

Age-specific response of a migratory bird to an experimental alteration of its habitat

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Summary

1. Recruitment, i.e. the influx of new breeding individuals into a population, is an important demographic parameter, especially in species with a short life span. Few studies have measured this parameter in solitary-breeding animal populations even though it may yield critical information on habitat suitability and functional connectivity.
2. Using a before-after, control-impact pairs (BACIP) experimental design, we measured: (i) the return rate and apparent survival rate of individually marked territorial males of a neotropical migrant bird species, the Ovenbird *Seiurus aurocapilla* Linnaeus and (ii) the age-specific recruitment rate. Study plots ($n = 10$) were paired: one was treated through single-tree selection harvesting (30–40% basal area removal) and the other acted as a control. We hypothesized that experienced males would out-compete inexperienced ones and tend to avoid settling in lower-quality, treated stands.
3. In the first year post-harvest, the mean density of territorial males was significantly lower in treated plots (–41%) than in controls and the difference remained relatively stable thereafter. This lower density mainly reflected a lower recruitment rate compared to controls (17.9 vs. 49.0% of males present), itself driven by a lower recruitment rate of experienced males (2.8 vs. 22.8%). Return rate was similar between controls and treated plots in the first year post-harvest (59 vs. 55%, respectively) but it decreased in treated plots during the second (–15.8% relative to controls) and third (–12.7%) year post-harvest. The trend was even stronger when considering only experienced males. The treatment was followed by a major expansion in mean territory size in treated plots (+49% relative to controls, 3rd year post-treatment).
4. Neither apparent survival rate nor recruitment rate varied as predicted. There was a strong year effect but no treatment effect on apparent survival rate, whereas male recruitment patterns were both year- and age-specific. Three years post-harvest, recruitment rate was sufficient to fill most territory vacancies in treated plots, due mainly to first-time breeders.
5. To our knowledge, this is the first study documenting the effects of experimental habitat alteration on recruitment rate in a songbird species using a BACIP design. The response of this male subpopulation highlights the influence of recruitment on the density of open populations of solitary-nesting birds and age-specific patterns in the response of individuals to habitat alterations.

Key-words: habitat selection, ideal despotic distribution, managed forest landscapes, recruitment, time-lagged response

Introduction

Monitoring the movements of individually marked animals before and after habitat alteration makes it possible to investigate behavioural and demographic responses in the context of rapidly changing environments (e.g. Burton *et al.* 2006;

Czertwytynski, Boyce & Schmiegelow 2007; La Puma, Lockwood & Davis 2007). In highly mobile animals, however, post-disturbance movements may be very difficult to document. The opposite approach, which consists in measuring recruitment into marked populations, may provide an efficient alternative. The degree to which local mortality (or emigration) will be compensated by immigration from elsewhere is expected to reflect local habitat suitability, the

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permeability of the landscape to movements, and the extent to which potential recruits are actually available from the regional population.

Recruitment plays a critical role in population dynamics, especially in short-lived species (Wauters, Matthysen & Dhondt 1994; Coulson, Lindström & Cotgreave 2002; Saether, Engen & Matthysen 2002; Hoffmann *et al.* 2003). For example, Ward (2005) found that low recruitment was the key factor underlying declines in isolated or peripheral colonies of Yellow-headed Blackbirds *Xanthocephalus xanthocephalus* Bonaparte. Schiegg, Walters & Priddy (2002) and Cooper & Walters (2002) observed a similar pattern in populations of Red-cockaded Woodpecker *Picoides borealis* Vieillot and Brown Treecreeper *Climacteris picumnus* Temminck, respectively.

Most songbirds exhibit very low fidelity to their natal site (Hann 1937; Nolan 1978; Greenwood & Harvey 1982; Paradis *et al.* 1998; Shutler & Clark 2003; Holmes, Rodenhouse & Sillett 2005). In fact, natal dispersal is thought to extend over tens or even hundreds of kilometres (Graves, Romanek & Navaro 2002; Hobson, Wassenaar & Bayne 2004; Tittler, Villard & Fahrig 2009; but see Dale *et al.* 2006). Hence, the replacement of local mortality and emigration depends to a large extent on the recruitment of individuals born elsewhere. Recruitment of locally born young can be high in colonial or cooperative-breeding species, as well as in isolated populations of solitary-nesting species (e.g. *c.* 50% for males in great tit *Parus major* Linnaeus and blue tit *P. caeruleus* Linnaeus; Matthysen, Adriaensen & Dhondt 2001; see also Crespín *et al.* 2006; Wilkin *et al.* 2006). In contrast, values recorded for open populations of migratory species are typically very low (e.g. 5.4% in Wood Thrush, *Hylocichla mustelina* Gmelin; Brown & Roth 2002). Again, these patterns indicate that functional connectivity among open populations of solitary-nesting songbirds is mainly ensured by natal dispersers.

Although the habitat-specific demography of songbirds has been investigated in some species (e.g. Holmes, Marra & Sherry 1996; *Dendroica caerulescens* Gmelin; Murphy 2001 *Tyrannus tyrannus* Linnaeus; VanderWerf 2004 *Chasiempis sandwichensis* Gmelin; Bears, Martin & White 2009 *Junco hyemalis* Linnaeus), little is known about the response of individuals from migratory species to habitat disturbance taking place between breeding seasons. In this study, we took advantage of an experimental silvicultural treatment to determine how individuals from a marked population respond to a major alteration of their breeding habitat taking place while they are wintering in the Neotropics. The treatment, single-tree selection harvesting, removed *c.* 30–40% of the original basal area of trees. We investigated post-treatment settlement patterns of marked individuals to ask whether habitat alteration influenced: (i) return rate; (ii) apparent survival rate; (iii) recruitment rate and (iv) the age structure of recruits.

Our focal species, the Ovenbird *Seiurus aurocapilla* Linnaeus, is a ground-nesting passerine that feeds on litter invertebrates (Van Horn & Donovan 1994). It responds negatively to disturbances that open the forest canopy (Gram *et al.*

2003; Guénette & Villard 2005) and, based on a meta-analysis, it is considered to be one of the two songbird species most sensitive to partial forest harvesting in North America (Vanderwel, Malcolm & Mills 2007). Ovenbird reproductive success has been shown to be positively correlated with the biomass of soil macroinvertebrates and with forest stand productivity (Seagle & Sturtevant 2005). Hence, this species appears to be a good indicator of the overall health of forest ecosystems.

We hypothesized that males would settle in study plots according to their niche 'gestalt' (*sensu* James 1971; Morton, Van der Voort & Greenberg 1993), i.e. that they would actively avoid recently altered stands. We further hypothesized that experienced males (after second-year, hereafter ASY) would out-compete inexperienced ones (second-year, hereafter SY) and settle preferentially in higher-quality stands (ideal despotic distribution – Fretwell & Lucas 1970). Therefore, we predicted that male (i) density; (ii) return rate; (iii) apparent survival rate; (iv) recruitment rate, and the proportions of (v) ASY recruits and (vi) returning ASY individuals would be lower in treated than in control plots after experimental harvesting (single-tree selection).

Materials and methods

STUDY AREA

The study was conducted in the Black Brook District, a 2000 km² managed forest owned by J.D. Irving Limited, in Northwestern New Brunswick, Canada (47°23'N, 67°40'W) (Fig. 1). The study area is characterized by a gently rolling topography with shade-tolerant deciduous stands on hilltops (25%), conifer stands in lowlands (20%), and scattered mixedwood stands (18%). The remainder of the land base is covered by spruce plantations (37%) (Etheridge *et al.* 2005, 2006).

Since the 1980s, the company has mainly managed tolerant deciduous stands through single-tree selection harvesting, a silvicultural treatment consisting in the removal of 30–40% of the basal area at *c.* 20-year intervals (G. Pelletier pers. comm.). The basal area of a stand refers to the cross-sectional area at breast height (1.35 m) of all woody stems ≥ 10 cm in diameter. Approximately 20% of the basal area is harvested by the creation of 5 m-wide skid trails whereas the remaining 10–20% is harvested through removal of single trees between trails. Skid trails are usually oriented in parallel directions, *c.* 20 m apart (Fig. 2), but their overall configuration varies as a function of site topography.

EXPERIMENTAL DESIGN

We used a before-after, control-impact pairs (BACIP) design, with five pairs of 25 ha study plots. Four of the ten study plots were square-shaped, the others being rectangular to fit within untreated deciduous stands (dimensions ranged from 500 × 500 m to 250 × 1000 m). We selected study plots dominated by mature or old shade-tolerant deciduous or mixedwood stands without recent (< 30 years) signs of human disturbance. The selected stands were co-dominated by sugar maple *Acer saccharum* Marsh and American beech *Fagus grandifolia* Ehrh, with lower densities of yellow birch *Betula alleghaniensis* Britton, balsam fir *Abies balsamea* Miller, and white or red spruce *Picea glauca* Moench, *P. rubens* Sarg. Plots within each pair were located 3–6 km apart (4.2 ± 1.0 km,

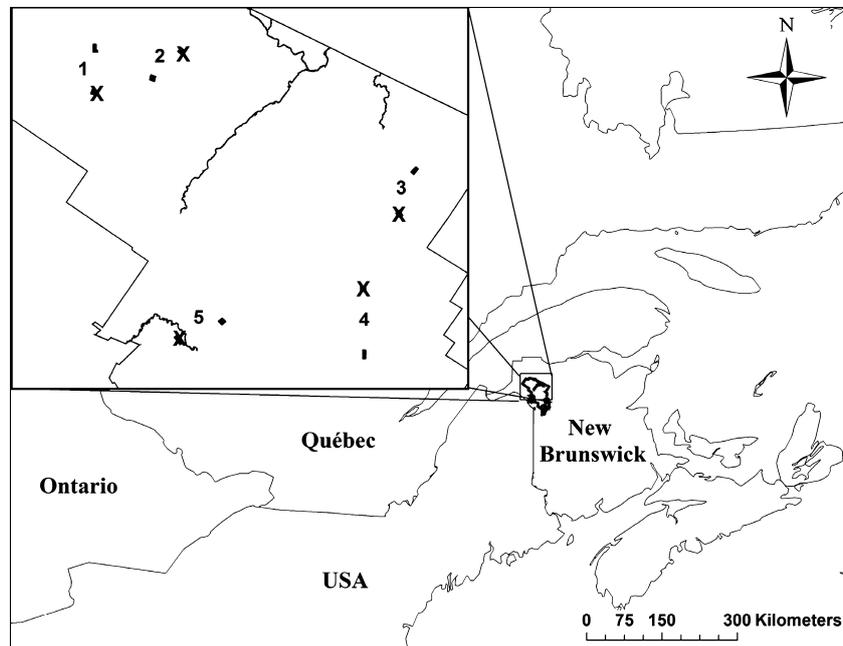


Fig. 1. Location of study plots in the Black Brook District, New Brunswick, Canada. Numbers indicate paired plots and × indicate plots treated through selection harvesting.

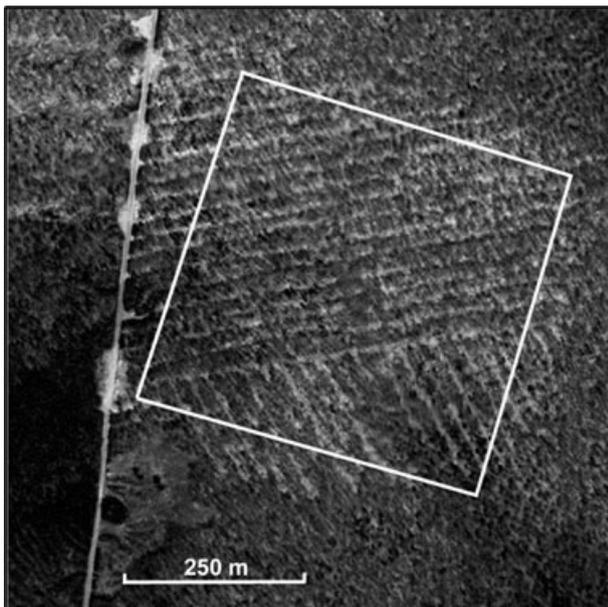


Fig. 2. Aerial photograph of a 25-ha treated plot taken in the first summer post-harvest. Pale, parallel lines correspond to skid trails and the broader vertical line to the left is an access road (courtesy: J.D. Irving Ltd).

mean \pm SD) and pairs of plots were separated by at least 7 km (23.8 ± 9.1 km; Fig. 1). This configuration was chosen to reduce the risk that the treatment would affect paired controls, and to ensure that plots within each pair would be located in similar landscape contexts. In December 2006, one plot of each pair was harvested using single-tree selection. The treatment was randomly assigned except for one pair, where harvesting was not possible on one of the plots owing to steep slopes. The basal area removed in a plot (30 or 40%) was

determined based on pre-harvest data on stand structure so that post-treatment basal areas would be as similar as possible across plots ($16.6 \text{ m}^2 \text{ ha}^{-1} \pm 0.7 \text{ SD}$). A 50 m buffer around treated plots was harvested to reduce the risk that territories near plot boundaries would include untreated forest. The BACIP design allowed testing treatment effects through the measurement of (i) the initial status of the Ovenbird population in treated plots and (ii) year effects (Bennett & Adams 2004).

DENSITY OF TERRITORIES, RETURN RATE, AND RECRUITMENT RATE

We estimated territory density in each plot by mapping the territories of all singing males (Bibby *et al.* 2000). Each year, every study plot was visited every 2–3 days, for a minimum of eight visits between 22 May and 5 July, from 0530 to 1000. Mapping was only conducted under suitable weather conditions (no wind/rain interfering with bird detection). We fitted ellipses around clusters of observations, using countersinging observations and locations of banded individuals. Territories which overlapped plots by <25% were excluded from density calculations. In 2006 (hereafter pre-harvest year), 2007, 2008, and 2009 (hereafter first, second, and third year post-harvest, respectively), we banded as many territorial males as possible in four (pre-harvest) and five (post-harvest) pairs of plots. In total, 245 of the 263 males (93.2%) holding a territory in our plots were captured and fitted with a unique combination of plastic colour bands, along with a numbered aluminium band from the Canadian Wildlife Service (capture rates were 91.6%, 96.6%, 97.5%, and 98.6% from 2006 to 2009, respectively). All territorial males that were unbanded when they settled in a plot (starting in the first year post-harvest for four pairs of plots and in second year post-harvest for the fifth pair) are hereafter referred to as ‘recruits’. Because SY males are breeding for the first time, they were considered as recruits in four pairs of study plots during the pre-harvest year and in five pairs during all three post-harvest years. Recruitment of ASY males and total recruitment could only

be estimated in four pairs of plots during the first-year post-harvest because it was impossible to distinguish ASY recruits from returning individuals in the plot pair where males were unbanded in the pre-harvest year. During post-harvest years, we searched every plot to determine the status of each singing male, i.e. either returning individual or recruit (except in the fifth pair during the first year post-harvest). Some recruits may have been unbanded individuals from the previous year that returned to our study plots, but the likelihood of such events was considered low enough to be negligible (18/263 territorial males), especially when accounting for mortality between years. We also searched for banded individuals in a 100-m band outside each study plot to detect short-distance dispersers.

We aged each individual as second (calendar) year (SY) or after second-year (ASY) based on the wear pattern of the third rectrix. Following Bayne & Hobson (2001), we used a rectrix tip angle of 84° to separate SY and ASY males falling between the critical values (77.92° – 90.05°) recommended by Donovan & Stanley (1995), i.e. 11.9% of individuals. Return rate was the percentage of males banded in year t that returned to the same plot in year $t + 1$. Age-specific return rates were also estimated to determine whether the probability of return of SY and ASY males varied according to treatment. Because the number of recruits and returning individuals per plot may be influenced by local density, we calculated the proportion of territorial males in a given year that were unbanded (recruits) or banded (returning individuals).

DATA ANALYSIS

To determine treatment effects on the behavioural response of the Ovenbird, we used linear mixed models (McCulloch & Searle 2001):

$$y = \mu + b_t + b_x + b_{\tau \times x} + b_m + b_{n(m)} + \varepsilon$$

where y is the response variable [i.e. density of territories, territory size, return rate (total, ASY, and SY males) and recruitment rate (total, ASY, and SY males)], μ is a constant, b_i is a parameter estimate, τ is the treatment (harvested vs. control; fixed effect), x is the year (fixed effect), $\tau \times x$ is the interaction between treatment and year (fixed effect), m is the landscape context of a given pair of plots (1–5; random effect), $n(m)$ is the plot (context) (1–10; random effect), and ε is the error term. For SY males, the analysis was based on four pairs of plots during the pre-harvest year. Given our BACIP design, a significant interaction between year and treatment would indicate a significant treatment effect on a response variable for which pre-harvest data were available. Treatment effects on variables only available for the post-harvest years [i.e. return rate (total, SY and ASY males) and recruitment rate (total and ASY males)] were quantified using the same linear mixed models, but a significant interaction only indicated a different treatment effect between years. These latter analyses were based on four pairs of plots during the first post-harvest year.

All mixed models were performed using the MIXED procedure in SAS 9.1 (SAS Institute 1999). This procedure allows controlling for the spatial pattern of our experimental design and explicitly modelling of the temporal autocorrelation associated with the repeated

measurement of plots using temporal autoregressive models. We performed multiple-comparison analyses to determine the treatment effect for the three post-harvest years separately, and to find out whether values remained stable over time in control plots. Adjustment of P -values for the LS-means was done using the Tukey–Kramer method.

Because the percentages of returning individuals and recruits (total, SY and ASY) were based on a variable number of individuals among plots, we also built GLMM from a Poisson distribution to account for this potential bias using the GLIMMIX Macro in SAS 9.1 (SAS Institute 1999). Because the results were qualitatively similar to those obtained using linear mixed models, we only report the latter. Recruitment and return rates data were arcsine-transformed to meet assumptions for homogeneity and normality of residuals. Data in tables and figures are presented in their original untransformed scale.

Apparent survival rates were estimated to determine whether a treatment effect on return rates might reflect higher mortality or long-distance dispersal, or simply higher breeding dispersal in the vicinity of treated plots. This approach also allows considering the individuals who 'skipped' a year (i.e. banded males that were absent in year $t + 1$, but were detected in year $t + 2$ or $t + 3$). Cormack–Jolly–Seber models were fit to mark–recapture data using the software MARK (White & Burnham 1999). Apparent survival rates (ϕ) could only be estimated for individuals banded during the pre-harvest year and first year post-harvest because at least two recapture sessions are required (Lebreton *et al.* 1992). A combination of 16 candidate models predicting apparent survival and recapture probability (P) were based on: (i) no factors (.); (ii) treatment (T); (iii) year (Y); and (iv) the treatment \times year interaction ($T \times Y$). We used an Akaike Information Criterion corrected for small sample size (AICc) to select the most parsimonious model and the likelihood ratio test to determine the significance of factors included in the best ranked model. The best-ranked model was considered as the most parsimonious if no other model had a $\Delta\text{AICc} \leq 2$. The best ranked model, i.e. with the lowest AICc value, was considered. The goodness of fit testing of the global model [i.e. $\{\phi(T \times Y) P(T \times Y)\}$] was performed using the median \hat{c} procedure (Cooch & White 2006). Model averaging was also performed to account for uncertainty in model selection (Cooch & White 2006).

Results

As predicted, there was a significant negative effect of the treatment on the density of territorial males ($F_{3,14} = 8.89$, $P < 0.001$). Density was respectively 41%, 36%, and 29% lower in treated plots than in controls in the first ($t_{1,24} = 3.58$, $P = 0.028$), second ($t_{1,24} = 3.22$, $P = 0.060$) and third year post-harvest ($t_{1,24} = 2.87$, $P = 0.125$; Table 1). Meanwhile, density remained stable in control plots between the pre-harvest year and the first year post-harvest ($t_{1,24} = -1.20$, $P = 0.926$), and between the first and second year post-harvest ($t_{1,24} = -0.30$, $P = 1.00$), but it increased

Table 1. Variations in Ovenbird density and territory size from the pre-harvest year to the third year post-harvest (mean \pm SD; $n = 5$)

	Pre-harvest		Post-harvest (1)		Post-harvest (2)		Post-harvest (3)	
	Control plots	Treated plots	Control plots	Treated plots	Control plots	Treated plots	Control plots	Treated plots
Density (/25 ha)	13.8 \pm 3.7	12.6 \pm 2.2	14.6 \pm 3.8	8.6 \pm 2.7	14.8 \pm 3.6	9.4 \pm 2.7	16.6 \pm 2.9	12 \pm 3.0
Territory size (ha)	1.00 \pm 0.15	0.90 \pm 0.09	1.24 \pm 0.11	1.57 \pm 0.14	1.34 \pm 0.19	1.96 \pm 0.22	1.27 \pm 0.22	1.89 \pm 0.23

slightly between the second and third year post-harvest ($t_{1,24} = -2.99$, $P = 0.098$).

Of the 188 males banded during the first 3 years of the study, 130 (69.1%) returned to the same study plot at least once. Returning males that were observed defending a territory outside of study plots in subsequent years (17; 12.3% in treated plots and 6.5% in controls) were not included in these calculations. Return rates were similar in treated plots and controls during the first year post-harvest. However, they were lower in treated plots during the second (-15.8%) and third year (-12.7%) post-harvest compared to controls, which resulted in an overall treatment effect ($F_{1,14} = 4.52$, $P = 0.052$; Fig. 3a). Irrespective of the treatment, there was also a trend toward a year effect on return rate ($F_{2,14} = 3.06$, $P = 0.079$; Fig. 3a). When considering only the return rate of males in year $t + 1$ that were ASY in year t , there were significant effects of year ($F_{2,14} = 4.70$, $P = 0.027$) and treatment (negative effect; $F_{1,14} = 4.92$, $P = 0.044$; Fig. 3b). No significant pattern was found for SY males (Fig. 3c).

The best-ranked and most parsimonious model predicting apparent survival rates included year as a predictor for both apparent survival and detection probability $\{\{\varphi(Y) P(Y)\}$; AICc = 515.6; AICc Weight = 0.42}. A correction for over-dispersion was not required because the global model fit was adequate ($\hat{c} = 1.19 \pm 0.035$ SE). Apparent survival rate of individuals banded during the pre-harvest year (0.83 ± 0.049 SE) was significantly higher than that of individuals banded during the first year post-harvest (0.64 ± 0.045 ; $\chi^2_1 = 6.85$, $P = 0.009$). The detection probabilities were $0.81 (\pm 0.053)$ and $0.94 (\pm 0.031)$, respectively. These values and the relative difference between years remained similar after model averaging (Table 2). The model with the lowest AICc value that included treatment as a predictor of apparent survival was poorly supported $\{\{\varphi(T \times Y) P(Y)\}$, Δ AICc = 4.68}.

In the first 3 years following harvesting, 145 recruits held territories in our study plots (note: only four pairs of plots could be surveyed in the pre-harvest year), 137 of which were captured and aged. Eleven banded ASY individuals resettled in a study plot after 'skipping' at least 1 year. Although habitat selection for 'skipping' individuals may have been based on different cues than first-time breeders in a study plot (e.g. previous year's reproductive performance), they were considered as recruits because they were immigrants into the plots and return rate in year $t + 1$ was based on the individuals occupying a plot in year t . Furthermore, the number of ASY recruits with (i.e. 'skipping' individuals) and without previous breeding experience in a study plot could not be teased apart during the first year post-harvest. Consistent with our prediction, the mean proportion of recruits was considerably lower (-31.0%) in treated plots than in controls in the first year post-harvest ($t_{1,14} = 3.49$, $P = 0.034$), but the opposite pattern was observed in the second year and third year post-harvest (+13.8% and +12.9%, respectively), as shown by the significant treatment \times year interaction ($F_{2,14} = 7.90$, $P = 0.005$; Fig. 4a). However, differences between treated and control plots in the second ($t_{1,14} = -1.41$, $P = 0.720$)

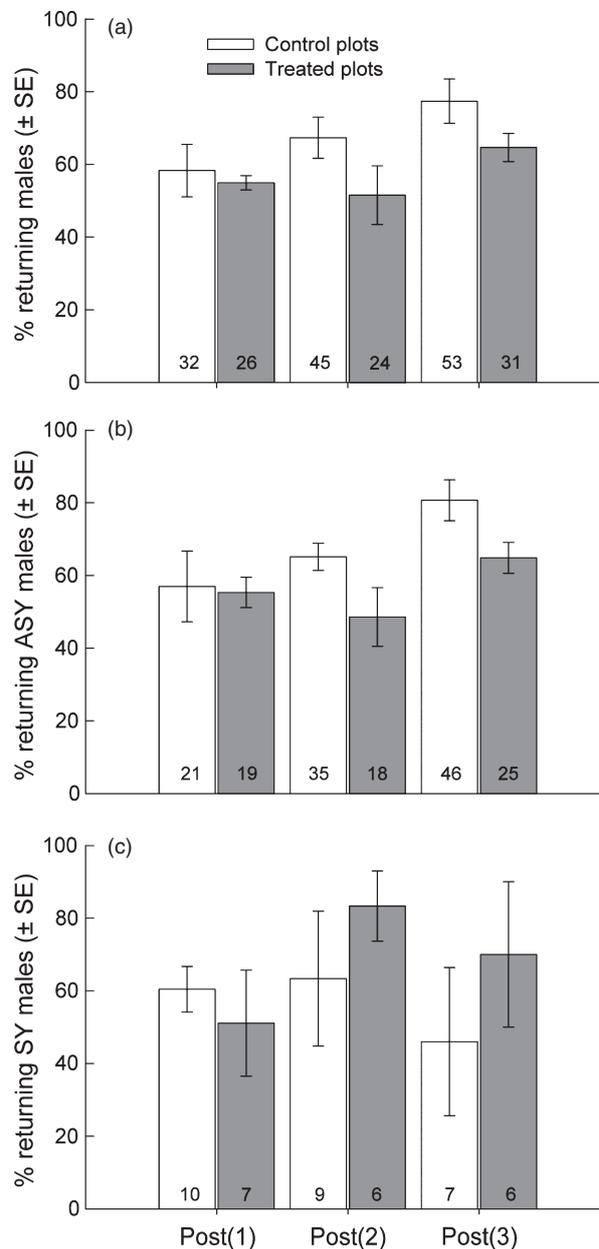


Fig. 3. Mean (\pm SE) return rate of total (a), ASY (b) and SY (c) male Ovenbirds (%) in treated plots and controls during the first (Post1; $n = 4$), second, and third year post-harvest ($n = 5$). The absolute number of returning individuals is indicated at the base of each bar. Note that two individuals could only be aged when they returned in year $t + 1$.

and third year post-harvest ($t_{1,14} = -1.30$, $P = 0.781$) were NS. The lower recruitment rate in treated plots during the first year post-harvest corresponded to a significantly lower proportion of ASY male recruits (-20.0%; $t_{1,14} = 3.37$, $P = 0.043$; Fig. 4b). However, as shown by the significant treatment \times year interaction, the treatment effect on the recruitment rate of ASY males varied among years ($F_{2,14} = 6.84$, $P = 0.009$). Again, the opposite trend was observed during the second year post-harvest (+17.1% $t_{1,14} = -1.74$, $P = 0.529$), whereas the percentage of ASY recruits was similar in both treated plots and controls during

Table 2. Apparent survival rate and probability of detection (\pm SE) from the full model $\{\varphi(T \times Y) P(T \times Y)\}$ before and after model averaging. The unconditional SE obtained from model averaging is presented in parentheses

	Apparent survival	Averaged apparent survival	Probability of detection	Averaged probability of detection
Post-harvest (1)				
Controls	0.863 (\pm 0.062)	0.807 (\pm 0.059)	0.831 (\pm 0.068)	0.849 (\pm 0.060)
Treated plots	0.796 (\pm 0.078)	0.799 (\pm 0.062)	0.785 (\pm 0.084)	0.835 (\pm 0.059)
Post-harvest (2)				
Controls	0.653 (\pm 0.056)	0.673 (\pm 0.059)	0.950 (\pm 0.034)	0.917 (\pm 0.039)
Treated plots	0.627 (\pm 0.075)	0.668 (\pm 0.057)	0.912 (\pm 0.059)	0.904 (\pm 0.052)

the third year post-harvest ($t_{1,14} = 0.94$, $P = 0.929$). A marginally significant treatment \times year interaction ($F_{3,22} = 2.97$, $P = 0.054$) suggests that the treatment effect on the recruitment of SY males varied among years. However, no significant treatment effect was linked to a specific post-harvest year due to the high degree of variation among treated plots.

There was a significant treatment \times year interaction effect on territory size ($F_{3,24} = 17.3$, $P < 0.001$; Table 1). In the pre-harvest year, mean territory size was similar between control and treated plots ($c. 1$ ha; $t_{1,24} = 0.78$, $P = 0.993$), whereas it increased in both treatments and controls, but to a greater extent in the former in the first year following the treatment ($+0.67$ ha; $t_{1,24} = -2.92$, $P = 0.113$; Table 1). Mean territory size increased again ($+0.4$ ha) in treated plots between the first and second year post-harvest ($t_{1,24} = -5.48$, $P < 0.001$) and then remained stable between the second and third year post-harvest. Although the method we used to delineate territories is not as precise as kernel analysis or other intensive approaches, the magnitude of the differences observed is such that the pattern appears to be robust.

Discussion

On the surface, treatment effects were simple and predictable. Density declined immediately after the treatment and remained relatively stable thereafter. Its percent reduction relative to controls was roughly equivalent to the percent basal area removed. Male return rate was also negatively influenced by single-tree selection harvesting, as expected. However, neither apparent survival nor recruitment rate varied as predicted. There was a strong year effect on apparent survival whereas recruitment patterns were both year- and age-specific.

In the first post-harvest breeding season, densities declined and male Ovenbirds increased the size of their territory, while no such patterns were seen in control plots. Territory expansion by returning males in treated plots may either reflect lower food abundance (Stenger 1958; Smith & Shugart 1987; but see Mazerolle & Hobson 2004) or a lower territorial pressure from neighbouring males. At peak fledging time, the abundance of soil invertebrates per unit area was indeed lower in treated plots than in controls (Haché & Villard, unpublished data), consistent with the former hypothesis.

Treatment effects on male return rates became significant in the second and third year post-harvest. Because experienced individuals are expected to defend territories of higher quality than inexperienced ones, we predicted that the treatment would promote the emigration of experienced males. Indeed, a lower proportion of ASY males returned to treated plots than to controls, especially in the second and third year post-harvest (Fig. 3b). This pattern is consistent with the hypothesis that treated plots and their particular structure represent lower-quality habitat or are perceived as such. However, in our focal population, breeding dispersal movements were very short, irrespective of the treatment. Only two returning individuals held a territory more than 100 m away from the one they occupied the previous year, though it should be noted that our data are biased against the detection of long-distance movements.

In spite of the observed decline in density and return rate following treatment, population response to harvesting was much less dramatic than expected from comparative mensurative studies (e.g. Bourque & Villard 2001; Jobes, Nol & Voigt 2004). In the same region, Bourque & Villard (2001) found Ovenbird densities similar to ours in control stands (16.5 ± 2.9 individuals per 25 ha; $n = 6$) but densities recorded in single-tree selection cuts 3–5 years post-harvest were $c. 60\%$ lower than the ones we recorded. The lower proportion of ASY and higher proportion of SY recruits in our treated plots in the third year post-harvest are consistent with a time-lagged response to the treatment (see also Wiens & Rotenberry 1985; Tilman *et al.* 1994; Nagelkerke *et al.* 2002; Schrott, With & King 2005).

Assuming that this phenomenon reflects lower food abundance, maintaining larger territories may incur significant costs in terms of food provisioning, with potential consequences on body condition of both parents and nestlings, and ultimately on their probability of survival. However, apparent survival rates varied as a function of year rather than harvest treatment. Because considerable variations in songbird survival rates have been reported elsewhere (Whitaker, Taylor & Warkentin 2008; Stutchbury *et al.* 2009), our results should be interpreted with caution, especially because individuals banded during the first year post-harvest had only two recapture sessions (years). Fewer recapture sessions (two vs. three) can lead to an overestimation of the probability of recapture and, consequently, an underestimation of apparent survival rate.

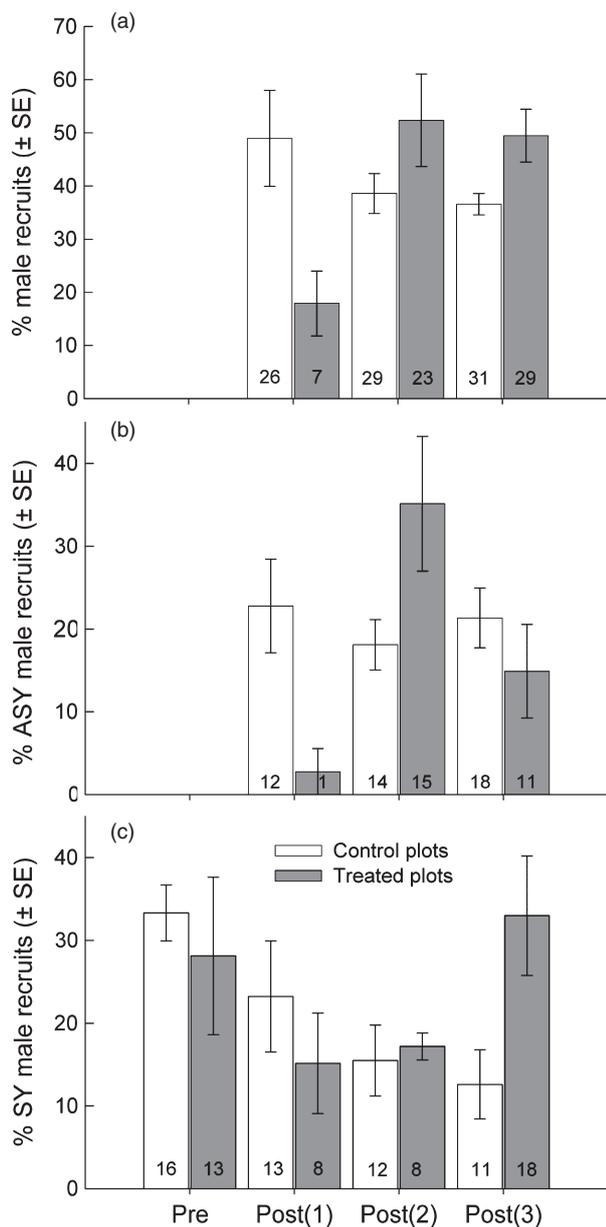


Fig. 4. Mean (\pm SE) proportion of territorial males that were recruits (a), ASY recruits (b), and SY recruits (c) in treated plots and controls during the first (Post1; $n = 4$; $n = 5$ for SY males), second, and third year post-harvest ($n = 5$). Percentages are calculated relative to the total number of territorial males present in each plot/year. The proportion of SY recruits during the pre-harvest year is also shown ($n = 4$). Only 8/145 recruits could not be aged, hence the discrepancies in some of the absolute numbers of recruits indicated at the base of each bar.

AGE-SPECIFIC HABITAT SELECTION BY RECRUITS

Individual songbirds are known to assess habitat quality based on previous experience (Stamps 2001). Hatch-year males have limited time to prospect for good-quality territories before fall migration. That time constraint is compounded by their lower ability to acquire a territory the following spring, assuming pre-emptive territory selection or

despotic behaviour by older males (Sherry & Holmes 1989; Holmes *et al.* 1996; Bayne & Hobson 2001). Older males may disperse from their previous territory for two main reasons: reproductive failure due to predation or unpaired status (Bayne & Hobson 2002; Porneluzi 2003), or inability to acquire their former territory or another one in the vicinity. In either case, these individuals would have gained more experience and a greater ability to assess habitat quality than males breeding for the first time.

In the first year post-harvest, the observed decline in Ovenbird density reflected an age-specific response of individuals to the treatment. As predicted, total male recruitment rate and recruitment rate of ASY males were significantly lower in treated plots than in controls. A lower recruitment rate of ASY males might reflect two non-mutually exclusive phenomena: (i) they responded negatively to experimentally altered habitat and (ii) they were unable to settle in treated plots due to habitat saturation (i.e. increased territory size of returning males). In contrast, the proportion of first-time breeders defending a territory during the first 2 years post-harvest was similar in treated and control plots. Hence, there was no evidence that younger males had to settle in treated plots as a result of despotic behaviour by older males, nor that they actually chose to settle in suboptimal habitat, suggesting high variability in SY males' perception of habitat quality or in their ability to defend a territory.

There was a surprising shift in recruitment pattern from the first to the third year post-harvest. During the second year post-harvest, many newly vacant territories were available to immigrants and recruitment rate increased accordingly, which apparently was not the case in the first year post-harvest. Another important change in the second year post-harvest was that 65% of the recruits in treated plots were ASY males, compared with only 11% in the first year post-harvest. However, this proportion increased to 38% in the third year post-harvest. Assuming that ASY males can accurately assess habitat cues, this suggests that they perceived habitat quality to be similar between control and treated plots during the second year post-harvest, or that they did not have the option to settle in better habitat in the vicinity.

TREATMENT EFFECTS ON POPULATION DYNAMICS

To our knowledge, this is the first study documenting the effects of experimental habitat alteration on recruitment rate in a songbird species using a BACI design. Although many studies have investigated the short-term effects of single-tree selection on the relative abundance of songbirds (Vanderwel *et al.* 2007 and references therein), very few have measured the effects of this treatment on density and none has investigated effects on recruitment, return rate, and apparent survival rate of marked individuals. There may be regional variations in the application of single-tree selection harvesting but our findings still provide insight into birds' behavioural response to major habitat change taking place overwinter.

Even though density remained relatively stable during the post-harvest years, data from Bourque & Villard (2001) suggest that it should decline sharply over the next several years as vegetation structure continues to change in response to canopy opening. In our study area, density does drop significantly as regeneration reaches the pole stage (c. 15–20 years post-harvest; Haché & Villard, unpublished data). At the landscape scale, many of the individuals reluctant to settle in partial cuts might still find suitable habitat elsewhere to breed successfully and contribute to the regional population (Whitaker *et al.* 2008). However, according to the current forest management plans for the region, the proportion of shade-tolerant deciduous stands managed under partial harvesting will increase over the next 20 years (Etheridge *et al.* 2006; Betts *et al.* 2007). Hence, mature closed-canopy forest is expected to become increasingly fragmented, which in turn may reduce the viability of local populations (Bayne & Hobson 2002; Ward 2005).

Although it is sensitive to habitat degradation and loss (Vanderwel *et al.* 2007; Betts & Villard 2009), the Ovenbird is not listed as a species at risk in Canada or in the United States. As a matter of fact, it is still widely distributed across North America and fairly abundant regionally (Sauer, Hines & Fallon 2008). Nonetheless, the fact that it is both sensitive to habitat alteration and widely distributed makes this species a prime focus for research because it offers the opportunity to identify key stressors and prevent their cumulative effects, which are at the root of regional extirpations and global population declines. We submit that preventive research should receive as much attention as species recovery if we are to avoid future ecological crises.

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