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Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of eastern Canada[1]

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Abstract: In the boreal forest, where tree cavities are mainly excavated by woodpeckers, many holes are incomplete excavations that are not suitable cavities for most other cavity users that form nest webs. We assessed cavity suitability for and use by a community of primary excavators and secondary users in managed and unmanaged landscapes in the boreal mixedwood forest of eastern Canada. We compared ground surveys of tree holes with direct inspections of the inside of potential cavities in remnant habitats surrounded by cutover areas and in large tracts of unharvested forest. We found that ground surveys overestimated suitable cavity abundance: only 38% of the potential cavities detected by ground surveys were suitable for nesting in both managed and unmanaged landscapes. Ground surveys of active nests correctly detected a greater proportion of primary (93%) than secondary cavity nesters (48%). In nest webs such as those of the boreal forest, where cavities are mainly created by woodpeckers, our results indicate that a large proportion of holes detected from the ground are not suitable for cavity nesters, thus overestimating the actual availability of nest sites. Furthermore, when nest cavities are active, ground surveys are satisfactory for detecting primary cavity nesters, but they are inadequate for detecting secondary cavity nesters.
Keywords: cavity abundance, cavity-nesting community, direct inspection, ground surveys, nest monitoring, primary and secondary cavity nesters.

Résumé : En forêt boréale, les cavités arboricoles sont excavées en majorité par les pics. Mais plusieurs des trous faits par les pics sont des cavités incomplètes et ne sont pas adéquates pour la plupart des autres utilisateurs de cavités faisant partie des réseaux de nidification. Nous avons évalué la qualité des cavités comme substrat de nidification et leur utilisation par une communauté d'excavateurs primaires et d'utilisateurs secondaires dans des paysages aménagés et non aménagés en forêt boréale mixte dans l'est du Canada. Nous avons comparé les résultats d'inventaires au sol des cavités arboricoles avec ceux d'inspections visuelles directes de l'intérieur des cavités potentielles dans des habitats forestiers résiduels entourés de zones coupées et dans des forêts intactes de grande superficie. Nous avons constaté que les inventaires au sol surestimaient l'abondance de cavités adéquates puisque seulement 38 % des cavités détectées comme potentielles à partir du sol étaient effectivement adéquates pour la nidification, et ce, autant dans les paysages aménagés que non aménagés. Les inventaires au sol de nids actifs détectaient correctement une plus grande proportion de nicheurs de cavité primaires (93 %) que secondaires (48 %). Dans des réseaux de nidification comme ceux de la forêt boréale où les cavités sont créées principalement par les pics, nos résultats indiquent qu'une grande proportion des cavités détectées lors des inventaires au sol n'est pas adéquate pour les espèces cavicoles, surestimant ainsi la disponibilité réelle de sites de nidification. D'autre part, lorsque les cavités abritent des nids actifs, les inventaires au sol détectent les excavateurs primaires de façon satisfaisante, mais ils ne permettent pas de détecter adéquatement les utilisateurs secondaires.
Mots-clés : abondance de cavités, communauté cavicole, inspection directe, inventaires au sol, nicheurs de cavité primaires et secondaires, suivi de nids.

Nomenclature: American Ornithologists' Union, online; Brouillet *et al*., online.

Introduction

Tree cavities are used as breeding sites or refuges by many vertebrate species in forest ecosystems worldwide (Newton, 1994; Bunnell, Kremsater & Wind, 1999; Martin & Eadie, 1999; Bai, Wichmann & Mühlenberg, 2003; Aitken & Martin, 2007; Wesolowski, 2007; Cockle, Martin & Wesolowski, 2011). Cavities are either created by natural decay processes or by primary cavity excavators (woodpeckers). Secondary cavity users do not excavate cavities and rely on cavities available at their breeding sites, whereas weak cavity excavators such as nuthatches or chickadees use either old natural and excavated cavities or excavate their own cavities in highly decayed trees (Martin & Eadie, 1999; Aitken, Wiebe & Martin, 2002; Norris & Martin, 2010). The trees utilized by cavity users are generally large, and they encompass a wide range of decay stages, from senescent trees to highly decayed snags (Martin, Aitken & Wiebe, 2004;

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Drapeau *et al.*, 2009). Such habitat attributes are more abundant in late-successional forests (Jonsson, Kruys & Ranius, 2005; Hannon & Drapeau, 2005); however, these forests have become greatly reduced by even-aged management at the landscape scale (Spies, Ripple & Bradshaw, 1994; Bergeron *et al.*, 2002). The interspecific relationships (primary *versus* secondary cavity users) and community structure of cavity nesters with respect to suitable cavities have been studied in recent years under the concept of "nest web" (Martin & Eadie, 1999; Martin, Aitken & Wiebe, 2004). Information concerning the abundance of suitable cavities and how cavity abundance is affected by forest management, for instance through nest site shortage, is essential for identifying ecosystems that may be vulnerable for cavity-nesting species (Newton, 1994; 1998).

Different methods for detecting suitable cavities have been evaluated based on efficiency, cost, and accuracy (Harper *et al.*, 2004; Koch, 2008). Ground surveys consist of visually inspecting trees and snags from the ground with binoculars to detect potential cavities (Sedgwick & Knopf, 1986; Dobkin *et al.*, 1995; Pattanavibool & Edge, 1996). Cavity users may also be detected by observing potential cavities (Martin & Geupel, 1993) or by flushing occupants by tapping or scraping at the base of trees with cavities (Aitken, Wiebe & Martin, 2002; Dudley & Saab, 2003). Ground surveys are among the quickest and least costly survey techniques (Harper *et al.*, 2004; Koch, 2008), but they are likely biased either because a proportion of potential cavities and occupants may remain undetected (source of underestimation) or because a proportion of potential cavities may be unsuitable for use by animals (source of overestimation) (Harper *et al.*, 2004; Koch, 2008; Cockle, Martin & Wiebe, 2008; Cockle, Martin & Drever, 2010). Direct inspection surveys consist of inspecting trees and potential cavities by climbing or using a camera mounted on a telescopic pole (Pattanavibool & Edge, 1996; Remm, Lohmus & Remm, 2006; Aitken & Martin, 2007; Huebner & Hurteau, 2007; Cockle, Martin & Wiebe, 2008; Koch, 2008). Whereas direct inspection may be more accurate than ground surveys, it is labour-intensive and time-consuming. Furthermore, some potential cavities may be inaccessible when located in decaying trees or snags that may be hazardous to climb or difficult to survey if located in the crown on inaccessible branches.

Recent studies undertaken in ecosystems where wood damage and decay are the main drivers for cavity formation have focused on the bias of cavity abundance generated by ground surveys (Harper *et al.*, 2004; Blakely *et al.*, 2008; Koch, 2008; Cockle, Martin & Drever, 2010; Rayner, Ellis & Taylor, 2011). In deciduous forest ecosystems, difficulties in detecting potential cavities using ground surveys were considered a source of error (underestimation), particularly when most potential cavities are located in branches in the tree canopy (Harper *et al.*, 2004; Rayner, Ellis & Taylor, 2010). In the tropical forests of Argentina, Cockle, Martin, and Drever (2010) found, after direct inspection, that many cavities detected in ground surveys were unsuitable for nesting, leading to overestimation of potential cavities.

In coniferous and mixedwood boreal forests of North America, most cavities used by the community of cavity nesters are located in trunks and are excavated by woodpeckers (Aitken, Wiebe & Martin, 2002; Martin, Aitken & Wiebe, 2004; Aitken & Martin, 2007; Cooke, 2009; Cockle, Martin & Wesolowski, 2011). Excavated cavities often have a regular entrance shape, and prior knowledge of the characteristics of woodpecker holes may facilitate their detection from the ground (Bull, Parks & Torgersen, 1997; Saab & Dudley, 1998). Woodpeckers are thus keystone species creating nest sites and shelters that are at the base of an array of ecological interactions with secondary cavity nesters and weak excavators. Woodpeckers may, however, excavate incomplete cavities that are not wide or deep enough for nesting (Hoyt, 1957; McClelland, 1979; Bull & Meslow, 1988; Hooper, Krusac & Carlson, 1991; Ojeda, Laura-Suarez & Kitzberger, 2007). Therefore, in ecosystems where cavities are mainly excavated by woodpeckers, an important issue when estimating the abundance of suitable cavities for the community of cavity users is to assess the importance of incomplete cavities in these forest ecosystems.

In this study, we compare ground surveys of potential cavities with direct inspections in remnant forest stands of a managed forest and in an unmanaged continuous forest. We predict that the proportion of incomplete excavations will be higher in remnant forest stands due to the greater habitat degradation (reduced density of large trees, reduced range of tree decay stages) that may occur within these habitats (Virkkala & Liehu, 1990; Andrén, 1997). We also report the rates at which primary and secondary cavity nesters are correctly detected by ground surveys in active nest cavities.

Methods

Study area

Our study area was located in the boreal mixedwood forest of northwestern Quebec in the balsam fir–white birch bioclimatic domain (Saucier *et al.*, 1998) at the southern fringe of the boreal forest of eastern Canada (48°30'N, 79°20'W). Sampled sites were located within or near the Lake Duparquet Research and Teaching Forest (LDRTF), in remnant mature forests embedded in an even-aged management cutover area outside the LDRTF that was harvested 10 to 20 y ago (hereafter managed forest landscape) and in a large (25 km^2) continuous forest mosaic located within the LDRTF (hereafter unmanaged forest landscape) with varying forest cover types. This mosaic was created under the influence of a variety of natural disturbances that resulted from 8 major fires (Bergeron, 1991; Dansereau & Bergeron, 1993) and 3 spruce budworm outbreaks, the most recent occurring between 1970 and 1987 (Morin, Laprise & Bergeron, 1993; Bergeron *et al.*, 1995). Stand composition within the LDRTF ranges from deciduous to mixed and conifer-dominated stands along a time-since-fire gradient; however, we concentrated our cavity sampling in forests (70–140-y-old) dominated by trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) in both landscapes. Mature forests (>70-y-old) dominated by aspen made up 27% and 60% of the total forest cover in the managed and unmanaged forest landscapes, respectively (MRNFQ, 2010).

Cavity suitability

In 2008, we carried out a survey to determine suitable cavity abundance in mature tracts dominated by aspen (>50%). We established plots of 20 × 400 m in mature tracts originating from wildfires that occurred between 1870 and 1923 (Bergeron, 1991; Dansereau & Bergeron, 1993) in both forest landscapes. We surveyed 6 plots in linear remnant forests in the managed forest and 5 plots in the unmanaged forest. Because tree species composition in the unmanaged forest was generally more heterogeneous, we used digital forest cover maps (MRNFQ, 2010) to select patches similar in vegetation structure and composition to habitats surveyed in the managed forest (Table I). Plots were visited by a team of 4 observers early in May before bud-break ended. All trees (DBH > 10 cm) were visually inspected from the ground with binoculars to record potential cavities originating from excavation or decay that appeared deep and wide enough to be usable for nesting. The observers walked the full 400-m length of each plot in pairs starting from opposite ends. Each pair of observers walked 10 m apart, 5 m on opposite sides of the centre of the plot. Each pair passed the other pair of observers coming the opposite way at the midpoint of the survey. Both pairs of observers went on to search for cavities that might have been missed by the previous observers. Each tree was thus examined by the 4 observers from different viewpoints.

All plots were considered independent because they were in different stands based on digital forest cover maps (MRNFQ, 2010) and were at least 400 m apart. All trees with potential cavities were marked with a sequentially numbered aluminum tag (Martin & Eadie, 1999). We subsequently inspected all potential cavities that could be reached with a TreeTop Peeper camera system using a 15-m telescopic pole on which we mounted a camera that could fit into an entrance hole with a diameter of >2 cm (Sandpiper Technologies, Manteca, California, USA). When inspected with cameras, potential cavities were classified as unsuitable (trial holes, incomplete excavations, hollow trunks, or wound without a chamber) or suitable. Suitable cavities had an entrance hole diameter of >2 cm and a chamber deep and wide enough to be occupied by mammalian or avian cavity nesters. Although we did not measure the depth of potential cavities, we estimated whether excavated chambers had been completed and if the depth of decayed cavities was sufficient (>10 cm). We did this by looking inside the cavity from the lower lip of the entrance to the bottom of the chamber.

TABLE I. Habitat characteristics of forest stands surveyed in 2008 to assess abundance of suitable cavities in a managed and an unmanaged forest landscape in the boreal mixedwood forest of eastern Canada.

Landscape	Proportion of aspen	10–25 cm DBH stem·ha^{-1} Mean ± SD	>25 cm DBH stem·ha^{-1} Mean ± SD
Managed forest	53%	260 ± 114	234 ± 75
Unmanaged forest	55%	623 ± 119	232 ± 42

Occupancy of active cavities

From the beginning of June to early July 2008 and 2009, we visited over 200 cavity-bearing trees in both the managed and the unmanaged forest to assess cavity nesters in active cavities. Some of the cavity-bearing trees selected to be surveyed were detected during the suitable cavity abundance survey (previously described) and others were cavity-bearing trees located in surrounding mature forest patches that had been detected as part of a long-term study on the eastern boreal nest web (Drapeau *et al.*, 2009). Nest webs describe the interactions between key species (excavators) that create suitable cavities and species that depend on suitable cavities for nesting (secondary cavity nesters) (Martin & Eadie, 1999). We selected trees with suitable cavities created by decay or by excavation by primary cavity-nesting species (Table II). We could identify the origin of the cavity 1) when we directly observed the species excavating or 2) through characteristics of entrance holes.

For each visit at an active nest, we followed the same protocol to assess the performance of ground surveys in detecting occupants of active nests. First, we tapped on the base of the tree with a large stick or a hammer and

TABLE II. Number of active nests where species occupancy could be confirmed using the ground survey method for primary and secondary cavity nesters in boreal mixedwood forest landscapes of eastern Canada in 2008 and 2009.

Species	Common name	Total number of nests detected	Nests confirmed using ground survey method
Primary cavity nesters		27	25
Sphyrapicus varius	Yellow-bellied sapsucker	14	13
Picoides pubescens	Downy woodpecker	3	3
Colaptes auratus	Northern flicker	9	8
Dryocopus pileatus	Pileated woodpecker	1	1
Secondary cavity nesters		25	12
Aegolius acadicus	Northern saw-whet owl	1	0
Bucephala clangula	Common goldeneye	7	5
Falco sparverius	American kestrel	1	1
Glaucomys sabrinus	Northern flying squirrel	7	5
Lophodytes cucullatus	Hooded merganser	1	0
Sciurus vulgaris	Red squirrel	2	0
	Anatidae sp.	5	1
	Sciuridae sp.	1	0

checked for visual or sound cues of activity by observing the cavity entrance and listening for begging for 2 to 3 min (Step 1) before visiting with the camera (Step 2). We noted whether evidence of nesting was detected at Step 1 or Step 2. If avian cavity users appeared in Step 1, we inspected the cavity with the camera to ensure it was not a false positive (absence of eggs, nestlings). To validate cavity use by Sciuridae, we inspected the inside of the cavity for the presence of young or, if they were not seen, of a nest (with fresh feces, straw, leaves, or bark).

Statistical analyses

We performed statistical analyses using R for Windows version 2.10.1 (Ihaka & Gentleman, 1996). We used the exact binomial test (Zar, 1984) to compare the proportion of potential cavities (ground surveys) that were classified as suitable cavities (direct inspection) with the probability that all potential cavities may be classified as suitable cavities. We derived cavity abundance to obtain cavity density (cavities·plot area^{-1}) for each plot. We used the *F*-test to compare the variances (Sokal & Rohlf, 1981) and the Shapiro–Wilk normality test to test assumptions of normality for the density variables (Shapiro & Wilk, 1965). We $\log_{10}$-transformed density variables because they were not normally distributed. We used a *t*-test to compare potential and suitable cavity densities of plots in managed *versus* unmanaged forests. We used Fisher's exact test of independence to compare the proportions of active primary and secondary nests correctly classified during ground surveys. Values are presented as means ± SD. The overall alpha level for statistical significance was 0.05.

Results

Cavity suitability

The effort spent to detect potential cavities during the ground surveys was 26.7 ± 5.5 observer-hours·ha^{-1}. We detected 270 potential cavities. We did not inspect 12 potential cavities because they were too high (>17 m); these cavities were excluded from further analysis. Under our definition of a suitable cavity, 98 potential cavities were considered suitable for use by cavity nesters. Overall, the proportion of suitable cavities was significantly lower (0.38, CI = 0.32–0.44, $P < 0.001$) than the proportion expected if all potential cavities were suitable cavities (*i.e.*, 1.0). This result was similar in managed (0.39, CI = 0.31–0.48, $P < 0.001$) and unmanaged forests (0.36, CI = 0.27–0.46, $P < 0.001$). Overall, unsuitable and suitable cavities were mostly excavated by woodpeckers (68% and 88%, respectively), as opposed to those resulting from wood decay (32% and 12%, respectively; $n = 204$ potential cavities with known origin). In the managed forest, we detected 34.0 ± 13.7 potential cavities·ha^{-1}, but only 12.4 ± 10.5·ha were suitable; in the unmanaged forest landscape, we detected 28.3 ± 10.0 potential cavities·ha^{-1}, but only 9.8 ± 4.0·ha were suitable. Density of potential and suitable cavities in managed ($n = 6$) and unmanaged forests ($n = 5$) did not differ (potential: $t_9 = 0.7$, $P = 0.52$; suitable: $t_9 = 0.1$, $P = 0.92$). Overall, suitable cavity density was 11.2 ± 8.0 per hectare.

Occupancy of active cavities

Of 40 mammal and bird species considered cavity users in the boreal mixedwood forest (Martin & Eadie, 1999; Darveau & Desrochers, 2001), 10 were detected in our study (see Table II). Weak cavity nesting species such as black-capped chickadees (*Poecile atricapillus*) and red-breasted nuthatches (*Sitta canadensis*) breed in our study area (Cadieux, 2011) but were not detected in our sampled cavities. We compared ground survey and direct inspection survey techniques for a total of 52 nests, of which 27 were primary cavity nesters and 25 were secondary cavity nesters. Nests of secondary cavity nesters were mainly Anatidae and Sciuridae, with also 1 American kestrel (*Falco sparverius*) and 1 northern saw-whet owl (*Aegolius acadicus*). A significantly higher proportion of nests of primary cavity nesters were detected without the use of a camera (93%) compared to those of secondary cavity nesters (48%) (Fisher's exact test of independence: $P < 0.001$).

Discussion

The low proportion of potential cavities classified as suitable (38%) after direct inspection indicates that ground surveys highly overestimate the suitability of woodpecker cavities in boreal mixedwood landscapes of eastern Canada. This may be an important bias in forest ecosystems where the availability of suitable cavities mainly depends on primary excavators (woodpeckers), such as in our study area (88%) or in the mixed forests of interior British Columbia, where 95% of suitable cavities were excavated by woodpeckers (Aitken & Martin, 2007). The actual availability of suitable cavities in nest webs driven by woodpecker holes could thus be more limiting for cavity users (Newton, 1994) than expected based on ground surveys of holes. Individual species preference may further limit availability of the nest site resource (Aitken & Martin, 2008).

Contrary to our prediction, the rate of incomplete excavations was not higher in remnant habitats of the managed landscape than in continuous forest blocks of the unmanaged landscape. Excavation behaviour of woodpeckers was not modified in the managed landscape, and cavity suitability for cavity users was similar to that in large forest blocks in the unmanaged landscape. Hence, within the time frame of our study (10 to 20 y after harvesting) remnant forests did not appear to be suboptimal habitats for cavity users with respect to cavity suitability. This may be partly explained by the fact that the same primary cavity nesting species were found in both studied forest landscapes (Drapeau, 2009). It may also be related to the availability of cavity-bearing trees (stems >25 cm DBH, Table I) that was comparable between the managed landscape and the unmanaged landscape.

In most forest ecosystems of North America, cavity abundance depends on woodpeckers and other excavating species (Martin & Eadie, 1999; Remm, Lohmus & Remm, 2006; Cockle, Martin & Wesolowski, 2011), and 1 or 2 excavating species often create most cavities (Martin & Eadie, 1999; Bednarz, Ripper & Radley, 2004; Saab, Dudley & Thompson, 2004). In our study, the yellow-bellied sapsucker was the most abundant primary excavator in both managed and unmanaged landscapes (Drapeau *et al.*, 2009). This species sometimes abandons nesting sites before completion (Lawrence, 1967). Hence, abundance of potential, but unsuitable, cavities is likely influenced by the propensity of some woodpecker species to abandon some of their excavations before completion.

Outside North America, wood damage and decay are the main drivers for cavity creation (Cockle, Martin & Wesolowski, 2011). In the Atlantic tropical forest of Argentina, Cockle, Martin & Drever (2010) found low numbers of suitable cavities (≥13 cm deep and ≥2.5 m high) from ground surveys (19%) when potential cavities (diameter ≥ 2 cm; interior depth unknown) were subsequently directly inspected. The bias of ground surveys to overestimate cavity suitability may thus vary among forest ecosystems depending on the relative importance of primary cavity excavators and natural decay processes in cavity creation. In any case, potential cavities are not a precise indicator of nest site availability.

Ground surveys may also underestimate the abundance of suitable cavities if cavities are not detected by observers. For example, in temperate forest systems where a large proportion of cavities are located on branches in the canopy, only 9–47% of potential cavities could be identified from ground surveys (Harper *et al.*, 2004; Blakely *et al.*, 2008; Koch, 2008). Some potential cavities in our study area may remain undetected, but we are confident that our ground survey estimates of abundance of potential cavities are less underestimated than in other forest systems (Harper *et al.*, 2004; Blakely *et al.*, 2008; Koch, 2008; Cockle, Martin & Wiebe, 2008). First, in our study area, trees are relatively small (*e.g.*, DBH over 40 cm is uncommon and tree height is generally under 25 m) and most cavities are found on trunks, where they are easier to detect from the ground (Rayner, Ellis & Taylor, 2010). Of the 115 active woodpecker nests detected in the study area in 2008 and 2009, 98% were located in the trunk (Ouellet-Lapointe, 2010). Second, our ground surveys were exhaustive and consistent (on average 26.7 ± 5.5 observer-hours·ha^{-1}). Variability in survey effort was attributed to differences in the tree density and walking difficulty among plots. Third, our results were similar to those reported by Aitken and Martin (2007) in mixed aspen–conifer forests of British Columbia when using a similar protocol to evaluate cavity abundance (ground surveys and subsequent direct inspection surveys). They reported a suitable cavity density of 12.3 per hectare, whereas our overall results were 11.2 suitable cavities·ha^{-1}, or 12.1 following their definition of a suitable cavity.

When using ground surveys to identify occupants of active cavities, we detected a greater proportion of primary than secondary cavity nesters. This is likely due to differences in behaviour between the 2 guilds. Primary cavity nesters (woodpeckers) generally excavate new cavities each year, which are easily identified by wood colour at the entrance and wood chips at the base of the tree (Bull, 1981). In addition, nestling begging is generally loud, and parents will often be seen at the entrance of the cavity tending the nestlings. In contrast, the secondary cavity nesters form a broader group (mammals and birds from different families, *e.g.*, owls, ducks, falcons) for which the response to tapping varies between species. Moreover, precocial birds, such as cavity-nesting ducks, could only be detected during incubation. Overall, direct inspection with a camera increased our ability to detect secondary cavity nesters in cavities. This result is most likely species-dependent and could differ for species that are more active at nest defence or at feeding nestlings. Furthermore, observing the nest for a longer period (20–30 min) would likely yield a higher detection rate (Martin & Geupel, 1993), particularly for secondary cavity nester species that leave the nest unattended or for species where adults frequently feed their mate or nestlings at the nest.

Although inspecting the inside of cavities results in more precise data (including the timing of breeding, clutch size, number and development of nestlings), its utility is defined by the trade-offs between the increased effort that it requires in the field and the level of accuracy required to reach specific research objectives. Our study indicates that in ecosystems where cavities are mainly generated by woodpeckers, such as boreal mixedwood forests, ground surveys overestimate cavity suitability for the community of cavity users but may be adequate for detecting primary cavity nesters in active nests. However, ground surveys yield low detection rates for secondary cavity nesters, which represent a critical group of species for assessing nest webs in these forest ecosystems.

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