# Do we create ecological traps when trying to emulate natural disturbances? A test on songbirds of the northern hardwood forest[1]

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**Abstract:** Forest management inspired from natural disturbances is often claimed to have more benign effects on biodiversity than more traditional approaches but this premise has rarely been tested. In the northern hardwood forest, selection harvesting could be seen as a surrogate for the combined effects of windthrow, moderate ice storms, and senescence. Here, we quantified the response of two focal species of forest birds (Brown Creeper (*Certhia americana* (Bonaparte, 1838)) and Ovenbird (*Seiurus aurocapilla* (Linnaeus, 1766))) to this treatment (30%–40% basal area removal) in the first 5 years postharvest using a replicated field experiment. We tested the possibility that selection harvesting creates ecological traps whereby individuals show a preference for a habitat type where their fitness is lower. We found that both focal species actually seemed to prefer control plots, where they reached a higher density than in treated plots. There was no evidence for a treatment effect on per capita productivity in either species. Hence, there was no evidence for an ecological trap. However, large-scale application of selection harvesting may have ecologically significant effects on productivity of the focal species per unit area of habitat. Future studies should test whether selection harvesting creates ecological traps for species naturally associated with canopy gaps.

**Résumé :** On prétend souvent que l'aménagement forestier inspiré des perturbations naturelles a des effets plus bénins sur la biodiversité que les approches plus traditionnelles, mais cette prémisse a rarement été testée. En forêt feuillue nordique, la coupe de jardinage pourrait être vue comme un substitut des effets combinés du chablis, des tempêtes de verglas d'intensité modérée et de la sénescence. Nous avons quantifié la réponse de deux espèces focales d'oiseaux forestiers (grimpereau brun (*Certhia americana* (Bonaparte, 1838)) et paruline couronnée (*Seiurus aurocapilla* (Linnaeus, 1766))) à ce traitement (prélèvement de 30–40 % de la surface terrière) dans les 5 premières années suivant la récolte, au moyen d'un dispositif expérimental répliqué spatialement. Nous avons évalué la possibilité que la coupe de jardinage crée des pièges écologiques en ce sens que les oiseaux montreraient une préférence pour un type d'habitat dans lequel leur dégré d'adaptation serait plus faible. Nous avons observé que les deux espèces focales semblaient préférer les sites témoins dans lesquels elles atteignaient des densités plus élevées que dans les sites traités. Rien n'indiquait que le traitement avait un effet sur la productivité per capita chez l'une ou l'autre des espèces. Il n'y avait donc aucun indice de piège écologique. Toutefois, l'application à grande échelle de la coupe de jardinage pourrait avoir des effets significatifs sur la productivité des espèces focales par unité de surface d'habitat. D'autres études devraient vérifier si la coupe de jardinage crée des pièges écologiques pour les espèces naturellement associées aux trouées du couvert arborescent.

[Traduit par la Rédaction]

## Introduction

Forest managers are often encouraged to design harvest plans and silvicultural treatments reflecting natural disturbances typical of their ecoregion (Bergeron et al. 1999; Gauthier et al. 2009; Long 2009). A basic premise behind this recommendation is that species have evolved under a certain set of natural disturbances and have acquired life history traits allowing them to adapt to the disturbances themselves or the resulting habitat conditions (Mutch 1970; Bunnell 1995; Perera and Buse 2004). Hence, managing the forest within the natural range of variability in stand or landscape structure is expected to have lower impacts on biodiversity than managing outside this range. That being said, it is often impractical to fully emulate natural disturbances in the context of timber management (Perera and Buse 2004), given the large portion of the tree biomass and nutrients left in the system when fire or insect outbreaks are the dominant disturbances. At the

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other extreme, natural disturbances may be too infrequent or limited in extent to allow economically viable treatments under the natural disturbance emulation paradigm.

Surprisingly few studies have been conducted to test the premise that natural disturbance based management actually has a lower impact on biodiversity than other practices such as sustained-yield forest management. Drapeau et al. (2009) examined the overall response of forest songbirds to percent cover of late-seral forest in their boreal landscape of northwestern Quebec and related this back to the percent cover of old forest expected to be present based on forest fire simulations. In two of the three songbird species examined, thresholds in probability of occurrence coincided with the lower bound of the historical range in old forest cover predicted from their fire model. Hence, they concluded that natural disturbance based management in this system would maintain large populations of these focal species. Robertson and Hutto (2007) compared the fitness of another migratory songbird, the Olive-sided Flycatcher (*Contopus cooperi* (Nuttall, 1831)), in burned and thinned forests of the northern Rocky Mountains of the United States. They hypothesized that a thinning harvest treatment would lure birds into low-quality habitat, i.e., that natural disturbance emulation would create an "ecological trap" (Dwernychuk and Boag 1972). They found that males defended territories earlier and reached a higher density in the harvested plot than in the burned plot, even though nesting success was higher in the burned plot. Robertson and Hutto (2007) concluded that harvesting or restoring forest habitat using natural disturbance patterns as a guide may lead to maladaptive habitat selection by species when the attractiveness of the newly created habitat cues does not reflect the fitness that will be achieved by most individuals settling there. In other words, it appeared that flycatchers were being trapped in low-quality habitat.

In contrast with natural disturbance emulation, plantation silviculture tends to create stand and landscape structures that contrast with those under which forest species have evolved. Nonetheless, some species may still show a preference for exotic plantations relative to nearby native habitat. For example, in the Czech Republic, Remeš (2003) found that a small migratory bird, the Blackcap (*Sylvia atricapilla* (Linnaeus, 1758)), settled earlier and reached higher densities in black locust (*Robinia pseudoacacia* (Linnaeus, 1753)) plantations than in native floodplain forests even though its reproductive success was significantly lower in the former.

Both Remeš (2003) and Robertson and Hutto (2007) suggested that focal species are trapped by a decoupling between habitat cues associated with food and habitat parameters influencing nest predation risk. This is in contrast with recent studies suggesting that songbirds can assess nest predation risk when selecting their future breeding territory (Morton 2005; Emmering and Schmidt 2011). However, both Remeš (2003) and Robertson and Hutto (2007) admitted that their studies lacked treatment-level replication and called for future studies investigating ecological traps using well-replicated designs.

In the northern hardwood forest of New Brunswick, Canada, uneven-aged management has been widely applied since the 1980s. It allows harvesting timber while increasing the commercial quality of treated stands and ensuring a strong natural regeneration (Nyland 2003; Neuendorff et al. 2007).

In this study, we used a replicated field experiment to monitor the response of two focal species of birds to a selection harvest treatment that removed 30%–40% of the basal area of trees in the winter of 2006–2007 (see Haché and Villard 2010 for details). This level of removal is typical of single-tree selection harvesting and under this silvicultural system, harvest entries are separated by 15–25 years, depending on site productivity (G. Pelletier, J.D. Irving Ltd., personal communication). Northern hardwood forests are characterized by small-scale, gap-phase dynamics whereby one or a few trees die from senescence, pathogens, or windthrow (Seymour et al. 2002; Fraver et al. 2009). Sporadic ice storms may also create relatively short-lived canopy gaps (Beaudet et al. 2007). Typically, the overall area disturbed does not exceed 1% per year (Runkle 2000; Fraver et al. 2009). Hence, the selection harvest treatment applied in this study exceeds this rate and the disturbance occurs all at once rather than being spread over a longer period. Nonetheless, selection harvesting is at the lower end of a gradient in forest management intensity in the northern hardwood forests of Canada and the northeastern United States (Nyland 1998) and it mimics to some extent the combined effects of windthrow, ice storms, and tree senescence (but see Angers et al. 2005).

To assess the potential of this silvicultural system to meet both economic and biodiversity conservation objectives, we must determine whether forest species most sensitive to harvesting maintain healthy populations in treated sites. In this study, we focused on the Ovenbird (*Seiurus aurocapilla* (Linnaeus, 1766)) and the Brown Creeper (*Certhia americana* (Bonaparte, 1838)), the two species of songbirds that have been shown to be the most sensitive to partial harvest treatments in North America (Vanderwel et al. 2007). We quantified their demographic response to determine whether selection harvesting can create ecological traps when applied to northern hardwood forests. More specifically, we asked (1) whether any of these focal species exhibits a preference for treated stands and (2) whether their demographic parameters suggest that fitness is lower in treated plots than in controls. Because nest predation is the main source of reproductive failure in songbirds (Ricklefs 1969; Martin 1992), we also asked (3) whether selection harvesting has an effect on the abundance of two important predators on Brown Creeper and Ovenbird nests, respectively, the Red Squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)) and the Eastern Chipmunk (*Tamias striatus* (Linnaeus, 1758)) (J.-F. Poulin, É. D'Astous, and M.A. Villard, unpublished data; Schmidt et al. 2008).

## Methods

### Study area

The study was conducted in the Black Brook District (47° 23′N, 67°40′W), a 2000 km² land base owned by J.D. Irving Ltd. The topography is characterized by rolling hills with northern hardwood forest codominated by sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and American beech (*Fagus grandifolia* Ehrh.) on hilltops (approximately 20% of the district) and coniferous stands dominated by balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* (Mill.) Britton, Sterns, & Poggenburg) at the bottom of

slopes (approximately 25%). Approximately 37% of the District is planted, mainly with black spruce and white spruce (*Picea glauca* (Moench) Voss), whereas the balance is covered by mixedwood stands (Etheridge et al. 2006).

## Experimental design

Brown Creeper data were collected in five pairs of study plots (25 ha each). Each pair comprised a treated plot (single tree selection, 30% or 40% basal area removal) and a control. The removal level was established to obtain similar post-harvest basal areas (16.6 m²/ha ± 0.7 SD). We have now monitored Ovenbird response to the selection harvest treatment within the same experimental plots every summer since 2006, or 2007 for the Brown Creeper. For the purposes of the present paper, we used a subset of two pairs of plots from 2008–2010 to monitor settlement patterns in Ovenbird males upon their return from spring migration and to determine treatment effects on per capita productivity.

## Bird survey methods

All bird detections were mapped using a standard spot mapping method (Bibby et al. 2000). We conducted eight spot mapping visits between sunrise and 0930 in each plot from the end of May until early July each year. In the case of the Brown Creeper, we also mapped individuals detected during intensive nest searching in early May each year. We also recorded detections of potential nest predators and used the mean number of detections per visit as an index of abundance for the Red Squirrel and the Eastern Chipmunk (Poulin et al. 2010). The Ovenbird male subpopulation was marked using unique combinations of colour bands along with a numbered aluminum band, whereas Brown Creepers were not banded except for 21 individuals in 2009.

For the Ovenbird, we monitored territory settlement patterns by mapping territories of males daily over the first week following their return from spring migration and every second day thereafter (Thériault et al. 2012). We conducted systematic nest searching throughout our study plots using preliminary maps of territories. All nests found were monitored every 3 days. In addition to nest searching, we monitored territories for recently fledged young (hereafter family groups). Ovenbird family groups could be assigned to specific territories when young were fed by a banded male or fledglings could not sustain flight. In the Brown Creeper, we made a specific effort to detect recently fledged young to confirm nest success in territories whose nest was too high to be monitored using a camera mounted on a telescopic pole.

## Statistical analyses

In the Brown Creeper, we could find the majority of active nests in the territories monitored, except for the few cases where nests were depredated or abandoned very early in the process (É. D'Astous, J.-F. Poulin, and M.-A.Villard, personal observation). Therefore, we searched for evidence for a preference between treated plots and controls by plotting the cumulative number of active nests found in either habitat type, pooling all sites. In the Ovenbird, saturation rate was estimated by plotting the increase in the number of males detected upon their return from spring migration. As returning (banded) males show different settlement patterns than re-

cruits (unbanded males) (Thériault et al. in review), we compiled the cumulative curves separately as a function of male status. We plotted the number of males detected, standardized according to the date of first settlement each year and averaged over the 3 year period (2008–2010).

Habitat quality was compared between treated and control plots using the following demographic parameters: nest density (Brown Creeper), density of territories (Ovenbird), and per capita reproductive success (both species). For the Ovenbird, we tested for a treatment effect on per capita reproductive success using a generalized linear mixed model (Poisson distribution) with treatment, male status (recruit/returning), year, and their interactions as fixed effects and study plot as well as study plot nested within plot pair as random effects. Brown Creeper per capita reproductive success was estimated through the monitoring of all known nesting attempts (including renests) for territories overlapping our study plots by >75% of their estimated surface. Because we could not access all creeper nests, we used a binary response variable (success or not) rather than the number of fledglings. Ovenbird per capita reproductive success was estimated as 50% of the brood size recorded at the last visit prior to the fledging date (approximately day 8). In territories where no nest could be found but a family group was detected, we used 50% of the mean brood size recorded in each habitat type across the 10 study sites of Haché and Villard (2010) for the 2008–2010 period (treated plots: 3.89 young, $n = 28$; control plots: 3.67 young, $n = 57$).

Finally, we used the same statistical approach to test for a treatment effect on the abundance of Red Squirrel and Eastern Chipmunk with treatment, year, and their interaction as fixed effects and study plot within plot pair as a random effect.

## Results

In the Brown Creeper, there was no evidence for a preference for treated plots. The number of active nests actually increased faster in controls than in treated plots (Fig. 1). In addition, nest density was significantly lower in treated plots than in controls in each of the 5 years after experimental selection harvesting, although there were significant year-to-year fluctuations (Table 1; Fig. 2). When comparing per capita productivity, there was no significant treatment effect ($F_{[1,7]} = 0$, $P = 0.99$), nor was there a year effect ($F_{[4,7]} = 0.81$, $P = 0.56$) or a treatment × year interaction ($F_{[4,7]} = 0.88$, $P = 0.52$).

In the Ovenbird, there was no evidence either for a preference for treated plots (Fig. 3). Actually, Thériault et al. (in review) found significant effects of treatment and male status (returning versus recruit) on arrival date of territorial individuals. There was also a trend toward a treatment × male status interaction. Males arrived later in treated plots than in controls, and recruits settled later than returning males. When comparing per capita productivity, there was no evidence for an effect of treatment ($1.07 \pm 0.95$ versus $0.94 \pm 1.00$ in controls versus treated plots; $F_{[1,63]} = 0.24$, $P = 0.623$) or male status ($1.12 \pm 0.97$ versus $0.85 \pm 0.96$; $F_{[1,63]} = 2.42$, $P = 0.125$) (Fig. 4).

There was no evidence for a treatment effect, nor a treatment × year interaction, on the abundance of Red Squirrel

**Fig. 1.** Cumulative number of active Brown Creeper (*Certhia americana*) nests present (pooled over a 4 year period: 2007, 2009, 2010, and 2011; see Methods) in plots treated by selection harvesting in 2006 (*n* = 5) and in control plots (*n* = 5) in the Black Brook District, New Brunswick, Canada. The year 2008 was omitted due to missing data on first egg dates. The *x*-axis represents the number of days elapsed since the first nest was found each year, and nests are added as a function of their first egg date.
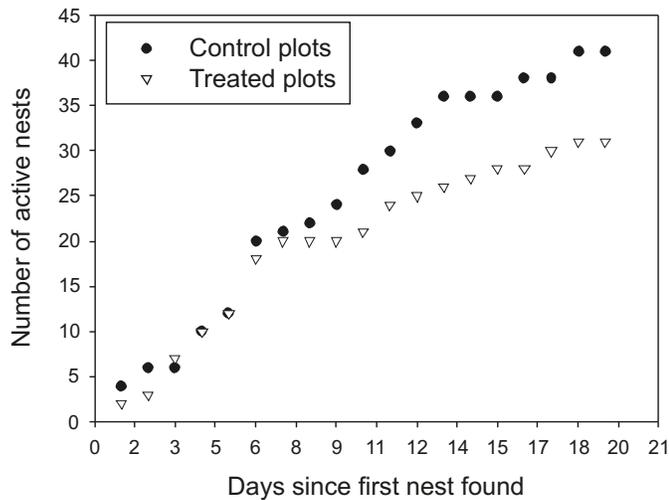


**Table 1.** Results of linear mixed models relating the maximum density of Brown Creeper (*Certhia americana*) nests per plot to treatment (single-tree selection harvesting versus controls), year, and their interaction.

| Explanatory variable | df | *F* | *P* |
|---|---|---|---|
| Treatment | 1,32 | 11.777 | 0.002 |
| Year | 4,32 | 10.424 | <0.001 |
| Treatment × year | 4,32 | 0.244 | 0.911 |

**Note:** Study plot and study plot nested within plot pair were entered as random effects (see Methods).

**Fig. 2.** Temporal variation in the maximum number of simultaneously active Brown Creeper (*Certhia americana*) nests (mean per plot ± SE) in plots treated through selection harvesting in 2006 (*n* = 5) and in control plots (*n* = 5).
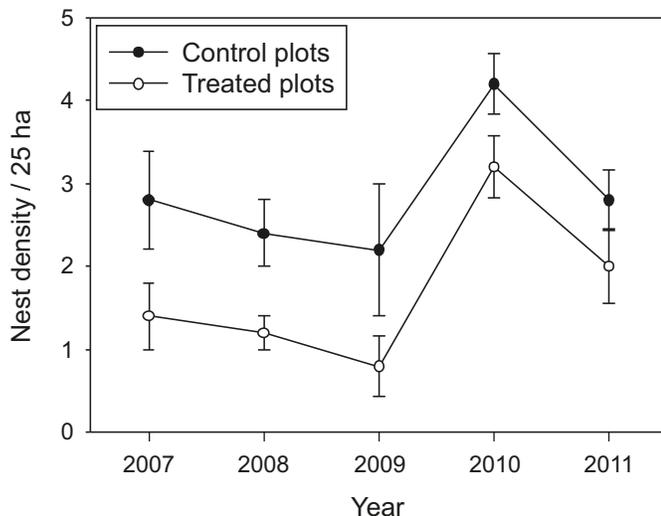


**Fig. 3.** Saturation rate by Ovenbird (*Seiurus aurocapilla*) males of plots treated through selection harvesting (*n* = 2) versus controls (*n* = 2) according to the cumulative number of territories occupied by banded males returning from previous years or unbanded recruits. Numbers on the *y*-axis represent means for three years (2006, 2007, and 2008). Sample sizes are as follows: returning to treatments, *n* = 40; returning to controls, *n* = 67; recruits in treatments, *n* = 28; recruits in controls. *n* = 42.
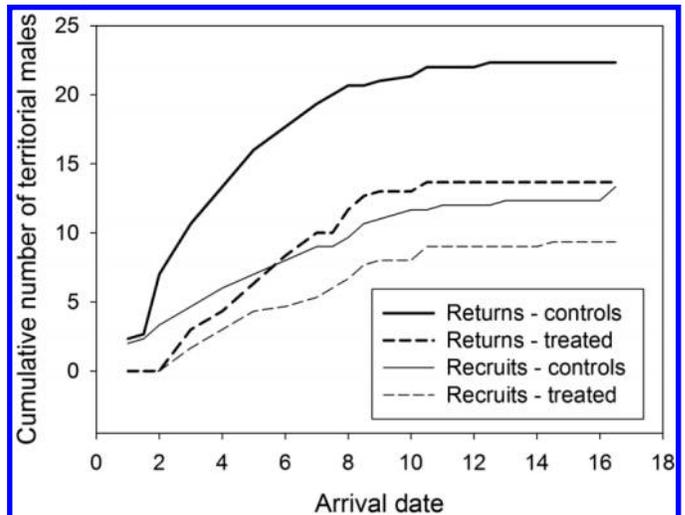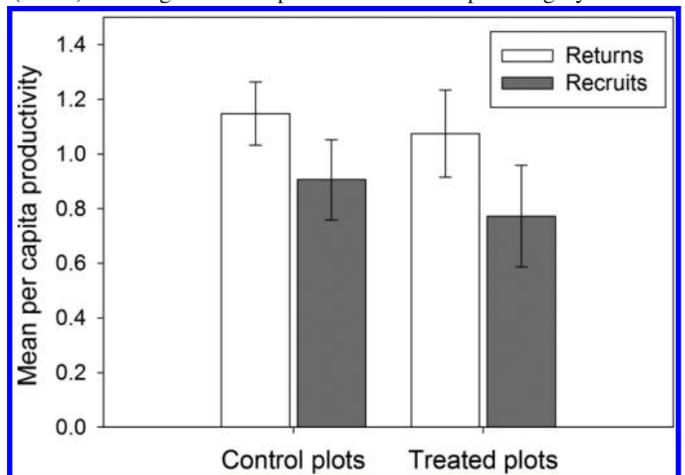


**Fig. 4.** Mean per capita productivity of Ovenbirds (*Seiurus aurocapilla*) in plots treated by selection harvesting (*n* = 2) and in controls (*n* = 2). See Fig. 3 for samples sizes of males per category.



or Eastern Chipmunk (Table 2). We only found a strong year effect (Table 2), the abundance of both species peaking throughout the study area in 2007 and (for chipmunk) 2010.

## Discussion

Several lines of evidence indicate that, in our study area, selection harvesting did not "trap" Brown Creepers and Ovenbirds into a low-quality habitat. In both species, treated plots actually appeared to be less preferred according to the rate at which new nests (Brown Creeper) or new males (Ovenbird) were detected by observers. Both species also reached lower densities in treated plots (Fig. 2) (Haché and Villard 2010), which suggests either that they recognized selection cuts as lower quality habitat or that they adjusted their

**Table 2.** Results of linear mixed models relating the abundance of two sciurid species known to depredate Ovenbird (*Seiurus aurocapilla*) and Brown Creeper (*Certhia americana*) nests to harvest treatment (selection harvesting versus controls), year, and their interaction.

| Explanatory variable | df | F | P |
|---|---|---|---|
| **Red Squirrel** | | | |
| Treatment | 1,32 | 0.30 | 0.589 |
| Year | 3,79 | 3.79 | 0.013 |
| Treatment × year | 4,32 | 0.58 | 0.678 |
| **Eastern Chipmunk** | | | |
| Treatment | 1,32 | 0.03 | 0.857 |
| Year | 5,40 | 15.03 | <0.001 |
| Treatment × year | 5,40 | 1.01 | 0.418 |

**Note:** Study plot and study plot nested within plot pair were entered as random effects (see Methods).

density according to resource levels. Indeed, there was no evidence that the selection harvest treatment caused a significant reduction in per capita reproductive success, as expected under an ideal free distribution (Fretwell and Lucas 1969). In the Ovenbird, we actually found higher mean brood sizes in treated plots shortly before fledging, but seasonal probability of success per territory was lower than in controls (S. Haché, M.-A. Villard, and E. Bayne, unpublished data), which explains the slightly lower per capita productivity observed.

In the same study region, Pérot and Villard (2009) also found evidence suggesting that the species can adjust its density as a function of perceived or actual habitat quality. Indeed, Haché and Villard (2010) reported a 49% expansion in mean territory size following selection harvesting. In the Brown Creeper, nest density was approximately 50% lower in treated plots than in controls in the first 2 years post-harvest, although it bounced back to some degree in the third and fourth years (Fig. 2).

Weldon and Haddad (2005) also performed a replicated field experiment to test for ecological traps in a species historically associated with disturbed habitat (forest edges), the Indigo Bunting (*Passerina cyanea* (Linnaeus, 1766)). They reported that birds preferred sites with more edge per unit area, yet experienced a lower seasonal fecundity than in less "edgy" sites. In that study, preference was determined on the basis of age structure: the proportion of older males was significantly higher in sites with more forest edge habitat. This is slightly different than using territory settlement sequence, as we have done, because territorial despotism by older males must be assumed.

Maladaptive habitat selection can have dire consequences for individuals and populations. In birds, examples of ecological traps include the failure of certain species to recognize evolutionarily recent changes in habitat quality resulting from climate change in semideserts (Hargrove and Rotenberry 2011), conspecific interactions with brood parasites in riparian vegetation (Latif et al. 2011), or agricultural practices (Pärt et al. 2007). Forest habitats may be better buffered against effects of rapid climatic change, and brood parasites such as the Brown-headed Cowbird (*Molothrus ater* (Boddaert 1783)) are essentially a nonfactor in managed forest landscapes of eastern Canada (e.g., Drapeau et al. 2000; Guénette and Villard 2005). Recent changes in silvicultural

practices, however, could potentially lead to unexpected responses in forest songbirds. Robertson and Hutto (2007) found evidence for an ecological trap in a similar case study (thinned site and control) but the abundance of potential nest predators was more than twice as high in their harvested plot than in a naturally disturbed plot. In our study system, we observed major temporal fluctuations in sciurid populations but no evidence for an effect of the selection harvest treatment on their abundance. Sciurids are thought to be the main predators on Brown Creeper nests, which might explain the wide fluctuations we recorded in the fledging success of this species (Poulin et al. 2010). In the Ovenbird, other nest predators (e.g., Blue Jay (*Cyanocitta cristata* (Linnaeus 1758))) are expected to play a significant role but their response to selection harvesting is relatively poorly known (Tarvin and Woolfenden 1999). Over the short term at least, Blue Jays have been shown to respond positively to group-selection harvesting (Tozer et al. 2010).

Because Brown Creepers are associated with older stands (Hejl et al. 2002; Poulin et al. 2008) and Ovenbirds are found in closed-canopy stands with a relatively open understory (Porneluzi et al. 2011), these species may not be attracted to sites where large trees have been removed, resulting in a significant opening of the canopy. However, some species have been shown elsewhere to respond positively to habitat conditions that do not necessarily fall within their "natural spectrum" (see Remeš 2003 above). Future studies should test the possibility of an ecological trap in species typically associated with a dense understory (e.g., Black-throated Blue Warbler (*Dendroica caerulescens* (Gmelin 1789)): Steele 1992; Chestnut-sided Warbler (*Dendroica pensylvanica* (Linnaeus 1766)): King and DeGraaf 2004). Such species would be expected to perceive selection cuts as attractive but their fitness might not justify this attraction. Sciurid nest predators apparently would not be a factor in such a trap but drier microclimatic conditions might affect invertebrate assemblages, a primary source of food for these passerine birds.

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