

Original Article

Habitat selection in site-faithful ovenbirds and recruits in the absence of experimental attraction

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Partial harvesting of forest stands has been shown to cause significant changes in the density of many bird species. However, the behavioral response of individuals to alteration of their habitat has rarely been investigated. Without this information, it is difficult to determine whether shifts in density reflect a response to habitat structure or the use of personal or public information. In this study, we compared the territory settlement sequence of male ovenbirds (*Seiurus aurocapilla*) with or without prior experience in our study plots upon their return from spring migration. We monitored settlement patterns in 2 pairs of 25-ha plots, 1 plot of each pair having been treated through selection harvesting (30–40% removal) in the winter of 2006–2007. From the second to the fourth year postharvest, control plots were first occupied at least 2–5 days earlier than treated plots. Males who bred successfully in a given year were more likely to return to the same plot the following year, independently of treatment. On average, banded males returning from previous years also tended to settle later in treated plots, but there was no treatment effect on the average settlement date of unbanded recruits. Recruits were never found to settle before the first returning male. Although patterns of first occupation suggest that ovenbirds preferred control plots, conspecific attraction (for recruits) and personal information (for returning individuals) seemed to play a greater role than vegetation structure in the habitat selection process. *Key words*: conspecific attraction; personal information; public information; ideal free distribution; *Seiurus aurocapilla*; structural cues hypothesis. [*Behav Ecol*]

INTRODUCTION

It is generally assumed that animals select their breeding territory in an attempt to maximize their fitness (Pulliam 1988; Křivan et al. 2008). The Ideal Free Distribution Theory assumes that 1) territory quality declines as local density increases, 2) individuals select territories that are most suitable to them (i.e., they are “ideal”), and 3) individuals within a habitat have identical expected fitness (they are “free”) (Fretwell and Lucas 1969). Although some of these assumptions are rarely met in nature, selection would be expected to favor individuals that make the best decisions. Some authors have reported distributions that appeared to conform to the ideal expectation (Lanyon and Thompson 1986; Calsbeek and Sinervo 2002; Beckmann and Berger 2003; Morris 2006; Griffen 2009). However, studies often relate the observed distribution of individuals to habitat parameters only once most of the individuals in a population have settled in a territory (e.g., Hobson and Bayne 2000; Holmes and Pitt 2007; Pérot and Villard 2009; but see Lanyon and Thompson 1986; Zając et al. 2006). Although this approach provides useful data on habitat requirements of a given species, it yields little information on the processes leading to the observed distribution. Without such information, it is difficult to identify the proximate cues used by animals to make their decisions.

Whether they have to decide among potential mates, foraging patches, or breeding territories, animals must first acquire information about the different alternatives available to them. They may do this either by interacting with the environment, thereby gathering “personal” information, or by monitoring the outcome of other individuals’ interaction with it (“social” information) (Danchin et al. 2004). Both these processes have been extensively studied. Some species may assess food abundance when selecting their territory (Bonnot et al. 2009), whereas others appear to use habitat parameters that are correlated with food abundance (Smith and Shugart 1987). For individuals that have reproduced at least once, the decision to return to a territory or habitat patch has also been shown to be strongly influenced by prior breeding success, another type of personal information (Pärt and Gustafsson 1989; Switzer 1997; Haas 1998; Porneluzi 2003). Information on personal breeding performance may also guide individual decisions between successive breeding attempts within a season (Jackson et al. 1989; Betts et al. 2008a).

Experimental studies further suggest that inadvertent social information provided by conspecifics could be particularly influential when individuals prospect for a future territory (Hahn and Silverman 2006; Nocera et al. 2006; Betts et al. 2008a; Boulonier et al. 2008). Aggregations of conspecifics could provide information on the location of potential territories and resources (location cues; Danchin et al. 2004). For example, male songbirds of several species have been shown to settle in habitats of marginal quality when conspecific playbacks were broadcasted shortly before (Fletcher 2007) or after the previous breeding season

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(Nocera et al. 2006; Betts et al. 2008b). Individuals may also cue in on the performance of conspecifics to estimate the quality of nearby patches (public information; Danchin et al. 2004). This type of information may be especially available to colonial species (Danchin and Wagner 1997; Brown et al. 2000), although it has also been shown to play a role in noncolonial species as well (Doligez et al. 2002, 2004; Pärt et al. 2011).

In this study, we investigate the selection of breeding territories in a marked population of ovenbird (*Seiurus aurocapilla*), a solitary-nesting passerine bird. Males returning from spring migration had the possibility of settling in 2- to 4-year-old selection cut plots (30–40% basal area removal) or in untreated control plots within northern hardwood forest. Previous studies on this species across its North American range have shown that partial harvesting causes a reduction in territory density, suggesting a reduction in habitat quality (Gram et al. 2003; Vanderwel et al. 2007; Pérot and Villard 2009). Haché and Villard (2010) have examined population-level processes potentially accounting for this reduction in density following selection harvesting. They found a reduction in recruitment rate in the first year post-harvest, followed by a reduction in return rate in later years, presumably because unsuccessful males tended to disperse to alternate breeding sites (e.g., Haas 1998) to increase their probability of nesting success (Chalfoun and Martin 2010). However, information use by individuals, which underlies the observed demographic changes, has rarely been documented.

We assessed the relative contribution of 3 potential sources of information (structural cues from the vegetation, location cues from conspecifics, and personal reproductive success) to habitat selection by ovenbird males from 2 categories: individuals with or without breeding experience in our study plots (hereafter returning males and recruits, respectively). We used the order of territory settlement (date of occupancy) upon the return from spring migration to assess the preference for a certain habitat type (Zajac et al. 2006; Arlt and Pärt 2007). Because returning males and recruits may respond to different habitat cues, we formulated predictions specific to each category.

In accordance with the “structural cues hypothesis,” we predicted that control plots would be occupied earlier and filled at a faster rate than treated plots, owing to the alteration of stand structure resulting from selection harvesting. This is an extension of Smith and Shugart’s (1987) hypothesis, which pertains specifically to the prediction of food abundance by birds using vegetation cues. With respect to location cues provided by conspecifics, we predicted that recruits in our study plots would cue on returning males to select their territory, thereby settling later. Finally, on the basis of personal information acquired by males, we predicted that returning individuals who failed to reproduce successfully in year t would have a lower probability to settle in the same study plot in year $t + 1$ (Porneluzi 2003). It should be noted that the use of structural cues by birds does not exclude the use of personal information or location cues.

METHODOLOGY

Study design

This study was conducted in the Black Brook District (47°23'N, 67°40'W), in northwestern New Brunswick, Canada (see Haché and Villard [2010] for a detailed description). We took advantage of the presence of a study design established in 2006 to determine the demographic response of ovenbirds through individual marking of the male subpopulation. Here, we monitored ovenbirds during the breeding season in four 25-ha plots located in mature stands dominated by broadleaved deciduous tree species (sugar maple, *Acer saccharum*; American

bee, *Fagus grandifolia*; yellow birch, *Betula alleghaniensis*). The study plots represent a subset of those monitored by Haché and Villard (2010). Plots within each pair were located 6.4 and 4.4 km apart, whereas plot pairs were separated by 13.2 km. This design allowed accounting for potential effects of landscape context while avoiding contamination of control plots by treatments. Indeed, we never detected movements of banded individuals between any of our plots.

The treatment, conducted in the winter of 2006–2007, was randomly assigned within each pair, and harvesting intensity (30–40% basal area removal) was adjusted so that residual stand structure would be as similar as possible among treated plots. The treatment consisted of clear-cut parallel bands (skid trails) approximately 5 m in width, separated by 20 m of selectively harvested (10–20% basal area removal) forest. This resulted in similar mean postharvest basal areas for the 2 treated plots. Plots had a 50-m buffer all around their boundaries. In control plots, this buffer was left uncut, whereas in treated plots, selection harvesting extended into the buffer. Owing to the intensity of forest management, we were unable to establish 4 equal-shaped plots. Therefore, although all plots covered 25 ha, plot perimeter varied slightly: 2000 and 2400 m for treated plots, and 2150 and 2300 m for controls (Figure 1).

Our focal species, the ovenbird, is a neotropical migrant songbird breeding in mature and old deciduous or mixed-wood forests (Porneluzi et al. 2011). It is relatively common in the study area (Guénette and Villard 2005) and prefers forest stands with a relatively closed canopy and deep leaf litter (Mattsson and Niemi 2006) for nesting and to forage on invertebrates (Porneluzi et al. 2011). We restricted our study to males because they are easier to detect and capture than females, and we preferred not to capture females at the nest to avoid potential impacts on reproductive success.

Bird surveys

In early May 2008 to 2010, we monitored the settlement patterns of male ovenbirds using a modification of the spot mapping method (Bibby et al. 2000). We recorded the location of each male in 25- × 25-m grid cells, as well as the unique color combination of leg bands on individuals returning from previous years. Ovenbirds are highly territorial, and they sing to advertise their territory (Hann 1937; Lein 1981). Males resume singing shortly after their return from spring migration (Porneluzi et al. 2011), and countersinging groups of males form quickly (Thériault S, Haché SA, Villard M-A, personal observations). Hence, we assumed that the absence of singing males indicated that no territory had been claimed.

In 2009, surveys started 1 day before males were first detected in our plots, whereas in 2008 and 2010, a few individuals were detected on the day of our first survey. Because individuals had been detected outside of our plots prior to those dates in both years, we cannot confirm that these were first-settlement dates, but they were considered as such for the purposes of the analyses. Surveys were performed daily and continued until the number of territorial males had remained stable for ≥ 3 days. In 2010, we performed surveys every other day after the first 6 days of settlement. We surveyed all 4 plots on any given survey day, except for 1 (day 8) in 2010, where we only surveyed 1 plot pair (pair 2) owing to logistical constraints. To account for annual variation in the phenology of spring migration, the settlement date of each individual in a given year was defined relative to the first individual detected (day 1) in our plots for that year. The rate of territory settlement was calculated as the total number of males settling in a plot

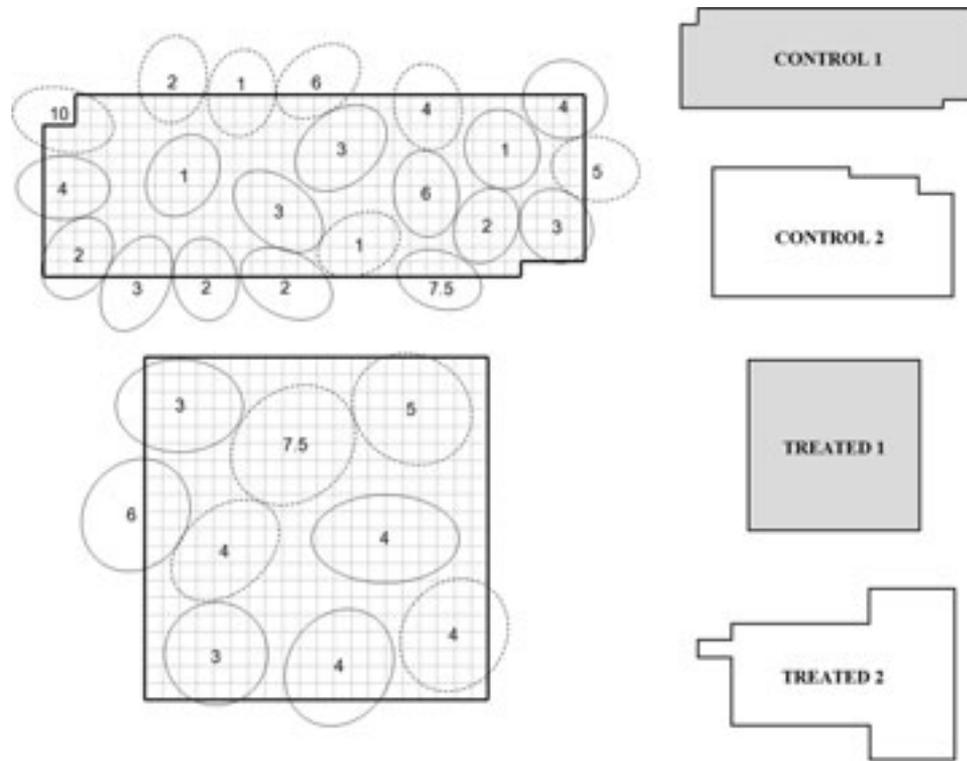


Figure 1

Settlement patterns in 1 pair of treated (a) and control (b) plots in 2009, and geometry of all 4 plots (right-hand side). Territories held by recruits are shown by dotted lines, whereas those held by site-faithful (returning) males are shown using solid lines. Numbers refer to settlement day relative to first settlement day in the 4 plots of the study area that year (i.e., day 1).

divided by the number of days between first and final male settlement in that plot.

From the last week of May until the end of June, we performed 8 additional spot mapping visits to delineate final territories (Haché and Villard 2010). For this purpose, we visited each plot every 2–4 days. Territories were considered to be located inside a plot if $\geq 25\%$ of the corresponding ellipses fell within a plot. To calculate territory density, we added the approximate proportions (0.25, 0.33, 0.5, etc.) of the territories that fell within plot boundaries. Unbanded territorial males (recruits) were captured using mist nets and given a numbered aluminum band and a unique combination of 3 celluloid color bands. Age (second year [SY] versus after second year [ASY]) was determined using the wear angle of the tip of the third rectrix (see Haché and Villard 2010).

To determine reproductive status, we monitored males regularly until the end of July and looked for signs of reproduction (e.g., presence of a female or nest, adult carrying food; see Haché and Villard 2010 for details). Breeding attempts were considered successful if parents were able to fledge at least 1 chick. Nests were declared unsuccessful if they were depredated or abandoned before at least 1 young fledged.

Habitat sampling

To characterize the effects of selection harvesting on stand structure, we estimated litter depth, shrub cover, and canopy closure in mid-July at the center of four hundred 25×25 -m cells covering the entire area of each study plot. Ovenbirds have been shown to respond to each of these 3 habitat parameters (Burke and Nol 1998; Guénette and Villard 2005;

Mattsson and Niemi 2006). We measured litter depth to the nearest millimeter, and shrub cover (height of 0.25–1.2 m) was estimated visually within a 2.5-m radius using a semi-quantitative scale (0–10, 10–25, 25–50, 50–75, 75–90, and 90–100%). We estimated canopy closure by holding a transparent sheet of Plexiglass (25×25 cm) overhead and counting the number of squares (5×5 cm) that were obscured by foliage or branches (Guénette and Villard 2005).

Statistical analyses

To test the effects of our predictor variables, we needed to account for the hierarchical experimental design and, in some cases, repeated measurements of our sampling unit (i.e., individual bird). For this purpose, we used generalized linear mixed models (GLMM). All analyses were conducted using SAS 9.2 (SAS Institute 2009).

Models testing the effects of treatment and year on first arrival dates and settlement rate included landscape context (plot pair) and plot nested within pair as random effects. Adding male status (returning male or recruit) as a fixed variable, we used the same model with settlement date as the response variable. We also tested for the effects of year and treatment on settlement date of returning males alone. Finally, we performed a GLMM with a logit link (binary distribution) to test the effects of breeding success on probability of return of individual males. All 2-way interactions were included in the models. Models testing for effects on settlement date and return probability used data at the individual scale. When repeated measures were taken (returning individuals), we accounted for within-sampling unit variation by using models including random slopes (Schielzeth and Forstmeier 2009).

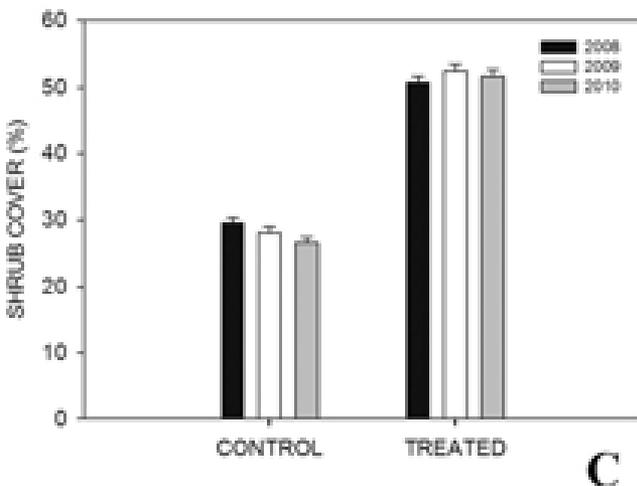
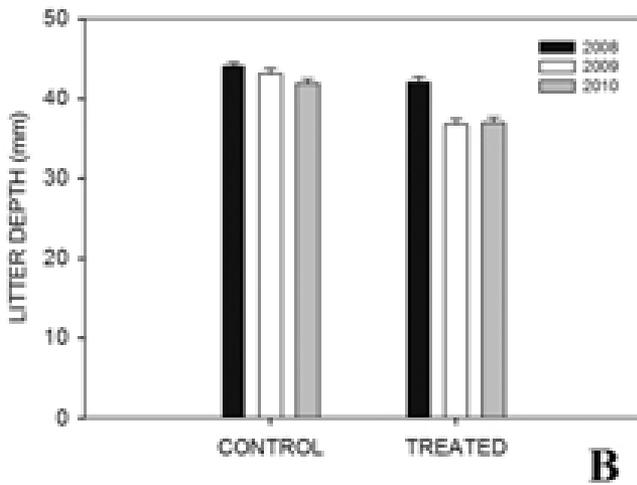
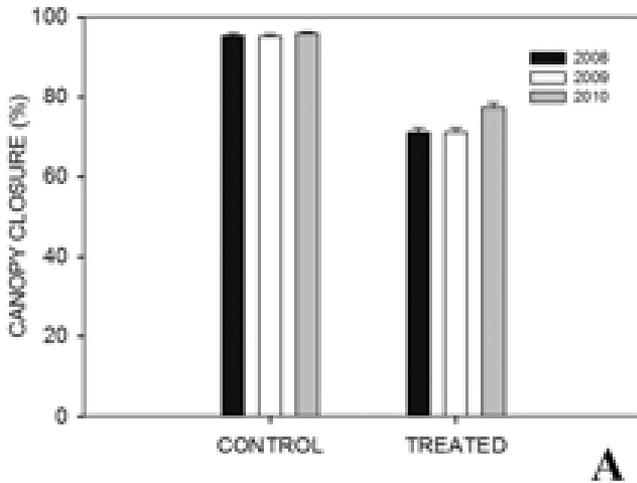


Figure 2 Comparison of habitat structure (mean \pm SE) in control and treated plots in years 2–4 (2008–2010) after experimental selection harvesting (30–40% removal). Habitat parameters were quantified in each 25- \times 25-m cell ($n = 400$ per plot/year).

We tested for differences in habitat structure (litter depth, shrub cover, and canopy closure) between control and treated plots using a GLMM including treatment (control

Table 1

Manova and univariate models of the 3 dependent variables included in the Manova on the effects of skid trails on habitat structure in 2 study plots treated through selection harvesting

Analysis and variables	df ^a	Treatment ^b	
		F value	P value
Manova Plot 1	3394	62.45	<0.0001
Manova Plot 2	3394	64.46	<0.0001
Canopy closure	1797	318.96	<0.0001
Shrub cover	1793	6.93	0.0086
Litter thickness	1797	34.31	<0.0001

^aThe degrees of freedom vary because shrub cover data were missing for 4 cells.

^bSkid trail versus intertrail forest.

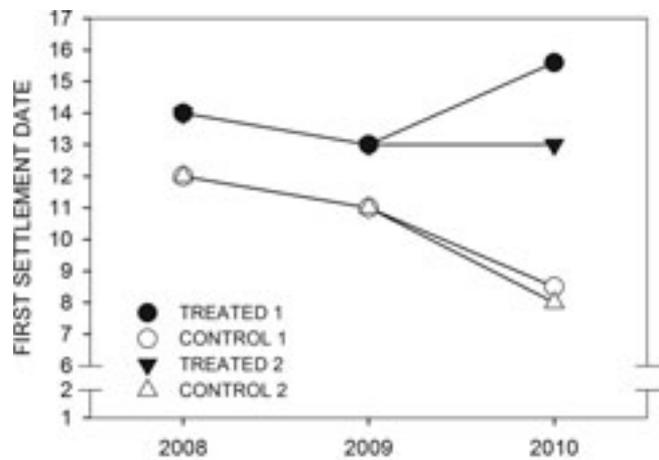


Figure 3 Date (in May 2008–2010) at which the first male(s) settled on territory in control and treated plots (1 = 1 May).

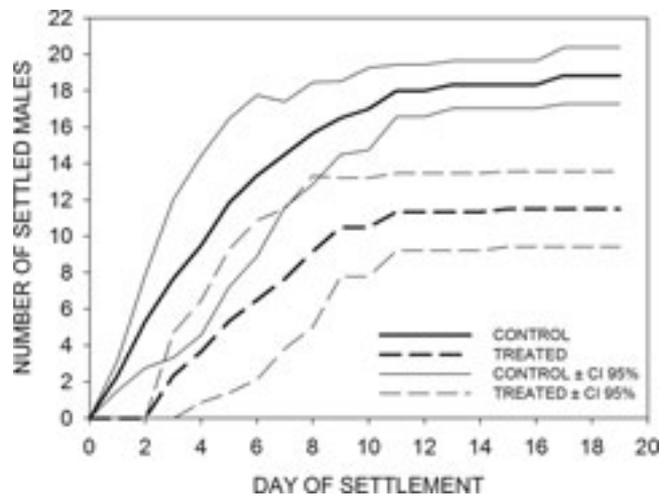


Figure 4 Saturation of control and treated (selection cut) plots by territorial male ovenbirds in the springs of 2008–2010 (mean and 95% confidence intervals). Day of settlement represents the number of days (-1) since the first male settled on a territory that year. Data are pooled for 2 control and 2 treated plots.

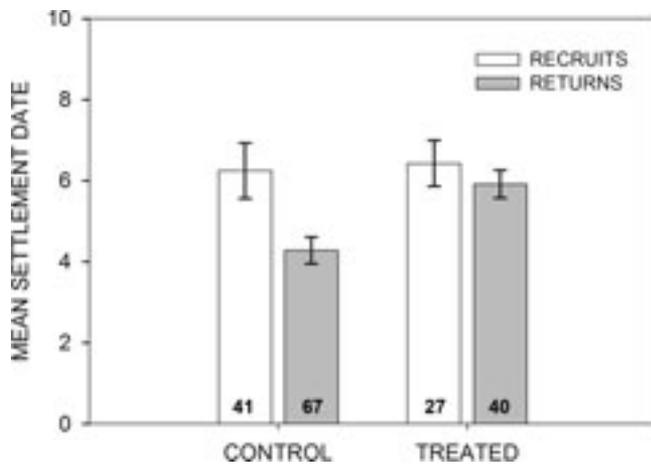


Figure 5

Mean (\pm SE) settlement date of male ovenbirds on breeding territories in treated and control plots in 2008–2010. Returns are males returning from previous year(s) whereas recruits are new (unmarked) males.

vs. cut), year, and treatment \times year as fixed effects. Random effects for this model were landscape context (plot pair) and plot nested within pair. We also performed a separate Manova in treated plots only, using the same 3 habitat parameters as dependent variables to determine whether stand structure differed between skid trails and intertrail forest. This analysis was conducted using 2010 habitat data only, assuming that differences in 2009 or 2008 would have been even greater (i.e., prior to substantial regeneration). We then analyzed treatment effects on each habitat parameter separately using GLMMs with plot as a random effect. Alpha for all of the tests was 0.05. Significant year effects were further investigated using Tukey–Kramer post hoc multiple comparisons tests.

RESULTS

At the plot scale, treatment \times year interactions were significant for all 3 vegetation parameters considered (canopy closure: $F_{1,4788} = 6.80$, $P = 0.001$; shrub cover: $F_{1,4768} = 3.77$, $P = 0.023$; litter depth: $F_{1,4785} = 4.06$, $P = 0.017$; Figure 2). Canopy closure and litter depth were negatively affected by treatment, whereas shrub cover increased but those relationships exhibited different year effects. When analyzing habitat variability within treated plots, all 3 parameters differed significantly between skid trails and intertrail forest (Table 1).

Across the 3 years, final ovenbird densities were $38.7 \pm 1.3\%$ (mean \pm SE) lower in treated plots than in controls (plot pair 1: 8.2 ± 0.2 vs. 15.1 ± 0.7 and plot pair 2: 10.4 ± 0.8 vs. 15.2 ± 0.9 territories). There were year-to-year variations in the dates at which the first males settled in our study area, the earliest settling on 8 May 2010 and the latest on 12 May 2008 (Figure 3). Settlement always began earlier in control plots, by 2–5 days ($F_{1,6} = 40.78$, $P < 0.001$; Figures 3 and 4), which is consistent with a preference for habitat structure in control plots (prediction 1). Earliest settlement dates for treated plots were 13–16 May (Figure 3).

Treatment ($F_{1,58} = 6.92$, $P = 0.011$) and year ($F_{2,58} = 39.50$, $P < 0.001$) had significant effects on the settlement date, males settling later in treated plots and over a longer period in 2010 (2008 vs. 2010: $t_{58} = -5.89$, $P < 0.001$; 2009 vs. 2010: $t_{58} = -8.31$, $P < 0.001$) than in 2008 and 2009. Although settlement periods were a few days longer in control plots, there was no treatment effect on settlement rate (prediction

2) once the first males had established their territory in treated plots ($F_{1,6} = 0.01$, $P = 0.909$; Figure 4). When considering instead the time required to reach 90% saturation, settlement rates for treatments and controls were 1.5 and 1.7 new males per day, respectively.

In contrast with prediction 3, there was only a trend for an earlier settlement of returning males ($F_{1,58} = 3.46$, $P = 0.068$) (Figure 5). In fact, groups observed on first settlement days often included both recruits (i.e., 6 of 13 individuals) and returning individuals. However, there was not a single instance in any plot-year where recruits were the sole occupants on the first day of settlement. The male status \times treatment interaction effect on settlement date ($F_{1,58} = 3.14$, $P = 0.082$) was not significant, but when restricting the analysis to returning males, treatment effect was significant ($F_{1,38} = 12.98$, $P < 0.001$). Returning males settled earlier, on average, in control plots (control = day 4.3 ± 0.3 , treated = day 5.9 ± 0.3 ; Figure 5). There was no such trend for recruits (Figure 5).

Finally, as expected from prediction 4, males breeding successfully in a given year were more likely to return to the same plot the following year ($n = 77$; $F_{1,30} = 9.08$, $P = 0.005$). Interactions for this model were not significant. Treatment had no effect on this decision ($F_{1,30} = 0.63$, $P = 0.435$), but there was tendency for a year effect ($F_{2,30} = 3.16$, $P = 0.057$).

DISCUSSION

We found evidence for the use of structural cues, location cues, and personal information by male ovenbirds settling on a breeding territory. First settlement took place 2–5 days later in treated plots than in matched controls each year, suggesting that males responded negatively to alterations in stand structure resulting from harvesting. However, once the first males had settled in treated plots each year, settlement rate became virtually identical to that of controls. Male recruits never settled in a given plot-year in the absence of at least 1 returning male, consistent with the use of location cues provided by conspecifics. The settlement pattern of returning males reflected their reproductive success the previous year, successful males being more likely to return than unsuccessful ones, irrespective of treatment. In a few instances, returning males skipped years, suggesting that some individuals dispersed between years in an attempt to increase their fitness (see also Chalfoun and Martin 2010).

In the same experimental system, Haché and Villard (2010) showed that the decline in territory density that immediately followed the selection harvest treatment was largely attributable to reduced recruitment. However, this phenomenon quickly disappeared in subsequent post-harvest years, suggesting that the initial drop in recruitment might be related to post-harvest territory expansion and stronger competition for remaining space, which would have been less important in the following years, as return rate decreased (Haché and Villard 2010). The settlement rates found in this study, as well as the lack of a treatment effect on mean arrival dates of recruits, suggest that they did not respond to structural cues per se. In fact, the presence of returning males seemed to be the main factor triggering the settlement of recruits (see also Betts et al. 2008a).

Because we did not control for the age of recruits, it could be argued that delayed arrival of recruits reflected later arrival from migration or lower competitiveness in territory acquisition (Sherry and Holmes 1989). However, this hypothesis can be rejected on several grounds. First, recruits included both inexperienced (SY) and experienced (ASY) breeders. In fact, when pooling data from the 3 years of the study, nearly half (46%) of the recruits were ASY individuals. Second, these

males arrived on day 6.26, on average, whereas SY males arrived on day 6.36. Finally, evidence for earlier migratory arrival of older males is equivocal (Morton 1992; Balbontin et al. 2009; Cooper et al. 2009). Hence, in this study, patterns associated with male status (recruit or not) did not seem to be confounded by age effects.

Experimental studies (Nocera et al. 2006; Betts et al. 2008b) suggest that in songbirds, the influence of social information may be stronger than that of structural cues. When structural differences between habitat types are not sufficiently obvious, prospecting individuals may face perceptual constraints, that is, they may be unable to perceive cues reflecting habitat quality in the limited time they have (*sensu* Abrahams 1986; Nocera et al. 2009). Indeed, we found that settlement periods were short, that is, 10–16 days (Figure 4) compared with 30–40 days in the sedge warbler (*Acrocephalus schoenobaenus*) (Zajac et al. 2006) and the willow warbler (*Phylloscopus trochilus*) (Reijnen and Foppen 1994). In our study area, males also arrive before leaf buds have fully opened (Thériault S, Haché SA, Villard M-A, personal observations), which may further reduce their ability to assess structural differences between treatments during the settlement period. Hence, males may rely on other cues, such as territorial conspecifics. However, 1 important question remains: Why did returning males settle later in treated plots?

The probability of return of individual males was associated with their reproductive success the previous year (personal information), but not with treatment (a surrogate for habitat structure), suggesting that per capita productivity was similar irrespective of habitat structure (Pérot and Villard 2009; Haché SA, Villard M-A, Bayne EM, unpublished data). These results are also consistent with those of Haché and Villard (2010), who observed in the same study region a significantly lower return rate in male ovenbirds in the second and third years postharvest, but not in the first year. Although the contrast in stand structure between treatments should have been more dramatic in the first year, males responded with a 1-year delay. Assuming that habitat quality was predictable between years (Valone 2007), individuals returned to their territory, irrespective of the selection harvest treatment applied overwinter. In this study, most returning males immigrated after plots were harvested and so were not exposed to abrupt changes in habitat quality. Yet, males breeding in treated plots returned later the following spring than those from control plots. Although there is no evidence for a treatment effect on per capita productivity, males returning to treated plots may have prospected for areas that could support higher ovenbird densities, thereby delaying their settlement.

Our results collectively point toward a critical role of returning males in the habitat selection process. These males influence the timing of immigration into specific sites and use personal information to guide their own settlement patterns. The fact that recruits never preceded the first returning males when settling on a territory suggests that they used returning males as indicators of suitable habitat and might have been able to identify them as such. Familiarity with a territory has been shown to be important in songbirds and other animal species (Pärt 1995; Piper 2011), and such familiarity might be expressed (and thus, detectable) through particular behavioral traits (e.g., vocalizations, degree of aggressiveness [e.g., Lanyon and Thompson 1986]). This intriguing possibility should be explored in future studies.

To our knowledge, this is the first study examining the potential roles of information provided by habitat structure, conspecific individuals, and personal experience on settlement patterns in a population where the experience of

individuals with specific sites (returning males vs. recruits) is known. In spite of its limitations, our design had the advantage of documenting settlement decisions by individuals that were not artificially attracted by playbacks, decoys, or other means. Few studies have documented conspecific attraction in the absence of experimental manipulation (Fletcher and Sieving 2010). Playback experiments designed to separate location cues provided by conspecifics from a response to habitat cues could lead to biases, for example, by attracting individuals to marginal habitat when they might otherwise have acted as floaters in good-quality habitat. Future studies could track males upon their return from migration to determine whether individuals from suboptimal habitat or first-time breeders do indeed sample the neighborhood for better territories. Because conspecific attraction is increasingly being used in the context of ecological restoration (e.g., Ahlering et al. 2010; Bradley et al. 2011; Kappes et al. 2011), its relative importance should be weighed against that of other habitat selection mechanisms.

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