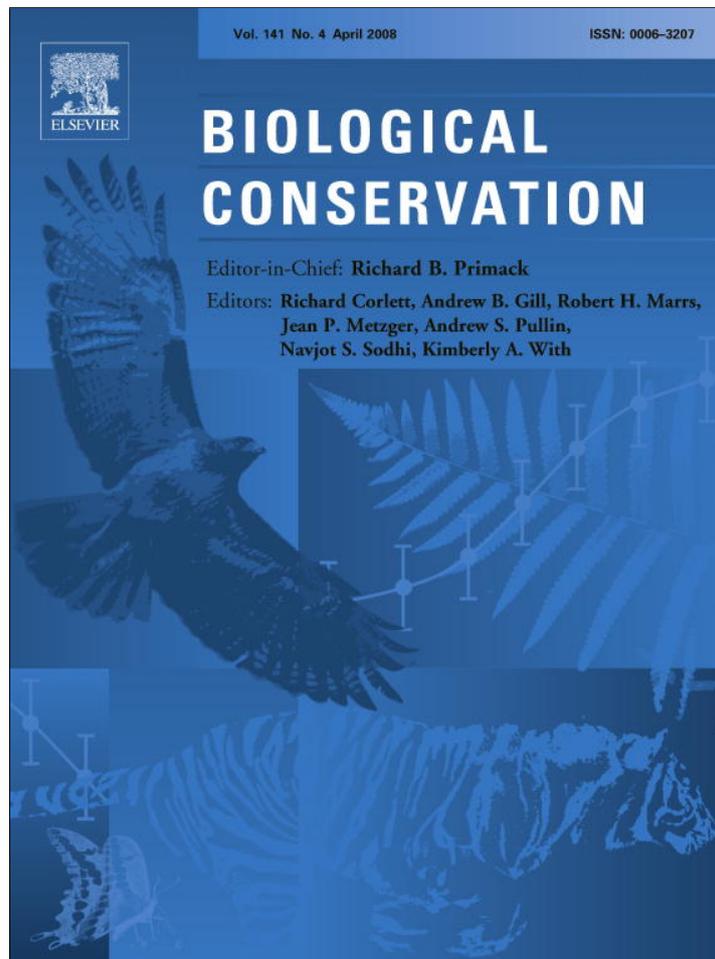


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Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (*Certhia americana*), as conservation targets

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ABSTRACT

Many bird species respond to forestry, even at moderate intensities. In New Brunswick, Canada, the Brown Creeper exhibits a negative, threshold response to harvesting intensity. This study aimed to determine whether (a) the threshold found in Brown Creeper occurrence is lower than eventual thresholds in its nesting requirements, and whether (b) the conservation of this species could be achieved through moderate-intensity harvest systems. Creepers are particularly sensitive to forestry because they nest on snags with peeling bark and they mainly forage on large-diameter trees. In northern hardwood stands, we compared habitat structure at local- ($r = 80$ m) and neighbourhood-scales ($r = 250$ m) around nest sites and sites not used by creepers. Over two years, we found 76 nests, 66 of which were paired with unused sites for comparison. At the local scale, densities of trees ≥ 30 cm dbh and snags ≥ 10 cm dbh, and the probability of presence of potential nest sites were significantly higher near nests than at sites where no creepers were detected. At the neighbourhood scale, the area of untreated mature forest was significantly higher around nests. Variance decomposition indicated that habitat variables at the local scale accounted for the majority of explained variation in nest site selection. We also found significant thresholds in the densities of large trees (127/ha) and snags (56/ha), and in the area of mature forest (10.4 ha). The conservation of breeding populations of Brown Creepers may thus require densities of large trees nearly twice as high as those associated with its probability of presence. Such a target seems to be incompatible even with moderate-intensity harvesting.

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1. Introduction

Forest management creates complex landscape mosaics composed of stands varying in floristic composition, age and dis-

turbance history (Lindenmayer and Franklin, 2002). Although low-intensity forestry may maintain habitat for some species, others are sensitive to reductions in specific forest stand structures (Vance and Nol, 2003; Fisher and Wilkinson, 2005;

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Guénette and Villard, 2005) or to overall loss and fragmentation of their habitat at the landscape scale (Villard et al., 1999; Lichstein et al., 2002; Cushman, 2006). Determining the ranges in forest management intensity over which species exhibit strong “threshold” responses may provide critical guidance for the development of biodiversity conservation targets (Fahrig, 2001; Bütler et al., 2004a; Guénette and Villard, 2005).

Research on threshold responses and the ecological processes underlying such thresholds is still in its infancy. A threshold can be defined as a sharp change in an ecological response corresponding to a small alteration in ecosystem conditions (Guénette and Villard, 2004; Huggett, 2005). A threshold may be breached when ecosystem conditions shift through time at a given location. Alternatively, threshold responses may be observed by measuring an ecological response variable (e.g. probability of species presence) along a gradient in ecosystem conditions (Bütler et al., 2004a; Homan et al., 2004; Guénette and Villard, 2005). For example, Guénette and Villard (2005) sampled forest birds in stands varying in structure and floristic composition and related those stand characteristics to the probability of species presence. In northern hardwood stands, they found a threshold of 66 large trees (≥ 30 cm diameter at breast height) per hectare, above which Brown Creepers (*Certhia americana*) were significantly more likely to be detected. Although this number represents a useful initial target for conservation and management, it still begs the question of whether meeting this target would be sufficient to expect reproduction and, ultimately, population persistence for this and ecologically-similar species. Authors who have addressed this issue have concluded that habitat requirements for reproduction may be substantially higher than those required for the mere presence of a species (Angelstam, 2004; Bütler et al., 2004b; Roberge et al., 2008).

Our study aims to determine whether the Brown Creeper exhibits threshold responses to stand structure variables when selecting nesting sites and if so, to compare these threshold values to those found by Guénette and Villard (2005) for the probability of presence at the local scale. Creepers (*Certhia* spp.) nest underneath pieces of bark peeling off from snags or declining trees (Cramp, 1993; Hejl et al., 2002). Therefore, they require a continuous supply of dying trees. They also require large surfaces of rough bark in order to find their food (invertebrates on bark surface and in crevices) (Mariani and Manuwal, 1990; Adams and Morrison, 1993). Both in Eurasia and North America, creepers have attracted the attention of conservation biologists owing to their potential value as indicators of sustainable forest management (Kuitunen and Helle, 1988; Kuitunen and Mäkinen, 1993; Bani et al., 2005; Suorsa et al., 2005; Wintle et al., 2005). However, Brown Creeper's life history remains surprisingly poorly known and so do the mechanisms underlying its sensitivity to forest management.

In northwestern New Brunswick, Canada, the Brown Creeper was among eight species of forest birds positively linked to the density of large-diameter trees and snags (Guénette and Villard, 2005). Current harvest practices in conifer-dominated stands make it unlikely that the structural requirements of these species can be met outside reserves. Mature stands are managed through clearcutting with retention

patches generally much smaller than 1 ha. In shade-tolerant deciduous stands, however, forest management systems include selection, shelterwood, and patch cutting, which might be compatible with the conservation of sensitive species such as the Brown Creeper. Single-tree selection harvesting attempts to emulate small scale natural disturbance by removing approximately one third of the basal area in each diameter class every 20 to 25 years (Nyland, 1998; Guillemette and Bédard, 2006). In the northern hardwoods and Acadian forests [typically mixedwood stands dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*)], the most frequent natural disturbance is windthrow, which usually alters approximately 1% of a particular area annually (Runkle, 2000; Mosseler et al., 2003).

Selection harvesting allows manipulating the residual density of large trees and snags and, thus, the value of post-harvest stands as habitat for species associated with these structures. Hence, a broader objective of this project was to determine whether the conservation of the Brown Creeper in deciduous forests can be achieved through adjustments in harvest systems or whether forest patches must be left untreated or managed through extended harvest rotations. Based on its ecological requirements, we expected that the Brown Creeper would represent an efficient umbrella for other species requiring a continuous supply of snags, a high density of large-diameter trees, and associated habitat features.

2. Methods

2.1. Study area

The study was conducted in the Black Brook and West Tobique districts (47°05'–47°50' N; 67°00'–67°50' W), two privately-owned managed forests adjacent to each other in northwestern New Brunswick, Canada. We searched for nests in 2005 and 2006 in scattered sites over a 5,000 km² area comprising ~25% of mature deciduous stands. In deciduous stands, the dominant species are sugar maple, American beech (*Fagus grandifolia*) and yellow birch. In these stands, the dominant silvicultural treatment is single-tree selection harvesting. See Bourque and Villard (2001) and Guénette and Villard (2005) for further details on the West Tobique and Black Brook districts, respectively.

2.2. Nest searching and monitoring

In 2005 and 2006, we intensively searched for Brown Creeper nests in mature and old (≥ 75 years) northern hardwood stands ($\geq 75\%$ of deciduous trees), irrespective of their harvest history. Because we did not mark individuals, we searched for nests in different locations and any nest found in 2006 within 500 m of a 2005 nest was excluded from the analyses. We chose a distance of 500 m in order to minimise the risk of resampling the same individual and especially the same habitat. In our study area, the area of creeper territories appeared to range between ~5 and 10 ha (J.-F. Poulin and M.-A. Villard, unpublished data). For comparison, we sampled vegetation in sites without creepers, which were located *a priori* on forest

inventory maps 500 m away from a known nest, in a random direction. Only points falling within deciduous or mixedwood stands were retained for sampling. Sites were visited a total of four times (2 with playback) during the months of June and July to assess creeper activity. We confirmed the absence of creepers by conducting a conventional 5 min point count followed by a 5 min playback of Brown Creeper vocalizations and an additional 5 min point count. The site was classified as unused if no individual was detected during two point count visits conducted between 10 and 30 June, before the fledging of the paired nest. This reduced the possibility of detecting the family group from that nest at the site deemed unused. Point count visits were conducted during the main nestling period of the first nesting attempt in our study area and individuals are not known to double-brood (Hejl et al., 2002; J.-F. Poulin and M.-A. Villard, unpublished data), although, creepers frequently re-nested if their first attempt failed. Sites were also classified as “transit” if activity, such as a family group, was detected during two other visits in June or during the vegetation sampling period in July. At 12 sites, individuals were detected but no nest was found in the vicinity. To validate the classification of certain sites as “unused”, we compared the delay of detection of individuals when using playbacks at nests vs. sites deemed to be unused by creepers.

2.3. Nest tree characteristics

For each creeper nest, we recorded the tree species used, its diameter at breast height (dbh) and decay stage (1 = alive; 2 = declining; 3 = dead with branches, intact; 4 = dead without branches, partially bare; 5 \geq 90% bare trunk). The percentage of bark remaining on the trunk was estimated to the nearest 10%. Finally, distance to the nearest edge (major road, clear-cut, conifer plantation) was measured using a global positioning system (GPS).

2.4. Vegetation sampling

Each year, vegetation data were collected in July, after young had fledged. Vegetation structure and composition were quantified at each nest and unused site along three 80-m transects oriented to the north, southeast and southwest. For nest sites, plots were centered on the nest. We recorded the species and dbh of all snags and trees (\geq 10 cm dbh) present within a 2-m wide band on either side of each transect. We also recorded the number of logs (\geq 10 cm in diameter) intersecting transects. At the center of the site and at 20 and 40 m along each transect, we measured canopy closure and shrub density (<1 m high) within a 2 m radius. Canopy closure was estimated by holding a transparent Plexiglas sheet (25 \times 25 cm) overhead and counting squares on a 5 \times 5 grid where more than 50% of the surface was obscured by foliage (Gu nette and Villard, 2005). We measured canopy height with a clinometer by choosing one representative tree in each of the four cardinal directions.

2.5. Habitat characterization at the neighbourhood scale

We quantified forest composition within a 250 m radius around each site using forest inventory data for the Black

Brook and West Tobique districts with ArcView GIS v.9. We distinguished five land cover types: untreated mature and old forest (deciduous, coniferous and mixedwood); treated deciduous forest; clearcuts and young conifer plantations (<15 years old); other forest (young, immature stands and plantations \geq 15 years old); and other silvicultural treatments (partially harvested mixedwood and coniferous stands). “Untreated mature forest” included mature and old stands, irrespective of their composition, because creepers do not exhibit clear preferences for stand composition (Hejl et al., 2002; Gu nette and Villard, 2005).

2.6. Statistical analyses

We calculated selection ratios for nest tree species and dbh class (balsam fir snags only) by comparing the proportion of used vs. available substrates in different categories. When the selection ratio was >1 and the 95% confidence interval did not include 1, the substrate type was considered to be selected. When the selection ratio was <1 and the confidence interval did not include 1, the substrate type was considered to be avoided. Finally, when the confidence interval included 1, the substrate was considered to be selected in proportion to its availability (Manly et al., 2002). We also plotted the distribution of nest locations from the nearest forest edge.

We compared the response time of individuals to conspecific playback between nesting and transit sites using an ANCOVA with site type (nesting vs. transit sites) as the covariate. A significant site type \times response time interaction would indicate that there is a difference in the time required to detect a response between the two types of sites. We applied a power transformation to the independent variable (proportion of occupied sites) in order to obtain a linear relation.

To identify variables influencing nesting habitat selection, we used discriminant function analysis (DFA) at each of the two spatial scales. We also performed another DFA with transit sites as a third group to examine whether vegetation at those sites differed from that around nests and unused sites. To account for the confounding effect of strong correlations among variables ($r \geq 0.7$), we selected the variable with the largest F value in a univariate one-way ANOVA (McGarigal et al., 2000). Because GPS locations of nest and unused sites could not be obtained for the entire West Tobique district, the sample size was lower at the neighbourhood scale than at the local scale.

We inspected the data to determine whether there was spatial autocorrelation in the significant discriminant variables using Moran's I. This was done separately for nests and unused sites. There was significant positive spatial autocorrelation in the density of large trees around nests. To assess the effects of this spatial structure on DFA results, we drew a 200 m buffer (slightly larger than a creeper territory; Davis, 1978) around each nest site location and randomly selected one site for each overlapping pair. We then performed another DFA with a single nest site per overlapping pair to assess the robustness of the original DFA to spatial autocorrelation. The same variables were selected with similar standardized and canonical correlation coefficients, suggesting that the original DFA was indeed robust.

To quantify the relative influence of each spatial scale on nest site selection, we used a variance decomposition technique (Lawler and Edwards, 2006). We fit three models: one full model and one for each of the two spatial scale investigated, which allowed us to determine the variation explained by each scale. We combined data available at both scales and ran a DFA for the full model, a model containing only local variables and one containing only neighbourhood scale variables. We determined the variation explained by subtracting to the full model each component of the variation. We then looked for evidence of thresholds in creeper response to individual habitat variables using univariate logistic regression and ROC (receiver operating characteristic) analysis. The binary dependent variable contrasted nest sites and unused sites. ROC analysis can be used to objectively identify a cutoff value maximizing the sum of specificity and sensitivity through an iterative approach (Zweig and Campbell, 1993; Guénette and Villard, 2004). The accuracy of the logistic model is assessed using the area under the ROC curve (AUC). Models whose AUC is >0.7 are considered to perform well whereas

an AUC of 1 would represent perfect discrimination (Swets, 1988).

3. Results

We found a total of 76 Brown Creeper nests over the duration of the study. Snags ($n = 73$) were highly selected as nesting substrates compared to live trees ($n = 3$). Balsam fir snags, spruce snags, and deciduous snags were strongly, slightly, and not preferred, respectively, as nesting substrates (Fig. 1a). The category “other (snags)” includes yellow birch ($n = 4$) and American beech ($n = 3$) snags, whereas “other (trees)” includes live stems of eastern white cedar (*Thuja occidentalis*, $n = 1$) and yellow birch ($n = 2$). Among balsam fir snags, creepers used stems with a dbh >20 cm in proportion to their availability whereas those whose dbh ranged between 10 and 19.9 cm were avoided (Fig. 1b). Of the 71 nest trees for which we measured substrate characteristics, mean dbh was

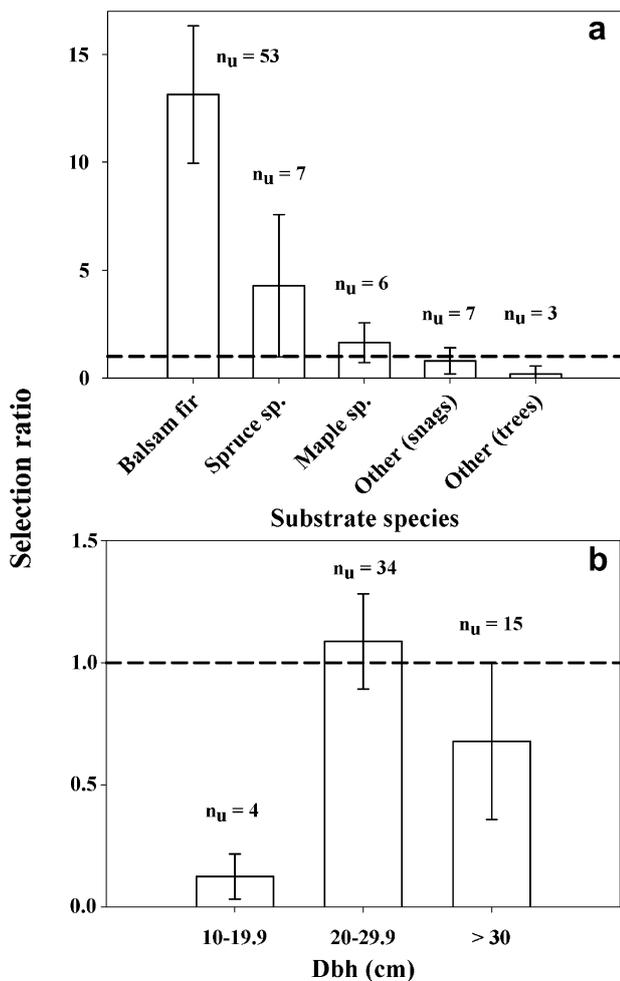


Fig. 1 – Selection ratios and their 95% confidence intervals for (a) tree species and (b) dbh classes of balsam fir snags used as nesting substrates by Brown Creepers. The dashed line represents the selection threshold (see Methods for details) and n_u corresponds to the number of substrates used in each category.

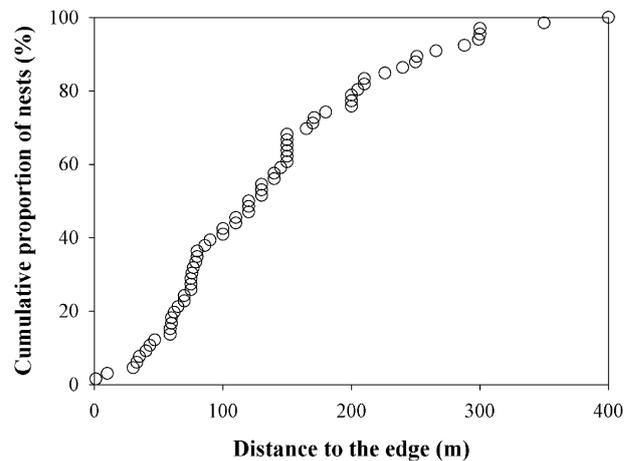


Fig. 2 – Cumulative proportion of nests as a function of their distance from the nearest edge ($n = 66$).

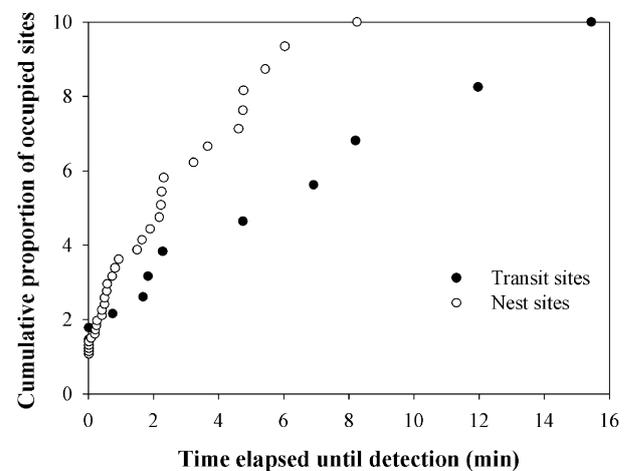


Fig. 3 – Cumulative proportion of occupied sites (power transformation) as a function of the time elapsed until first detection of a Brown Creeper individual at nest sites ($n = 34$) and transit sites ($n = 12$) when broadcasting a conspecific playback.

31.9 cm (± 13.6 SD, range: 15.1–95.6 cm) and height of nest entrance was 3.7 ± 1.9 m above ground (range: 1.1–9.0 m). Mean proportion of bark left was $57 \pm 25\%$. The mean distance from a nest to the nearest forest edge was 143.4 ± 88.7 m (range: 10–400 m) and 38% of the nests were located ≤ 100 m from the nearest edge (Fig. 2).

Table 1 – Model composition and variation explained by three discriminant function analyses contrasting Brown Creeper nest sites and unused sites at local (radius = 80 m) and neighbourhood (radius = 250 m) scales (n = 75)

| Model | Variables ^a | % Of variation explained |
|---------------------|--|--------------------------|
| Full | Large trees + snags + pot_nest + mature | 42.6 |
| Local scale | Large trees + snags + pot_nest | 40.7 |
| Neighbourhood scale | Mature | 12.8 |

^a Large trees: density of trees ≥ 30 cm dbh/ha; snags: density of snag ≥ 10 cm dbh/ha; pot_nest: presence/absence of other potential nest site; mature: area of untreated mature/old forest (ha).

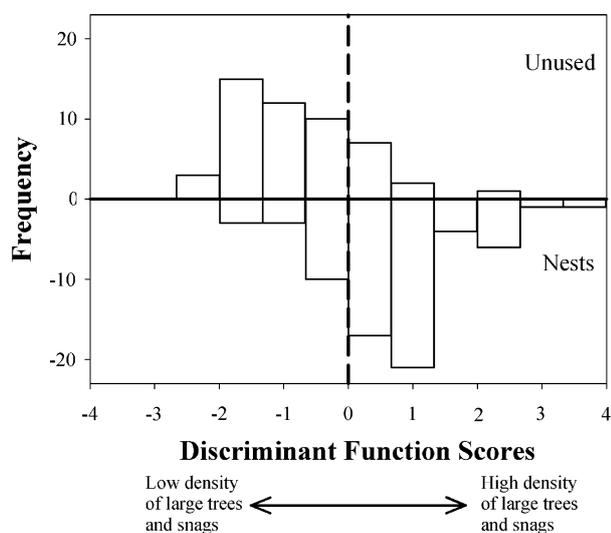


Fig. 4 – Frequency of discriminant function scores for unused sites (n = 50) and nest sites (n = 66).

Not surprisingly, the detectability of Brown Creepers was significantly lower in transit sites than at nests (Fig. 3). The site type * response time interaction was significant, indicating that individuals took longer to respond to conspecific playback at transit sites ($F = 142.6$, $df = 1$, $P < 0.01$). At nest sites, 33 out of 37 males were detected at the first visit, one responded to playback only at the second visit, and activity was recorded at two nests but males did not respond, whereas activity was never detected at one nest due to nest failure. At transit sites, 10 males were detected during the first playback visit whereas only one was first detected during the second visit.

We performed a separate DFA at each spatial scale, and a third DFA included variables from either scale (Table 1). There were significant differences in habitat structure between nesting and unused sites at the local scale (Wilk's $\lambda = 0.66$, $r = 0.59$, $P < 0.01$, $n = 116$; Fig. 4). In decreasing order of importance, the presence of another potential nest site and densities of large trees (≥ 30 cm dbh) and snags, respectively, were the most significant discriminant variables (Table 2). The DFA correctly classified 78.4% of observations. Density of smaller trees (10–30 cm dbh), canopy closure, canopy height, shrub density and the number of logs were excluded by the stepwise selection. Transit sites had a similar mean density of large trees as nest sites, but their mean density of snags was similar to that of unused sites (Table 2). When included in a separate exploratory DFA, the first discriminant function explained 95% of the variation (Fig. 5). Transit sites

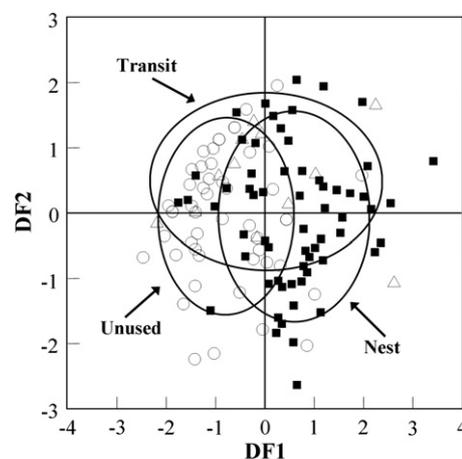


Fig. 5 – Discriminant function (DF) scores for unused sites (n = 50), nest sites (n = 66), and transit sites (n = 12).

Table 2 – Standardised discriminant coefficients and canonical correlations from a discriminant function analysis contrasting nest sites and unused sites, as well as descriptive statistics at the local scale (r = 80 m)

| | Standardized coefficient | Canonical correlation | Mean (SD) | | |
|-------------------------------------|--------------------------|-----------------------|---------------------|-----------------------|------------------------|
| | | | Nest sites (n = 66) | Unused sites (n = 50) | Transit sites (n = 12) |
| Density of large trees (stems/ha) | 0.674 | 0.564 | 147.9 (59.4) | 101.7 (52.7) | 152.8 (52.3) |
| Density of snags (stems/ha) | | | 84.4 (43.3) | 56.0 (56.3) | 59.9 (61.7) |
| Presence of potential nest site (s) | 0.722 | 0.641 | n/a | n/a | n/a |

were segregated by the second discriminant function and points were mostly located in the positive portion of the plot. However this function had low discriminant power (5%).

A significant difference between nests and unused sites was also found at the neighbourhood scale, but the area of untreated mature forest was the only variable selected (Wilk's $\lambda = 0.85$; correct classification = 71.8%; $r = 0.39$, $P < 0.01$, $n = 78$). When adding the four variables selected *a priori* (density of

large trees, density of snags, presence of a potential nest site and area of untreated mature forest) in a model combining both spatial scales, the difference between nesting and unused sites was still significant and the model explained 42.6% of the variation (Wilk's $\lambda = 0.59$; correct classification = 82.5%; $r = 0.65$, $P < 0.01$, $n = 63$; Table 3). Variance decomposition showed that local components explained most of the variation (i.e. 29.8%; Table 4), neighbourhood scale explained only an additional 1.9%.

At the local scale, the probability of presence of a creeper nest corresponded to distinct thresholds in densities of large trees (127 stems/ha, AUC = 0.713; Fig. 6) and snags (56 stems/ha, AUC = 0.704; Fig. 7). At the neighbourhood scale, the probability of presence of a nest was much higher when the area of mature/old untreated forest was ≥ 10.4 ha (AUC = 0.714; Fig. 8), i.e. 53% of the area considered (19.6 ha).

Table 3 – Standardised discriminant coefficients, canonical correlations and descriptive statistics at local and neighbourhood-scales from a discriminant function analysis contrasting nest sites and unused sites

| | Standardized coefficient | Canonical correlation | Mean (SD) | |
|-------------------------------------|--------------------------|-----------------------|---------------|-----------------|
| | | | Nest (n = 47) | Unused (n = 28) |
| Density of large trees (stems/ha) | 0.602 | 0.346 | 150.7 (61.7) | 114.6 (54.9) |
| Density of snags (stems/ha) | 0.187 | 0.163 | 86.7 (42.3) | 72.5 (59.4) |
| Presence of potential nest site (s) | 0.860 | 0.737 | n/a | n/a |
| Area of mature forest (ha) | 0.287 | 0.444 | 11.9 (6.0) | 9.1 (6.3) |

Table 4 – Variation explained by habitat variables when contrasting nest sites and unused sites

| Isolated component of variation | % Of total variation explained |
|--------------------------------------|--------------------------------|
| Pure (local) | 29.8 |
| Pure (neighbourhood scale) | 1.9 |
| Shared (local + neighbourhood scale) | 10.9 |

Pure deviance is solely linked to factors at a given scale and shared variation reflects cross-correlation at both scales.

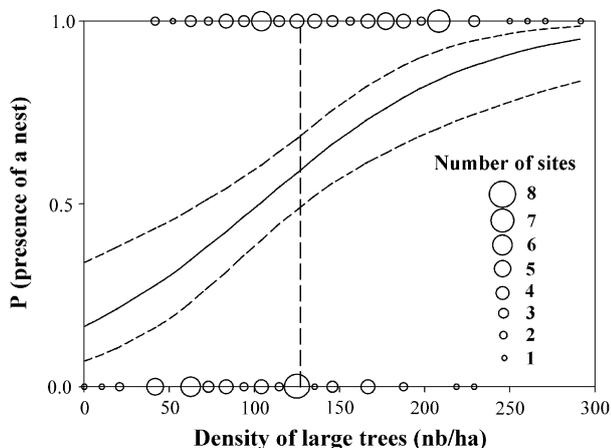


Fig. 6 – Probability of presence of a nest as a function of the density of large trees (≥ 30 cm dbh). Dashed curves represent 95% confidence intervals and the vertical dashed line indicates the ROC threshold value.

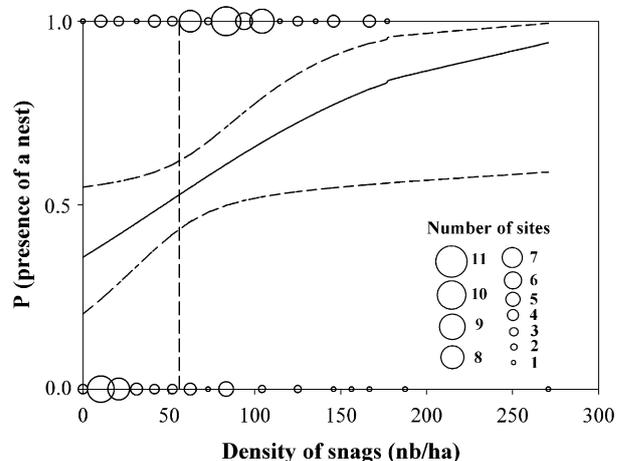


Fig. 7 – Probability of presence of a nest as a function of the density of snags (≥ 10 cm dbh). Dashed curves represent 95% confidence intervals and the vertical dashed line indicates the ROC threshold value.

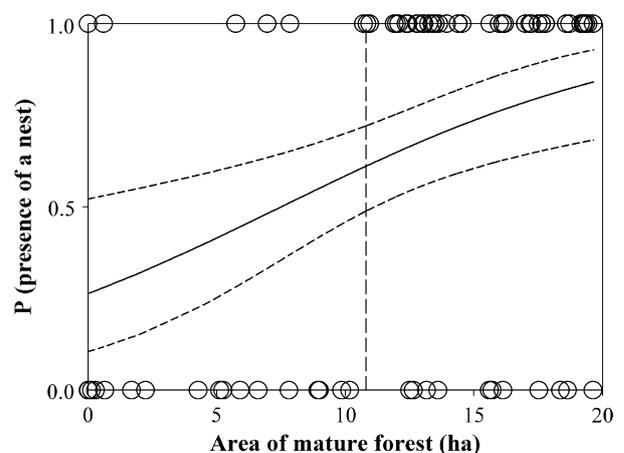


Fig. 8 – Probability of presence of a nest as a function of the area of mature forest within a 250-m radius (i.e. 19.6 ha). Dashed curves represent 95% confidence intervals and the vertical dashed line indicates the ROC threshold value.

4. Discussion

Brown Creeper nest sites were characterized by higher densities of large-diameter trees (≥ 30 cm dbh) and snags than unused sites. The threshold we found in the density of large trees (127 stems/ha) was nearly twice as high as that reported by Guénette and Villard (2005) for Brown Creeper's probability of presence in the deciduous stands of the same study region (66 stems/ha). This high threshold value combined with the positive threshold response to the area of untreated mature forest at the neighbourhood scale strongly suggest that Brown Creeper conservation cannot be achieved through low-intensity harvest systems. Based on the threshold we found in the area of untreated mature/old forest, patches of at least 11 ha should be left untreated to provide suitable nesting habitat. Such patches are likely to meet the requirements of many other species of birds (Guénette and Villard, 2005), herbaceous plants (Ramovs and Roberts, 2003) or epiphytic lichens (Edman et al., 2008) that are sensitive to forest harvesting. However, conservation strategies for northern hardwood forests should also integrate the requirements of species that are more area-demanding than the Brown Creeper, such as the Barred Owl (*Strix varia*).

The persistence of creeper populations implies a constant supply of snags providing suitable nesting substrates. Other studies conducted in northeastern North America (e.g. Davis, 1978 in Michigan; Peck and James, 1987 in Ontario) also reported that creepers usually nest on snags, but more than half of the nests were found on deciduous rather than coniferous snags. In our study area, the strong preference exhibited by creepers for balsam fir snags as nesting substrates is somewhat intriguing because we only surveyed deciduous stands and, therefore, balsam fir was not a dominant canopy species. Relative to other coniferous species, balsam fir has a thinner bark which tends to dry out more quickly (Chang, 1954). This may partly explain why fir snags produce large slabs of bark flaking off the trunk, creating suitable nest sites. Other factors such as short longevity and susceptibility to spruce budworm (*Choristoneura fumiferana*) defoliation may also increase snag recruitment relative to the other tree species present (MacLean, 1984; Burns and Honkala, 1990). As creepers are closely linked to balsam fir for nesting in our study area and this tree species is vulnerable to budworm defoliation, one might conclude that creeper populations should fluctuate as a function of budworm outbreaks. However, balsam fir defoliation by spruce budworm tends to decrease significantly as the deciduous content of a given stand increases (Su et al., 1996). Thus, in deciduous stands, balsam fir snag recruitment might be more strongly linked to self-thinning than to budworm outbreaks.

At the local scale, the presence or absence of other potential nesting substrates was the most significant discriminant variable, along with densities of large trees and snags. This is consistent with other studies showing that creepers are associated with old forest attributes. Large trees are essential to the recruitment of new snags through death from natural causes (Vanderwel et al., 2006). In our study region, snag recruitment has recently been influenced by the spread of beech bark disease and the last spruce budworm outbreak in deciduous and mixed stands respectively (Chokkalingam

and White, 2001). Higher availability of snags will increase the creeper's probability to find suitable nesting substrates. Furthermore, a higher density of potential nest sites may provide better concealment to actual nests by forcing visual predators to survey more microsites matching their search image (Martin and Roper, 1988).

Transit sites were very similar to nest sites except for snag density (Table 2, Fig. 5). This may explain why creepers were present but not nesting in the vicinity of those sites. Our sample size of transit sites was low but our results still suggest that the vicinity of nests has a higher density of snags than the periphery of a territory. The greater distance from the nest may also explain why individuals were taking longer to respond to playback in transit sites (Fig. 3).

Brown Creepers' association with large-diameter trees is probably linked to their quality as foraging substrates. Larger trees support a higher biomass of bark-dwelling invertebrates, especially spiders, owing to their deeper bark furrows (Jackson, 1979; Mariani and Manuwal, 1990). The greater bark surface of these trees also allows individuals to reduce the number of flights required per unit of energy intake (Franzreb, 1985; Mariani and Manuwal, 1990). In this study, it was not possible to determine whether large trees or snags were the limiting factor in the selection of a nesting site. However, results from a selection harvesting experiment (Poulin and Villard, submitted for publication) suggest that the density of foraging substrates may be limiting.

In Washington State, Blewett and Marzluff (2005) reported that Brown Creepers responded both to forest cover at the landscape scale (1 km² blocks) and to local habitat conditions (snag density). Here, we also found that Brown Creepers respond significantly to mature/old forest cover at a neighbourhood scale. The 250-m radius approximately corresponds to twice the area of a creeper territory (J.-F. Poulin and M.-A. Villard, unpublished data). Nearly two-thirds (62%) of creeper nests were located ≥ 100 m away from an edge. *Certhia* sp. seems to be edge sensitive and are more likely to nest over a 100 m from the nearest edge (Kuitunen and Mäkinen, 1993; Brand and George, 2001). In Finland, Kuitunen and Mäkinen (1993) found similar results in the Eurasian Treecreeper (*C. familiaris*): 65% of the nests (in nestbox grids) were located >100 m from the edge, even though the birds could have selected nestboxes located 30, 80, 140 or 200 m from the nearest edge. This apparent edge avoidance by creepers may reflect their relatively high area requirements (Davis, 1978; this study). Edge territories would likely have to be elongated to encompass enough trees to meet the energetic requirements of a breeding pair (Kuitunen and Mäkinen, 1993). Other studies have reported that the probability of finding *Certhia* spp. nests increased when continuous untreated stands of mature forest exceeded 10 ha (Hinsley et al., 1996; Drolet, 1997). For comparison, Suorsa et al. (2005) reported a threshold in the area of untreated mature/old forest of 6.5 ha (200 m radius) using an arbitrary cut-off value of 0.5 on the y-axis. Using the same cut-off value for our data, we obtained a threshold of 7.5 ha (250 m radius). This striking similarity reinforces our impression that parallels can be drawn between the two species.

Our results suggest that thresholds in species occurrence may be misleading from a conservation perspective. Indeed,

the few studies which compared thresholds linked to presence-absence vs. reproduction of the same species have shown that threshold values are higher for the latter (e.g. greater proportion of suitable habitat or basal area of snags) (Angelstam, 2004; Bütler et al., 2004a,b). Occurrence thresholds may be used to identify sensitive species within a large assemblage. Thereafter, it is possible to focus on the most sensitive species to acquire more refined data (e.g. on probability of reproduction, or even probability of successful reproduction), which in turn yields thresholds more likely to ensure the persistence of the focal species and their ecological associates.

Low-intensity harvest systems seem unlikely to maintain suitable habitat for breeding populations of Brown Creeper. In the northern hardwoods forest region, uneven-aged silvicultural systems have been applied largely without reference to biodiversity conservation. Whereas a certain number of species may be robust to such silvicultural systems, our results indicate that managing deciduous stands over entire landscapes through selection harvesting may pose a threat to species such as the Brown Creeper. Thus, conservation targets must be established at the landscape scale and they should include the maintenance of patches that are left unmanaged, or managed under extended harvest rotations, to provide a sufficient amount of foraging substrates and a continuous renewal of snags to meet creeper nesting requirements. We propose that patches be left untreated and managed as a network of shifting reserves. Such patches should also provide suitable habitat for a wide variety of forest taxa with high requirements for large-diameter trees, dead wood, and associated features. Current harvest regulations in New Brunswick require the protection of patches of old shade-tolerant hardwoods ≥ 40 ha, but the target density of large-diameter trees (≥ 30 cm dbh) within these patches is only ≥ 60 stems/ha (DNR, 2005). Our data indicate that such patches would have a high probability to accommodate at least 3–4 creeper territories if they have multiple cores of ca. 3 ha (radius ~ 80 – 100 m) with high densities (≥ 127 stems/ha) of large trees. The generality of such guidelines remains to be tested, but we submit that they likely reflect the energetic requirements of breeding pairs (see also Bütler et al., 2004b for Three-toed Woodpecker, *Picoides tridactylus*).

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