elicit settlement, thereby reducing search and settlement costs (Mönkkönen *et al.* 1999; Forsman *et al.* 2002; Nocera, Forbes & Giraldeau 2006).

The study occurred in 25 deciduous riparian patches in Montana, which is the primary breeding habitat for both species in this region, along approximately 150 km of the Madison and Upper Missouri Rivers, May–July, 2003–05. Riparian patches were dominated by narrowleaf cottonwood *Populus angustifolia* (James), and a variety of willow species (e.g. *Salix amygdaloides* Anderss., *S. exigua* Nuttall). Other tree and shrub species included water birch *Betula occidentalis* (Hook.), mountain alder *Alnus incana* (Linnaeus), rose *Rosa* spp., and snowberry *Symphoricarpos albus* (L.) (Blake).

## EXPERIMENTAL DESIGN

From 2003 to 2005, I used a song playback experiment to test the avoidance and attraction hypotheses for using social cues in habitat selection. Manipulating songs of each species to change social cues within plots is a powerful and appropriate method because both species sing often, breed in forests with substantial subcanopy structure (thus limiting availability of visual cues), use vocalizations in competitive interactions, and use song in mate attraction (Briskie 1994; Martin *et al.* 1996; Sherry & Holmes 1997).

The experimental design consisted of comparing habitat use in pre-treatment years to treatment years over two paired year combinations, 2003–04 and 2004–05. This design allows for the control and testing the effect of pre-treatment densities within sites and the control of natural annual variation in population density. The design focuses on the use of social information when settling into areas after spring migration. While some experimental evidence suggests birds use information gained in the previous breeding season for settling (e.g. Doligez, Danchin & Clobert 2002), most evidence to date on the use of social cues suggests that cues are often used during the spring settlement period (Alatalo, Lundberg & Bjorkland 1982; Mönkkönen *et al.* 1990; Thomson *et al.* 2003; Ward & Schlossberg 2004; Hahn & Silverman 2006). I considered individual point count locations (50-m fixed radius; 0.79 ha) in different riparian patches (plots hereafter) as the sampling unit (see also Nocera *et al.* 2006). Plot size was large enough to accommodate multiple males within the plot boundaries, based on the known small territory sizes of both species (typically 0.07–0.18 ha for flycatchers, 0.1–0.66 ha for redstarts; Briskie 1994; Sherry & Holmes 1997; Hahn & Silverman 2006). In 2003, six plots were chosen to span a gradient of subcanopy structure, as part of a larger study on riparian bird productivity. All six plots were used in 2003–04. To select plots used for the 2004–05 paired combination, I identified plots with suitable vegetation to reduce any confounding of vegetation quality, based on the occurrence of each species from a larger random sample of 75 riparian patches (166 plots) covering over 500 km of the Missouri and Madison Rivers, 36 (72 plots) of which fell within the study area used here. Based on suitable vegetation characteristics, 19 plots within the study area were randomly selected. All plots were > 500 m apart.

The experiment consisted of two treatments – redstart playback plots ( $n = 7$ ) and flycatcher playback plots ( $n = 7$ ) – and control plots ( $n = 11$ ), which were similar to playback areas except no bird songs were manipulated. Control plots estimated natural annual variation in population densities. As in all other playback experiments testing for the use of social cues in habitat selection (Ward & Schlossberg 2004; Hahn & Silverman 2006; Nocera *et al.* 2006), control playbacks, such as songs from another species unlikely to be competitors with the focal species, were not used because of

logistical constraints. However, another behavioural playback experiment on these two species showed no general effect of playbacks (Martin *et al.* 1996).

Treatments were randomly assigned, but flycatcher treatments were stratified by pre-treatment year flycatcher abundance (mean number of detections/point) for unoccupied ( $n = 3$ ), low (1–2;  $n = 2$ ) and high (> 2 detections/point;  $n = 2$ ) abundance plots to ensure that treatments were applied across the natural range of densities and to assess if density influences the use of social cues. I chose this approach because for migratory birds, density effects on habitat selection can be assessed by estimating settlement as a function of density in the previous year (Newton 1998; Hahn & Silverman 2006), when birds show consistent patterns of habitat use (and/or site fidelity) among years. For least flycatchers, densities in one year were positively correlated with densities in the following year in control plots ( $F_{1,9} = 7.64$ ,  $P = 0.022$ ,  $r = 0.68$ ; when excluding one outlier,  $P = 0.002$ ,  $r = 0.85$ ), suggesting that densities in the previous year may be a useful indicator of density in the current year (see also Perry & Andersen 2003). Redstart treatments were not stratified by pre-treatment redstart abundance because redstarts occurred only in 33% of the plots at the start of the study (i.e. two of the six plots in 2003).

Each treatment consisted of two playback stations, 100–120 m apart, with each station pointed toward the centre of the study plot (where point counts were conducted; see below). This cue addition increased ‘apparent’ male density in each plot by 2.56 males  $\text{ha}^{-1}$ ; natural density of males in occupied control and pre-treatment plots ranged from 0.66 to 3.4 males  $\text{ha}^{-1}$  for flycatchers and 0.64–2.56 males  $\text{ha}^{-1}$  for redstarts. Playbacks commenced on 5 May in 2004 and 1 May in 2005 and continued daily until 7–10 July. I continued playbacks throughout the breeding season because males often sing throughout this period and some migratory songbirds may move within the breeding season after nest failure (Briskie 1994; Sherry & Holmes 1997; Fletcher, Koford & Seaman 2006). Although social cues, such as song, may provide different types of information early vs. late in the breeding season, density estimates from early (1 June–15 June) and later in the breeding season (16 June–10 July) were not different in treatment plots (paired  $t$ -test:  $t = -1.05$ ,  $P = 0.32$ ). Each playback station consisted of a portable stereo mounted 1–2 m up a tree or shrub, wired to a timer and a deep-cycle marine battery. Stereos broadcasted songs at full volume (approximately 90 dB) from a CD from 04.00 to 10.00 h each day, mimicking the primary vocalization period for each species (see also Ward & Schlossberg 2004). Each CD contained 60 min of song tracks and 5 min of silent tracks in a random order. Timers played stereos for 65 min, shutdown the system for 5 min, and then repeated broadcasting the CD. For both species, local dialects recorded in Montana were broadcasted.

To estimate bird densities during the breeding season, my assistants and I surveyed each plot once during two

periods in each year: 1–15 June and 16 June–10 July. I used 10-min, 50-m fixed-radius point counts for surveying birds (cf. Nocera *et al.* 2006), with one point count location centred in each plot (50–60 m from each stereo). Both species are thought to be highly conspicuous (Sherry & Holmes 1997; Perry & Andersen 2003), such that this sampling effort should be adequate for understanding habitat use. Surveys were conducted between sunrise and 5 h later, when birds are most active. Surveys were not conducted during high wind velocities ( $\geq 25 \text{ km h}^{-1}$ ) or during precipitation. Before surveys, observers turned off portable stereos. During surveys, observers recorded all birds seen or heard, including how individuals were detected (by song, visual, or call), sex of individuals, time interval of detection (four equal intervals: 0–2.5, 2.5–5 min, etc.), and distances of birds from the centre point. To ensure accurate delineation of birds within or outside plots, distances to birds were estimated using a laser range finder. Note that these density estimates do not provide information on individual movements, which would require marking individuals, or explicit data on breeding status. Instead, densities only explicitly provide information on how habitat use is influenced by the addition of social cues.

While estimating densities provides crucial information on habitat selection behaviours, arrival dates provide another valuable measure of habitat preference (Newton 1998). In 2005, I estimated arrival dates on a subset of plots (four flycatcher, four redstart, six controls) by conducting point counts at each plot every 1–3 days (mean = 2.8 days;  $n = 137$  surveys) between 3 and 31 May. At least one plot of each treatment was surveyed daily during this period. A species was considered to have arrived in a plot if it was detected on at least two consecutive visits.

Finally, at each point-count station I measured vegetation after the bird surveys to determine if there was any bias in treatment applications such that differences in vegetation structure could explain patterns of habitat use. To do so, I estimated metrics related to canopy, shrub and ground cover (see Appendix 1). Overall, there was no evidence for differences in vegetation structure among plot types (Table S1; Wilks'  $\lambda = 0.56$ ,  $F_{16,30} = 0.62$ ,  $P = 0.84$ ).

#### STATISTICAL ANALYSES

Based on point counts during the breeding season surveys, I estimated bird density (birds per hectare) by correcting raw counts with estimated detection probabilities, which were estimated using a removal model in Program MARK (see Appendix 2). I was unable to estimate detection probabilities for American redstarts due to their rarity in the study area (see below). For redstarts, I focus on changes in occurrence among treatments. Results for redstarts should be treated cautiously due to their rarity, but I provide these results for comparison among other relevant investigations (Sherry & Holmes 1988; Hahn & Silverman 2006).

To test for the attraction and avoidance hypotheses during the breeding season, I used a two-step approach. I first developed models to test hypotheses for using social cues while controlling for pre-treatment population densities and natural annual variation in population density. I tested for the effects of treatments on flycatcher density during the treatment year using ANCOVA, with flycatcher density during the pre-treatment year as a covariate, which controls for effects of pre-treatment density in responses to treatments. For redstarts, I focused on changes in redstart occurrence (–1, local extinction; 0, no change; 1, local colonization) using ordinal logistic regression (i.e. cumulative logit analysis; Allison 1999). I used this approach in lieu of using logistic regression for treatment year occurrence data, because that approach is less sensitive to detecting avoidance and would require more parameters for estimation. The hypotheses for using social cues in habitat selection were analysed using three a priori contrasts within the ANCOVA and ordinal logistic regression: (1) conspecific responses (conspecific – control); (2) heterospecific responses (heterospecific – control); and (3) differences in cue use (conspecific – heterospecific). Subtracting responses in controls in the first two contrasts accounts for natural annual variation in population densities.

My second step included testing for the effects of population density on the use of social cues by flycatchers by comparing models that reflect different hypotheses for density effects to a density-independent model. If population density influences the use of social cues in this experiment, density in the treatment year should vary based on pre-treatment densities for treatments relative to controls (a significant treatment  $\times$  density interaction), whereas for density-independent responses, the treatment year densities should be independent of pre-treatment densities. I compared a treatment-only model (density-independent) to a model that incorporated pre-treatment density and its interaction with treatment as covariates (linear density-dependent), and a model that included pre-treatment density<sup>2</sup> and its interaction with treatment as covariates (nonlinear density-dependent model; see Forsman *et al.* 2002; Fletcher 2006) using Akaike's Information Criterion (adjusted for sample size; AIC<sub>c</sub>) and AIC<sub>c</sub> model weights (Burnham & Anderson 1998). A model selection approach was used here because it allows for simultaneously comparing different models that reflect biological hypotheses (Johnson & Omland 2004).

Patterns of arrival were analysed using a proportional hazards model (Allison 1995), with treatment as a fixed effect and pre-treatment year density (birds per hectare) as a covariate. I included pre-treatment density as a covariate because for some species older animals may arrive earlier to the breeding grounds and are more likely to show site fidelity (Switzer 1993; Lemon *et al.* 1996). A proportional hazards model is appropriate for time-to-event data, such as arrival dates, and it allows for the censoring of data (Allison 1995), which is particularly useful for arrival data in situations where

**Table 1.** Comparison of models describing the influence of population density on the use of social cues by least flycatchers, based on the relative Akaike's Information Criterion (adjusted for sample size;  $\Delta AIC_c = AIC_{ci} - \min AIC_c$ ),  $AIC_c$  model weights ( $w_i$ ), and variation explained ( $R^2$ )

Model	$AIC_c$	$\Delta AIC_c$	$w_i$	$K^*$	$R^2$
Density-independent	100.4	13.2	0.001	3	0.12
Linear density effects	89.6	2.4	0.234	6	0.61
Nonlinear density effects	87.2	0.0	0.765	9	0.79

\* $K$  = number of parameters in the model.

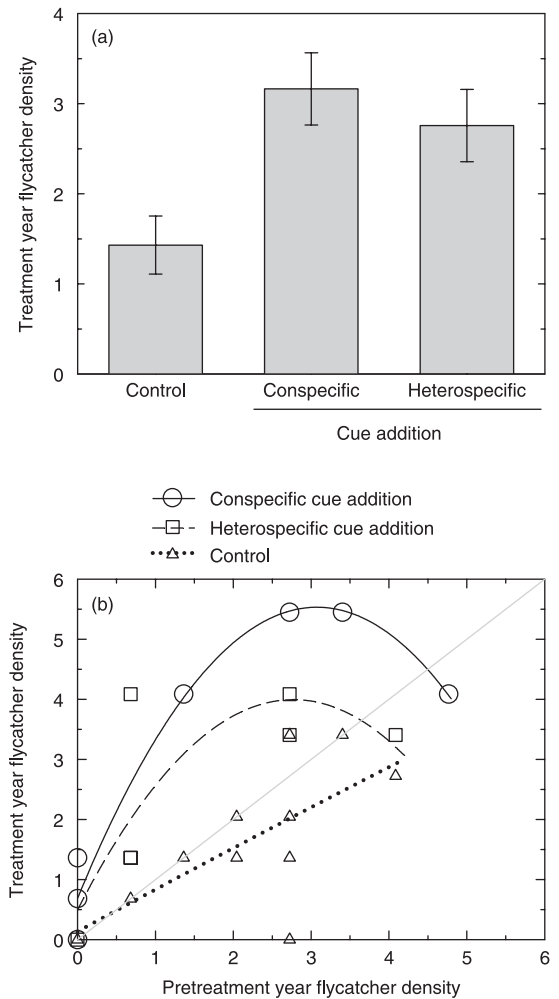
no animals may arrive to some sites during the sampling period. Arrival date was considered the midpoint between the last unoccupied and first occupied visit.

**Results**

For breeding surveys conducted from 2003 to 2005, my assistants and I accumulated 154 detections of least flycatchers but only 10 detections of American redstarts, with flycatchers being detected in 23 of the 25 sites, and redstarts in five of the 25 sites, in at least one year. For least flycatchers, the best model to explain detection probability was a constant detection probability (Table S2), estimated at 0.94. I used this estimate of detection probability for estimating flycatcher density in the remaining analyses. Note that using detections for least flycatchers without correcting for detection probability produced similar results.

In the year prior to the treatment, densities of flycatchers were similar among plot types ( $F_{2,22} = 0.49$ ,  $P = 0.49$ ). Yet the treatments had a strong effect on least flycatcher density ( $F_{2,21} = 6.51$ ,  $P = 0.006$ ; Fig. 1a), with flycatchers showing positive responses to both conspecific ( $F_{1,21} = 11.28$ ,  $P = 0.003$ ) and heterospecific treatments ( $F_{1,21} = 6.55$ ,  $P = 0.018$ ), but there was no evidence for different responses to conspecific and heterospecific cues ( $F_{1,21} = 0.52$ ,  $P = 0.48$ ). Not only was the average density approximately two times greater in treatment plots than in controls (Fig. 1a), but the addition of conspecific cues resulted in some plots having higher densities than the natural range of observed densities in control plots (control plot density range: 0–4.09 birds ha<sup>-1</sup>; conspecific addition density range: 0–5.44 birds ha<sup>-1</sup>). Comparing models that reflect different hypotheses for the effect of population density suggest that nonlinear density effects were most supported by the data (Table 1). Based on the nonlinear model, attraction was strongest by flycatchers in plots with moderate pre-treatment densities (Fig. 1b).

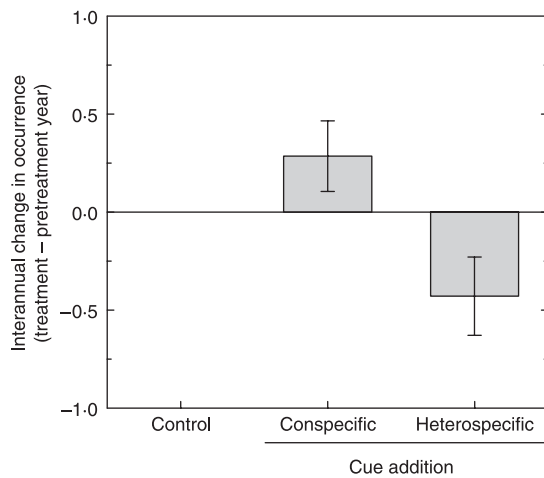
Although American redstarts were rare in the study area, interannual changes in the occurrence of redstarts differed among treatments (Nagelkerke's  $R^2 = 0.59$ ,  $\chi^2_1 = 13.81$ ,  $P = 0.001$ ; Fig. 2), with redstarts responding differently to conspecific and heterospecific cues ( $\chi^2_1 = 13.62$ ,  $P = 0.002$ ). Redstarts showed negative responses to heterospecific treatments ( $\chi^2_1 = 6.66$ ,  $P =$



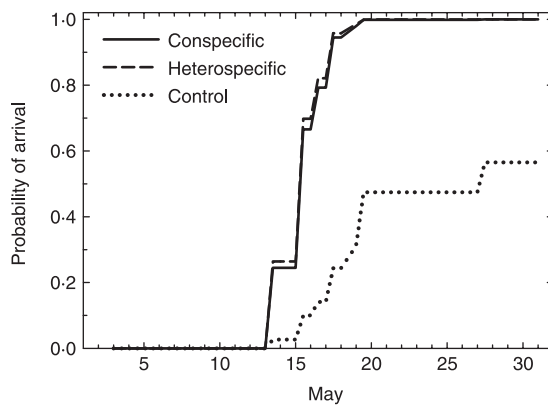
**Fig. 1.** Response of least flycatchers to experimental playback treatments in riparian habitats, 2003–05. (a) Least squares estimates ( $\bar{x} \pm 1$  SE) for flycatcher densities (birds per hectare; corrected for detection probability) with added conspecific cues ( $n = 7$ ), heterospecific cues ( $n = 7$ ), and controls (no added cues;  $n = 11$ ), controlling for pre-treatment year flycatcher density. (b) Density of least flycatchers during the treatment year as a function of pre-treatment year density, which highlights the nonlinear effect of population density on attraction. Data points are mean estimates for each plot, and predicted lines come from an ANCOVA that included an interaction of treatment and density<sup>2</sup> (see Table 1). Solid grey diagonal line shows 1 : 1 relationship, or no change between years.

0.010) and weaker, positive responses to conspecifics ( $\chi^2_1 = 4.18$ ,  $P = 0.041$ ; Fig. 2).

For surveys conducted during the arrival period in 2005, we accumulated 75 detections of least flycatchers but no detections of redstarts. When including pre-treatment flycatcher density as a covariate ( $\chi^2_1 = 4.59$ ,  $P = 0.032$ ), there was marginal evidence for flycatcher arrivals differing among plot types ( $\chi^2_1 = 4.76$ ,  $P = 0.093$ ), where flycatchers arrived to plots with conspecific ( $\chi^2_1 = 4.13$ ,  $P = 0.042$ ) and heterospecific cues ( $\chi^2_1 = 4.09$ ,  $P = 0.043$ ) sooner relative to controls (Fig. 3), suggesting that even the first settlers use social cues when available.



**Fig. 2.** Interannual changes in occurrence ( $\bar{x} \pm 1$  SE) of American redstarts in plots with added conspecific cues ( $n = 7$ ), heterospecific cues ( $n = 7$ ), and controls (no added cues;  $n = 11$ ), 2003–05.



**Fig. 3.** Patterns of arrival for least flycatchers in relation to conspecific cues ( $n = 4$ ), heterospecific cues ( $n = 4$ ) and controls ( $n = 6$ ), 2005. Predicted estimates are taken from a proportional hazards model, testing for treatment and controlling for pre-treatment year flycatcher density (birds per hectare) as a covariate.

## Discussion

Social cues and interactions are not typically incorporated into habitat selection theory, and even when cues and interactions are addressed, negative interactions have been emphasized (Rosenzweig 1981; Morris 2003). Yet there is accumulating experimental evidence that animals do indeed use social cues to elicit settlement (Alatalo *et al.* 1982; Stamps 1988; Mönkkönen *et al.* 1990; Muller 1998; Forsman *et al.* 2002; Ward & Schlossberg 2004; Nocera *et al.* 2006), as well as other social information, such as the performance of others (i.e. public information; Doligez *et al.* 2002; Danchin *et al.* 2004). This study provides a unique example that the way animals use social cues for selecting habitats can be diverse and dynamic, depending on source of information (i.e. conspecifics or heterospecifics) and population density.

Interestingly, least flycatchers were not only attracted to conspecific cues but also heterospecific cues, even though flycatchers are known competitors with redstarts. The use of heterospecific cues has generally focused on avoidance behaviours in most taxa, from mites (Pallini *et al.* 1997) to mammals (Danielson & Gaines 1987). To date, theoretical and empirical research on heterospecific attraction has primarily focused on how migratory birds may use information on residents when settling for breeding (e.g. Mönkkönen *et al.* 1990; Mönkkönen *et al.* 1999; Forsman *et al.* 2002; Thomson *et al.* 2003). However, in this experiment both species are migratory and flycatchers typically arrive to Montana earlier each spring than redstarts. Because flycatchers are dominant over redstarts and have similar foraging strategies (Sherry & Holmes 1988; Martin *et al.* 1996), redstart cues may contain valuable information with little fitness costs involved. While these cues may not be normally available to flycatchers during migration in Montana, flycatchers may typically use these cues during breeding and post-breeding forays (Nocera *et al.* 2006). Alternatively, in other areas of their breeding ranges, redstarts arrive to the breeding grounds prior to flycatchers (B.A. Hahn, personal communication), such that flycatchers could use these cues in spring settlement decisions in some areas. But, why should flycatchers have used this information when redstarts were rare in this area? Least flycatchers and American redstarts overlap broadly in their breeding range (Briskie 1994; Sherry & Holmes 1997), and in other parts of Montana, both species are locally abundant (Fletcher, unpublished data). Thus, redstart cues are likely available to flycatchers in many areas, such that redstart cues may often provide reliable information. The rarity of redstarts in this area may also actually increase the quality of information relative to areas where redstarts are common and thus occur across a gradient of habitat quality. In any case, results presented here suggest that heterospecific attraction may be more common by operating under broader contexts than originally envisioned. Consequently, the potential use of heterospecific attraction should be considered in any system with asymmetrical interspecific competition.

Recent theory predicts that at very low population densities, individuals gain little from using social cues, because these cues are typically unavailable to guide habitat selection, whereas at very high population densities, habitat saturation and the potential costs of competition may outweigh any benefits from using attraction (Mönkkönen *et al.* 1999; Greene & Stamps 2001; Fletcher 2006). Therefore, social attraction should be strongest at moderate population densities. This is the first experimental evidence that describes such density-dependent attraction, even though it is often speculated about in theoretical and empirical investigations (Mönkkönen *et al.* 1999; Forsman *et al.* 2002; Thomson *et al.* 2003). Yet, this could be common for many taxa. For example, Donahue (2006) recently provided experimental evidence for conspecific attraction

in porcelain crabs *Petrolisthes cinctipes* (Randall), and simulation models suggested that attraction should be strongest at moderate densities in some situations.

For least flycatchers, declines in attraction at high population densities are most easily explained by interference intraspecific competition for limited resources because of habitat saturation, while the strong attraction at moderate population densities could arise for at least two different proximate reasons. First, sites with moderate population densities should contain more conspecific social cues, thereby providing a greater social stimulus for arriving birds in both treatments. This explanation suggests that individuals respond more to conspecific/heterospecific abundance rather than their mere presence, and predicts that experiments broadcasting songs of more individuals in unoccupied sites will elicit greater responses. Second, sites with moderate densities may have been more suitable sites to flycatchers, in terms of habitat or other resources, such that the combined suitability and added social cues elicited stronger responses. However, treatments were randomly assigned and positive responses were not observed in control plots of moderate pre-treatment densities, reducing the likelihood of this explanation. Regardless of why density effects occur, such density-dependent variation could influence metapopulation dynamics. Biologists have noted that attraction can decrease colonization rates and increase rescue effects in metapopulations (Ray *et al.* 1991; Reed & Levine 2005); density-dependent attraction behaviours may additionally result in complex rescue effects by inducing a potential threshold in rescue from attraction, which may increase or decrease stability and the likelihood of extinction, depending on total population size in the landscape (Fletcher 2006).

A variety of ultimate factors have been invoked to explain why attraction may evolve and why such behaviours may be most beneficial at moderate population densities (Stamps 1988). Increased mating success is often used to explain attraction at moderate to low densities in many species (Stephens & Sutherland 1999), and some evidence suggests that least flycatchers may have 'hidden leks', where males settle in aggregations due to extra-pair copulatory behaviours (Tarof *et al.* 2005; Fletcher & Miller 2006). Yet, similar patterns of attraction were seen with heterospecific cues, suggesting that other factors may at least partly explain the use of social cues in settlement by this species. The use of social cues as an indirect measure of habitat quality or potential interspecific Allee effects (e.g. predator dilution) might help explain the consistent attraction by flycatchers to both conspecific and heterospecific cues.

Despite the fact that American redstarts were relatively rare in the study area, redstarts were attracted to conspecific cues and consistently avoided heterospecific cues. While these results should be interpreted cautiously, results are consistent with known settlement patterns of redstarts in other areas. For example, Hahn & Silverman (2006) recently documented redstarts

using conspecific attraction in a landscape containing relatively high densities of redstarts. Sherry & Holmes (1988) also documented evidence for heterospecific avoidance by redstarts when they removed least flycatchers from plots and found that redstarts increased in abundance in those areas. Results presented here on flycatcher attraction to redstarts suggest that there may be an ongoing ecological and evolutionary arms race, whereby redstarts provide inadvertent cues that flycatchers use to their advantage. The consequences of this information transfer will likely depend on which species tends to settle first in an area and whether this information transfer occurs predominantly between or within years in natural systems (see, e.g. Nocera *et al.* 2006). Where redstarts settle later than flycatchers, or where flycatchers attain information from redstarts from the previous year, redstarts may be able to reduce costs by dispersing to new areas.

Because habitat selection has strong fitness consequences and influences virtually all subsequent decisions animals make for breeding, documenting the proximate cues animals use for habitat selection is an important first step for understanding the broad implications of these behaviours. For example, there has been a recent call for manipulating social cues to promote settlement by rare species to suitable habitat, which may provide a viable complement to habitat-based conservation strategies (Stamps 1988; Reed & Dobson 1993; Ward & Schlossberg 2004). Yet results from this experiment suggest that manipulating social cues can potentially have nontarget effects on other members of the community. Implications of attraction can also manifest in important, although unappreciated, ways in contemporary landscapes. Fletcher (2006) illustrated that individuals using conspecific attraction should display patterns of sensitivity to habitat fragmentation. Interestingly, fragmentation sensitivity has been suggested for least flycatchers and American redstarts in this region (Tewksbury *et al.* 2002), as well as for some other vertebrates that use conspecific attraction in other regions (cf. Fletcher 2005; Nocera *et al.* 2006). Identifying the ultimate causes for using social cues will also be critical for predicting when, where, and in what species attraction or avoidance likely operates. In doing so, we will better understand the generality and complexity of these processes, their importance to ecological theory, and when these behaviours should be incorporated into conservation strategies.

### Acknowledgements

Thanks to T. Smucker, A. Peterson, and J. Csoka for their hard field work, and to the numerous landowners that allowed bird songs to be broadcasted from their properties. PPL-Montana, the Bureau of Land Management, and the US Department of Agriculture provided support for this project. Thanks to S. Schlossberg for advice on playback stations. This manuscript benefited from constructive reviews by J. Fontaine, G.

Hays, C. Miller, M. Mönkkönen, J. Nocera, J. Orrock, Y. Ortega, B. Robertson, J. Sauer, S. Schlossberg, and two anonymous reviewers.

## References

- Ahlering, M.A. & Faaborg, J. (2006) Avian habitat management meets conspecific attraction: If you build it, will they come? *Auk*, **123**, 301–312.
- Alatalo, R.V., Lundberg, A. & Bjorkland, M. (1982) Can the song of male birds attract other males? An experiment with the Pied Flycatcher, *Ficedula hypoleuca*. *Bird Behavior*, **4**, 42–45.
- Allison, P.D. (1995) *Survival Analysis Using SAS: a Practical Guide*. SAS Institute Inc., Cary, NC.
- Allison, P.D. (1999) *Logistic Regression Using the SAS System*. SAS Institute, Inc., Cary, NC.
- Briskie, J.V. (1994) Least flycatcher (*Empidonax minimus*). In *The Birds of North America*, Number 99 (eds A. Poole & F. Gill). Academy of Natural Sciences, Philadelphia, PA; American Ornithologists' Union, Washington, DC.
- Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M. & Stephens, D.W. (2005) Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, **20**, 187–193.
- Danchin, E., Giraldeau, L.A., Valone, T.J. & Wagner, R.H. (2004) Public information: from nosy neighbors to cultural evolution. *Science*, **305**, 487–491.
- Danielson, B.J. & Gaines, M.S. (1987) The influences of conspecific and heterospecific residents on colonization. *Ecology*, **68**, 1778–1784.
- Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.
- Donahue, M.J. (2006) Allee effects and conspecific cueing jointly lead to conspecific attraction. *Oecologia*, **149**, 33–43.
- Fletcher, R.J. Jr (2005) Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology*, **74**, 342–352.
- Fletcher, R.J. Jr (2006) Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist*, **168**, 207–219.
- Fletcher, R.J. Jr & Miller, C.W. (2006) On the evolution of hidden leks and the implications for reproductive and habitat selection behaviours. *Animal Behaviour*, **71**, 1247–1251.
- Fletcher, R.J. Jr, Koford, R.R. & Seaman, D.A. (2006) Critical demographic parameters for declining songbirds breeding in restored grasslands. *Journal of Wildlife Management*, **70**, 145–157.
- Forsman, J.T., Seppanen, J.T. & Mönkkönen, M. (2002) Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London Series B*, **269**, 1619–1623.
- Fretwell, S.D. & Lucas, H.L. Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.
- Greene, C.M. & Stamps, J.A. (2001) Habitat selection at low population densities. *Ecology*, **82**, 2091–2100.
- Hahn, B.A. & Silverman, E.D. (2006) Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters*, **2**, 337–340.

- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Lemon, R.E., Perreault, S. & Lozano, G.A. (1996) Breeding dispersions and site fidelity of American redstarts (*Setophaga ruticilla*). *Canadian Journal of Zoology*, **74**, 2238–2247.
- Martin, P.R. & Martin, T.E. (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, **82**, 189–206.
- Martin, P.R., Fotheringham, J.R., Ratcliffe, L. & Robertson, R.J. (1996) Response of American redstarts (suborder Passeri) and least flycatchers (suborder Tyranni) to heterospecific playback: The role of song in aggressive interactions and interference competition. *Behavioral Ecology and Sociobiology*, **39**, 227–235.
- Mönkkönen, M., Helle, P. & Soppela, K. (1990) Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? *Oecologia*, **85**, 218–225.
- Mönkkönen, M., Hardling, R., Forsman, J.T. & Tuomi, J. (1999) Evolution of heterospecific attraction: using other species as cues in habitat selection. *Evolutionary Ecology*, **13**, 91–104.
- Mönkkönen, M., Forsman, J.T. & Thomson, R.L. (2004) Qualitative geographical variation in interspecific interactions. *Ecography*, **27**, 112–118.
- Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.
- Muller, K.L. (1998) The role of conspecifics in habitat settlement in a territorial grasshopper. *Animal Behaviour*, **56**, 479–485.
- Newton, I. (1998) *Population Limitation in Birds*. Academic Press, Inc., San Diego, CA.
- Nilsson, P.A. (2006) Avoid your neighbours: size-determined spatial distribution patterns among northern pike individuals. *Oikos*, **113**, 251–258.
- Nocera, J.J., Forbes, G.J. & Giraldeau, L.-A. (2006) Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society of London Series B*, **273**, 349–355.
- Pallini, A., Janssen, A. & Sabelis, M.W. (1997) Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia*, **110**, 179–185.
- Perry, E.F. & Andersen, D.E. (2003) Advantages of clustered nesting for least flycatchers in north-central Minnesota. *Condor*, **105**, 756–770.
- Ray, C., Gilpin, M. & Smith, A.T. (1991) The effect of conspecific attraction on metapopulation dynamics. In: *Metapopulation Dynamics: Empirical and Theoretical Investigations* (eds M. Gilpin & I. Hanski), pp. 123–134. Academic Press, Inc., New York.
- Reed, J.M. & Dobson, A.P. (1993) Behavioral constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution*, **8**, 253–256.
- Reed, J.M. & Levine, S.H. (2005) A model for behavioral regulation of metapopulation dynamics. *Ecological Modelling*, **183**, 411–423.
- Rosenzweig, M.L. (1981) A theory of habitat selection. *Ecology*, **62**, 327–335.
- Sherry, T.W. & Holmes, R.T. (1985) Dispersion patterns and habitat responses of birds in northern hardwoods forests. In: *Habitat Selection in Birds* (ed. M.L. Cody), pp. 283–310. Academic Press, Inc., London.
- Sherry, T.W. & Holmes, R.T. (1988) Habitat selection by breeding American redstarts in response to a dominant competitor, the least flycatcher. *Auk*, **105**, 350–364.
- Sherry, T.W. & Holmes, R.T. (1997) American Redstart (*Setophaga ruticilla*). *The Birds of North America*, Number 277 (eds A. Poole & F. Gill). Academy of Natural Sciences, Philadelphia, PA; American Ornithologists' Union, Washington, DC.

- Stamps, J.A. (1988) Conspecific attraction and aggregation in territorial species. *American Naturalist*, **131**, 329–347.
- Stamps, J.A. (1991) The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology*, **28**, 29–36.
- Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.
- Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.
- Tarof, S.A., Ratcliffe, L.M., Kasumovic, M.M. & Boag, P.T. (2005) Are least flycatcher (*Empidonax minimus*) clusters hidden leks? *Behavioral Ecology*, **16**, 207–217.
- Tewksbury, J.J., Black, A.E., Nur, N., Saab, V.A., Logan, B.D. & Dobkin, D.S. (2002) Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. *Studies in Avian Biology*, **25**, 158–202.
- Thomson, R.L., Forsman, J.T. & Mönkkönen, M. (2003) Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. *Oecologia*, **134**, 431–438.
- Wagner, R.H. (1998) Hidden leks: sexual selection and the clustering of avian territories. *Avian Reproductive Tactics: Female and Male Perspectives* (eds P.G. Parker & N.T. Burley), pp. 123–145. Ornithological Monographs 49. American Ornithologists' Union, Washington, DC.
- Ward, M.P. & Schlossberg, S. (2004) Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology*, **18**, 519–525.

Received 31 October 2006; accepted 6 February 2007