Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird

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Abstract. According to the ideal despotic distribution (IDD), dominant individuals gain a fitness advantage by acquiring territories that are of higher quality, thereby forcing other individuals into lower quality habitat. In contrast, the ideal free distribution (IFD) predicts that local density is a function of habitat quality, but that individuals achieve the same fitness in different habitat types as a result of density-dependent variation in territory size. Although the IFD represents an alternative, population dynamics of territorial species are generally expected to be driven by an IDD. We tested the predictions of IFD and IDD by monitoring the demographic response of the Ovenbird (*Seiurus aurocapilla*) to selection harvesting (30–40% tree removal) during the first five years postharvest in five pairs of 25-ha study plots, each comprising a control (undisturbed) and a treatment (harvested plot). In the first year following harvesting, Ovenbird territory size increased in treatment plots relative to controls, whereas density, productivity per unit area, and the abundance of litter invertebrates decreased. Treatment effects declined consistently as stands regenerated, and most effects were no longer significant by the fifth year postharvest. However, there was no treatment effect on daily nest survival rate nor on per capita productivity. These results are consistent with the IFD, whereby similar per capita productivity is achieved across habitat types through density adjustments facilitated by changes in territory size. To our knowledge, this is the first study providing evidence for an IFD in a territorial bird species.

Key words: adaptive habitat selection; density dependence; habitat alteration; habitat quality; litter invertebrates; Neotropical migratory songbirds; partial harvesting; population dynamics; population regulation; private information; Seiurus aurocapilla; *territoriality.*

Introduction

Population dynamics of territorial species are often described as being driven by an ideal despotic distribution (IDD), whereby more experienced/competitive individuals secure territories where their fitness is maximized (Holmes et al. 1996, Petit and Petit 1996, Murphy 2001, Calsbeek and Sinervo 2002). This scenario implies that dominant individuals force subordinates into lower quality habitat where the subordinates achieve lower fitness. Each year, individuals from lower quality territories try to improve their fitness by moving into higher quality habitat, but not vice versa (e.g., Reijnen and Foppen 1994). A specific case of the IDD, the ideal preemptive distribution (IPD), suggests that individuals select the best territories, whose availability decreases with increasing density (Pulliam and Danielson 1991). Preemptive behavior tends to result in higher quality territories being secured earlier by more experienced or dominant individuals, allowing them to achieve higher fitness than those forced to defend lower quality territories (Sergio and Newton 2003).

Although the IDD and IPD make intuitive sense and are the processes put forward to explain source–sink dynamics (Pulliam 1988) and population regulation through site dependence (Rodenhouse et al. 1997), some authors suggest that these models do not adequately describe patterns observed in the field, mainly because the assumption of constant territory size within and among habitat of different quality is rarely met (Ridley et al. 2004, Piper 2011). A key prediction from the IDD is differential per capita productivity as a function of habitat quality, which results from despotic behavior (i.e., interindividual differences in competitive ability) and territoriality (Ridley et al. 2004). However, some studies show that site familiarity could compensate to some degree for low habitat quality and allow individuals to achieve unexpectedly high fitness (reviewed by Piper [2011]). This could lead to patterns consistent with predictions from the ideal free distribution (IFD; Fretwell and Lucas 1969), whereby density is adjusted through territory size to match local habitat quality (cf. habitat matching rules; Morris 1994). Under an IFD, population regulation is more likely to be driven by density-dependent factors acting simultaneously on different vital rates, irrespective of habitat quality

(Nevoux et al. 2011; see also Morris 1994). There is also evidence that despotic behavior may not necessarily result in an ideal despotic distribution as it may not prevent per capita productivity of individuals in good quality habitat from being density dependent, owing to variation in territory size (Ridley et al. 2004).

The IFD is also a simplistic model for explaining territory settlement patterns because, like the IDD, it assumes that private information does not influence habitat selection ("familiarity blindness" or "site indifference"; Schmidt 2001, Piper 2011). Site fidelity has been shown to be influenced by past reproductive success (e.g., Switzer 1997, Tremblay et al. 2007, Thériault et al. 2012). In addition, both the IDD and IFD models assume that individuals have perfect (ideal) knowledge about resource availability and density dependence functions. However, there is evidence that nonideal habitat selection by dominant individuals can occur (Arlt and Pärt 2007, Hollander et al. 2011; reviewed by Chalfoun and Schmidt 2012). Ecological traps (preference for lower quality habitat; Battin 2004) and perceptual traps (avoidance of high-quality habitat; Gilroy and Sutherland 2007, Patten and Kelly 2010) are extreme cases of nonideal habitat selection (Pärt et al. 2007).

In spite of their relative simplicity, IDD and IFD models provide a useful theoretical framework to explore species–habitat relationships and interindividual differences in competitive ability (Boulinier et al. 2008). For example, based on empirical models, Haugen et al. (2006) found that 40 years of variation in the distribution of pike (*Esox lucius*) in a lake composed of two basins with contrasting productivity was consistent with an IFD. The presence or absence of habitat-specific variation in per capita productivity can have very different consequences for population dynamics, not to mention conservation (Morris 2003). For example, given similar population size and habitat quality, an IDD implies that a portion of the population contributes disproportionately to population growth, whereas individual contribution to population growth is more uniform under an IFD, irrespective of habitat quality. Hence, the loss of high-quality sites may have disproportionately negative effects in species following an IDD not only because the region's best territories would be lost, but it would potentially threaten the reproduction and survival of dominant individuals. Populations can also be anywhere along a "free" to "despotic" continuum owing to spatiotemporal variation in population size and habitat quality (Ridley et al. 2004). Knowing where a regional population falls along this gradient would yield insight into the effective population size of a focal species.

In this study, we tested predictions of the IFD and IDD on the demographic response of the Ovenbird (*Seiurus aurocapilla*), a Neotropical migratory songbird, to an experimental alteration of its habitat (selection harvesting) in five pairs of study plots (one control, undisturbed study plot and one treated plot, harvested study plot) over a six-year period (1 year pre- and 5 years postharvest). In the same study area, Pérot and Villard (2009) found patterns in density and the proportion of territories producing at least one young that were consistent with an ideal free distribution, whereas Thériault et al. (2012) found no evidence that Ovenbird males preferred plots treated through selection harvesting and, hence, no evidence that the treatment created ecological traps. Here, we examined the magnitude and duration of effects of selection harvesting on Ovenbird density, territory size, productivity (per unit area and per capita), and daily nest survival rate to determine whether adaptive habitat selection (sensu Morris and MacEachern 2010) occurred in response to experimental disturbance. On the basis of the IFD, we predicted a negative effect of treatment on density (through an increase in territory size) and productivity per unit area, but no treatment effect on productivity per capita. In contrast, the IDD would predict that per capita productivity will be lower in treated plots than in controls, assuming that the former represent lower quality habitat. We also estimated the abundance and biomass of litter invertebrates during the peak of the Ovenbird nestling period because they represent the main source of food exploited by Ovenbirds (Stenger 1958), and food abundance is a key component of habitat quality on both the breeding and wintering grounds (Smith and Shugart 1987, Strong and Sherry 2000, Seagle and Sturtevant 2005). We predicted that, as treated stands regenerate, the magnitude of negative treatment effects on Ovenbird demography and abundance of litter invertebrates would decrease. This, in turn, should decrease the influence of either IFD or IDD on population dynamics, as partially harvested plots gradually become functionally equivalent to controls.

Methods

Study area

The study was conducted in northwestern New Brunswick, Canada (47°23′ N, 67°40′ W), within a 2000-km^2 forest district privately owned by J. D. Irving, Limited (between St. Quentin and St. Leonard, New Brunswick, Canada). This intensively managed forest landscape is characterized by hardwood stands (25% of total area; sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and American beech [*Fagus grandifolia*]), conifer stands (20%; black spruce [*Picea mariana*], white spruce [*Picea glauca*], jack pine [*Pinus banksiana*]), mixedwood stands (18%), and spruce (*Picea* spp.) plantations (37%; Etheridge et al. 2005).

For 30 years, J. D. Irving has managed hardwood stands and hardwood-dominated mixedwoods using partial harvest treatments, selection harvesting being the most widely used. This treatment typically removes 30–40% of the basal area (cross-sectional area at breast height [1.35 m] of all stems with a diameter ≥10 cm) every 20–25 years. The creation of skid trails (5 m wide)

accounts for 20% of the basal area removal, the extra 10–20% being harvested in the residual forest between skid trails (Gaetan Pelletier, *personal communication*).

Focal species and experimental design

The Ovenbird is considered to be one of the vertebrate species most sensitive to forest management in the northern hardwood forest (Vanderwel et al. 2007, 2009). Its fledging success has been shown to be positively correlated with the biomass of litter macroinvertebrates and productivity of mature deciduous forest stands (Seagle and Sturtevant 2005).

From 2006 to 2011, we have used a before and after-control and impact paired (BACIP) design to measure the demographic response of Ovenbird to the treatment (selection harvesting), while controlling for plot and year effects. Each year, we have quantified density, territory size, productivity (per unit area and per capita), and daily nest survival rates in 10 study plots (25 ha each) that were spatially paired (see Haché and Villard 2010). The average distance was 4.2 ± 1.0 km (mean $\pm$ SD) between paired plots and 23.8 ± 9.1 km among pairs. In December 2006 and January 2007, one plot of each pair was treated through selection harvesting, including a 50-m band harvested around each treated plot, whereas the other plot was left intact and used as a control. Every year, we individually marked territorial males in all study plots using unique color band combinations (see Plate 1), except in one pair of study plots in 2006.

Territory size and configuration were estimated using spot mapping (Bibby et al. 2000). We mapped all detections of territorial males during eight visits to each plot and drew ellipses around clusters of detections using countersinging and locations of banded males for guidance (see Haché and Villard 2010 for details). Only territories that overlapped study plots by $\geq 25\%$ were considered in density estimates, which were obtained by adding all territories and territory fractions (fractions estimated as overlap of 0.25, 0.33, 0.50, 0.66, and 0.75). Throughout the breeding season, we performed systematic nest searching and balanced the effort across territories, irrespective of local density. Each nest was monitored every 2–3 d until the young fledged or the nest was depredated or abandoned. Productivity per capita was calculated as one-half of the number of young fledged per territory. Breeding success was also attributed to banded males seen with a family group, or to territories where we saw fledglings unable to sustain flight with an unbanded adult. In those instances, the mean number of young fledged per nest in the treatment vs. control was used to estimate productivity. The proportion of males with unknown breeding status was 25.2%, and it did not differ between treatment and controls (23.8% and 25.8%; Appendix A). In the analyses, we assumed that those "unknown" territories had failed (see Appendix A for details). Productivity per unit area (per 25 ha) was estimated by adding the contribution of all breeding pairs to a given study plot.

For example, a pair that produced four fledglings and had 25% of its territory overlapping a study plot was considered to have contributed 1 young to the plot's productivity.

In four pairs of study plots, we sampled Ovenbird food items (frequency of occurrence and biomass) during the peak of the nestling period (1–12 July) over five breeding seasons (one year pre- and four years postharvest). We collected all invertebrates (≥ 2 mm) detected in the litter of a 0.2-m^2 quadrat over a 3-min period (Willson and Comet 1996, Van Wilgenburg et al. 2001). Sampling was conducted at 60 predetermined locations in each study plot. We then estimated the frequency of occurrence and biomass of invertebrates (all taxa), and those of ground beetles (Coleoptera) and land snails (Gastropoda) in each study plot. Stenger (1958) showed that taxa found in Ovenbird stomach contents were proportionate to their availability in the corresponding territories. We compiled data on gastropods separately because calcium limitation may have important implications for Ovenbird productivity (Pabian and Brittingham 2007). Finally, we also compiled Coleoptera (imagoes and larvae) data separately because adults of many forest bird species have been shown to forage extensively on them (Holmes and Robinson 1988). The biomass of each group was quantified for each study plot (see Appendix A for further details on the sampling method).

Statistical analyses

Different variables were sampled at different levels of our hierarchical experimental design. Territory size and per capita productivity were measured at the territory level, abundance of invertebrates at the quadrat level, whereas density and productivity per unit area, and biomass for each group of invertebrates were measured at the study plot level. Furthermore, pairs of plots were clustered at the landscape context level. To test for treatment, year, and treatment $\times$ year interaction effects on different demographic parameters and invertebrate abundance and biomass, we used variations of linear mixed and generalized linear mixed models (Appendix A). Appropriate hierarchical levels were included as random effects as a function of the sampling unit of each response variable. Temporal autocorrelation associated with the repeated measurement of sampling units was explicitly considered by specifying a first-order autoregressive structure to each model. To distinguish treated plots and controls for the duration of the study, the five harvested plots were also considered as treated during the preharvest year. We also used post hoc multiple comparison analyses to test for treatment effects in specific years. Consequently, a significant treatment $\times$ year interaction was required to infer a treatment effect. Using similar statistical analyses, we also explored heterogeneity in food abundance within treated plots by testing for a difference in the abundance of litter invertebrates in samples collected on skid trails and in
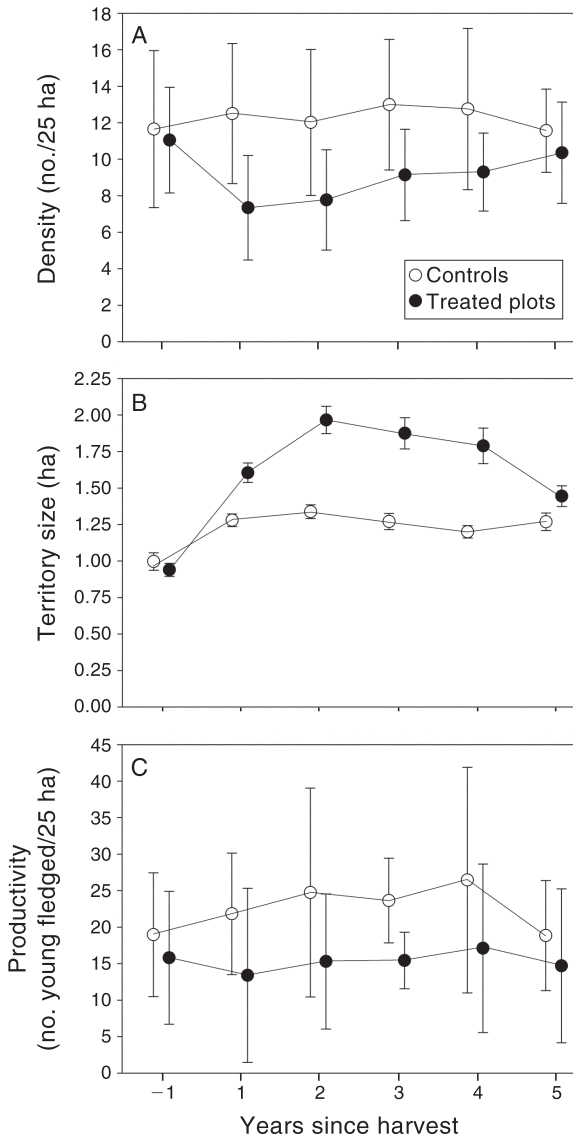
FIG. 1. (A, B) Density and territory size of territorial Ovenbird (*Seiurus aurocapilla*) males, and (C) productivity per unit area in intensively managed forest plots treated by selection harvesting (30–40% tree removal) and in controls one year preharvest (−1 on *x*-axis) and the first five years postharvest (1–5 on *x*-axis). Values are means with 95% CI.

the residual forest, and to determine how it evolved as stands regenerated. We then used a post hoc multiple comparison analysis to test for treatment effects in specific years. Lastly, a logistic exposure model was used to estimate the treatment, year, and treatment × year interaction effects on daily nest survival rate (Shaffer 2004). Because only one random effect can be included in the model using this procedure, four a priori models with treatment, year, and treatment × year interaction as predictors were compared using an AIC approach. The first model had no random effect, and the three others had one of the three random effects accounting for the

nonindependence of our sample units (i.e., nest inden-
tification, plot, and landscape context).

RESULTS

We monitored a total of 784 territories (458 in controls/326 in treated plots) over the six years, 721 (92%) of which were held by banded males. In total, 349 males were banded and 197 (105/92) returned for at least one breeding season. We found 229 nests (148/81). Of these, 135 (59%; 90/45) were successful. There were 3.66 ± 1.1 young fledged per nest (mean ± SD; $n = 85$) in controls and 3.98 ± 1.1 young fledged per nest ($n = 42$) in treated plots (brood size was unknown for eight successful nests). In monitored territories where no nest could be found, 212 (128/87) family groups were detected.

There was a significant treatment × year interaction effect on the density of territorial males ($F_{5,40} = 7.3$, $P < 0.001$). Significant negative treatment effects were observed for the first four years postharvest (Fig. 1A; Appendix B: Table B1). Territory size followed a similar pattern, with a significant treatment × year interaction effect ($F_{5,759} = 40.0$, $P < 0.001$). Territories were significantly larger in treated plots than in controls in all postharvest years, but to a lesser extent during the fifth year postharvest (Fig. 1B; Appendix B: Table B2). There was only a significant negative treatment effect on mean productivity per unit area ($F_{1,40} = 17.6$, $P < 0.001$). When analyses were conducted separately for each year, productivity per unit area was only significantly lower in treated plots during the first four years postharvest (Fig. 1C; Appendix B: Table B3). In contrast, we found no effects of treatment or year on per capita productivity (Fig. 2A; Appendix B: Table B4), nor daily nest survival rate (Fig. 2B). The best ranked model estimating daily nest survival rate included landscape context as a random effect ($k = 13$, AIC = 626.86, AIC weight = 0.60). The ΔAIC values for models with other levels of random effects or no random effect were >2, suggesting substantially less support. Treatment effects on territory size, density, and productivity per unit area, as well as the lack of evidence for treatment effects on per capita productivity and daily nest survival rate are consistent with predictions from an IFD.

There was a significant treatment × year interaction effect ($F_{4,1912} = 15.7$, $P < 0.001$) on total abundance of litter invertebrates, with lower abundances in treated plots than in controls during the first four years postharvest (Fig. 3A; Appendix B: Table B5). The same treatment × year interaction effect was observed for the abundance of Coleoptera ($F_{4,1912} = 5.1$, $P < 0.001$; Appendix B: Fig. B1.A) and Gastropoda ($F_{4,1912} = 3.2$, $P = 0.013$; Appendix B: Fig. B1.B, Tables B6–B7). In contrast, when considering total invertebrate biomass, only year ($F_{4,24} = 4.4$, $P = 0.008$) and treatment ($F_{1,24} = 19.5$, $P < 0.001$) effects were significant. Total biomass was significantly lower in treated plots than in controls during the first four years of the study, including the
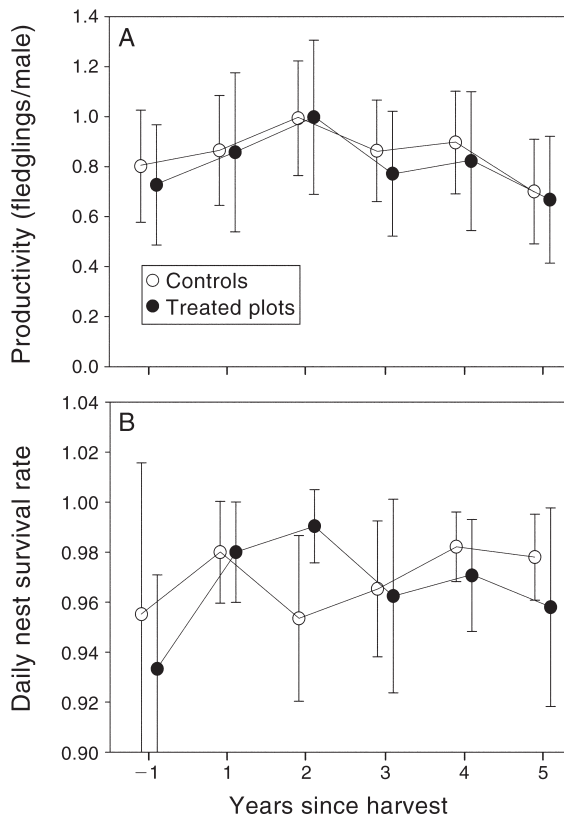
Fig. 2. (A) Productivity per territorial Ovenbird male and (B) estimated mean daily nest survival rate in treated plots and controls one year preharvest and the first five years postharvest. Values are means with 95% CI.

the contention that food abundance is a key factor underlying the observed IFD.

DISCUSSION

Ovenbird demographic parameters and their relationship to variations in the abundance of litter invertebrates were consistent with predictions from the ideal free distribution (IFD; Fretwell and Lucas 1969) despite the
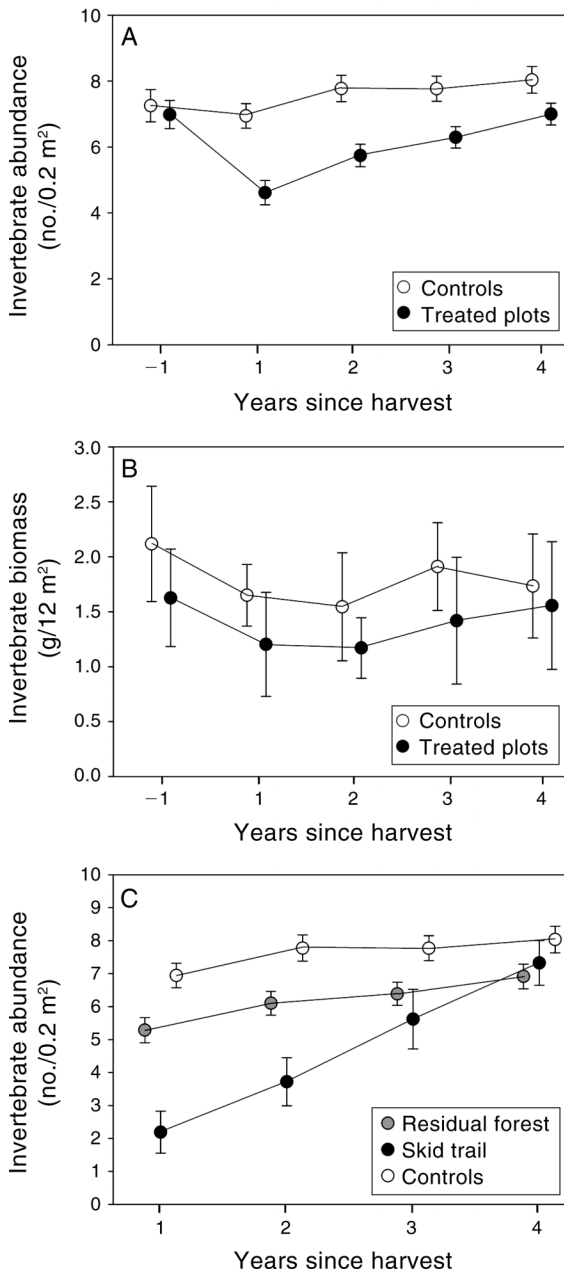

Fig. 3. (A) Abundance of invertebrates (per sampling point) and (B) total biomass of invertebrates (per study plot) in treated plots and controls, and (C) abundance of invertebrates per sampling point in skid trails vs. inter-trail forest in treated plots and in controls. Values are means with 95% CI.

preharvest year (Fig. 3B; Appendix B: Table B8). Similarly, only year ($F_{4,24} = 3.6$, $P = 0.020$) and treatment ($F_{1,24} = 26.8$, $P < 0.001$) had significant effects on biomass of Coleoptera (Appendix B: Fig. B1.C), whereas only year was a significant predictor of biomass of Gastropoda ($F_{4,24} = 5.1$, $P = 0.004$; Appendix B: Fig. B1.D). However, when testing for year-specific treatment effects, the difference in biomass of Coleoptera was only significantly lower in treated plots than in controls during the first three years postharvest ($P \leq 0.006$; Appendix B: Tables B9–B10). The difference in total abundance of invertebrates ($F_{3, 949} = 25.2$, $P < 0.001$; Fig. 3C), Coleoptera ($F_{3, 949} = 2.9$, $P = 0.033$), and Gastropoda ($F_{3, 949} = 4.4$, $P = 0.005$; Appendix B: Fig. B1 [panels E, F]) in skid trails vs. residual forest varied as a function of number of years postharvest. Total abundance of invertebrates was significantly lower in skid trails than between trails during the first two years postharvest and the importance of this effect decreased consistently as stands regenerated (Appendix B: Table B11). A similar pattern was observed for the abundance of Coleoptera and Gastropoda (Appendix B: Tables B12–B13). The treatment effects we observed on food abundance were consistent with variations in territory size, density, and productivity per unit area, supporting

PLATE 1.   A color-banded male Ovenbird (*Seiurus aurocapilla*) delivering food to the nest. Photo credit: Jonathan Frenette.

fact that our focal species is strongly territorial. Density, through changes in territory size, was adjusted to match local habitat conditions, resulting in similar per capita productivity between treatment plots and controls. The fact that per capita productivity did not vary between habitat types with contrasting Ovenbird densities represents strong evidence against an ideal despotic distribution (IDD). As stands regenerated, treatment effects became weaker, and they were barely detectable by the fifth year postharvest, suggesting that treated plots were becoming functionally equivalent to controls.

Density-dependent effects on songbird territory size (Ridley et al. 2004, Sillett et al. 2004, Pons et al. 2008) or small-mammal home range size (Abramsky et al. 1979, Pusenius and Schmidt 2002) have been shown in many species. The absence of posttreatment crowding in this study suggests that subordinate males could not force territorial individuals to share resources, or that they found alternative territories elsewhere in the study area. Territory size was negatively correlated with food abundance (see also Stenger 1958, Smith and Shugart 1987) and postharvest adjustments in territory size by males banded in the preharvest year indicate a high degree of behavioral plasticity and adaptive habitat

selection (see also Haugen et al. 2006, Morris and MacEachern 2010, Chalfoun and Schmidt 2012). The observed pattern is also consistent with food-value theory (Stenger 1958, Marshall and Cooper 2004), which predicts that males from treated plots would increase the size of their territory to compensate for the postharvest decline in food abundance. This response seems to have allowed Ovenbirds to achieve similar per capita productivity, irrespective of treatment. As clear-cut skid trails regained similar abundances of litter invertebrates as inter-trail forest, territory size decreased and treatment effects on demographic parameters almost all became nonsignificant by the fifth year postharvest.

Although the average quality of a territory apparently did not differ between treatment and controls, the cues that are used by returning migrants to assess habitat quality and secure the resources required to attract a mate and produce young remain unclear. Site familiarity, private information (i.e., information from previous breeding experience; Piper 2011), information on predator activity (Emmering and Schmidt 2011), natal habitat preference (Davis and Stamps 2004), social information (Danchin et al. 2004, Pärt et al. 2011), or

cues provided by habitat structure (James 1971, Smith and Shugart 1987) may all play a role (see ecology of information; Schmidt et al. 2010). Further studies should strive to tease apart these non-mutually exclusive factors, as exemplified by van Bergen et al. (2004), Betts et al. (2008), Mariette and Griffith (2012), and Thériault et al. (2012).

Very few studies have presented empirical evidence in support of an ideal preemptive distribution (Sergio and Newton 2003, Zajac et al. 2006, Petty and Grossman 2010). In our study area, Thériault et al. (2012) found that male Ovenbirds returning from previous breeding seasons settled first in any given plot, alone or with a few unbanded recruits, and that settlement started 2–5 days earlier in controls than in selection cut plots. This may be seen as evidence for preemptive habitat occupancy by individuals familiar with the plots. However, the fact that some plots were first occupied by a combination of returning males and recruits suggests that public information provided by experienced breeders is a more likely mechanism underlying habitat selection by recruits (see location cues; Danchin et al. 2004). The settlement pattern observed by Thériault et al. (2012) does not necessarily lead to a rejection of IFD predictions: higher quality habitat may be selected first and lower quality habitat later as density increases in controls (Giraldeau 2008). There also was no evidence for a treatment effect on apparent survival rate of male Ovenbirds during the first four years of this study (Haché and Villard 2010). The same study reports a lower recruitment rate in treated plots than in controls during the first year postharvest. This probably reflected the increase in territory size of returning individuals in response to the treatment, because recruitment rate became similar between treated and control plots over the next two years (Haché and Villard 2010).

These results and those reported in this study are all consistent with an IFD in a territorial songbird. Such a finding is somewhat unexpected for birds. Indeed, the IDD tends to receive more support than the IFD (reviewed by Rodenhouse et al. 1997, Piper 2011). Yet, there is a growing body of evidence suggesting that the IFD can indeed apply to birds (Weidinger 2000, Sebastian-Gonzalez et al. 2010, Quaintenne et al. 2011) and many other taxa (Beckmann and Berger 2003, Rieger et al. 2004, Haugen et al. 2006, Morris and MacEachern 2010).

We showed that in a moderately altered ecosystem, individuals can adjust the size of their territory as a function of food abundance and, in turn, exhibit similar per capita productivity as their conspecifics from higher density habitat. This is further evidence that density can be a good indicator of productivity per unit area (Bock and Jones 2004, Pérot and Villard 2009), though not necessarily per capita (Skagen and Yackel Adams 2011). Hence, mosaics of varying habitat quality do not necessarily exhibit spatial source–sink dynamics. Temporal source–sink dynamics, where density-dependent factors act irrespective of habitat quality, also need to be considered (Nevoux et al. 2011). Future studies should also consider that individual distributions most likely fall in a continuum between IDD to IFD rather than being either one or the other (Ridley et al. 2004). Lastly, subtle habitat-specific effects on population dynamics should be given consideration. For example, there is evidence that defending territories in habitat of lower quality can incur a cost in terms of survival rate over long time periods (A. Vernouillet, M.-A. Villard, and S. Haché *unpublished manuscript*). In the Ovenbird, stress levels and sex ratio in nestlings have also been shown to differ between partially harvested and control plots (Leshyk et al. 2012). Ultimately, this may reduce male fitness and, thus, population growth rates among habitat types varying in quality (Arlt et al. 2008). For these reasons, relatively subtle impacts of human activities on population dynamics deserve careful attention when considering our ever-expanding ecological footprint.

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SUPPLEMENTAL MATERIAL

Appendix A

Additional details on methods used to determine breeding status of territorial Ovenbirds, invertebrate sampling design, and statistical analyses (*Ecological Archives* E094-074-A1).

Appendix B

Results from the multiple comparison analyses testing for year-specific treatment effects and figures presenting mean abundance and biomass of Coleoptera and Gastropoda for each year and habitat type and mean abundance between skid trails and inter-trail forest within treated plots (*Ecological Archives* E094-074-A2).