

# Foraging patterns of pileated woodpeckers in a managed Acadian forest: a resource selection function

Jérôme Lemaître and Marc-André Villard

**Abstract:** We analyzed the relative influence of foraging substrate characteristics as predictors of the probability of use by the pileated woodpecker (*Dryocopus pileatus* L.) and determined threshold values for significant predictors. We sampled used and available substrates around 126 stations distributed in an intensively managed forest in northwestern New Brunswick, Canada. We developed a resource selection function (RSF), validated by a resampling procedure, and compared selection ratios for significant predictors. Diameter at breast height (DBH) of trees and snags was the most significant predictor, probably reflecting nesting selection by its main prey, carpenter ants (*Camponotus* spp.). The pileated woodpecker preferred deciduous substrates with DBH >35 cm and coniferous substrates with DBH >30 cm. Among deciduous substrates, it preferred snags over living trees, but there was no such preference for coniferous substrates. American beech (*Fagus grandifolia* Ehrh.) was clearly preferred over all other species. The RSF we developed and the thresholds we obtained should help forest managers and conservation planners assess habitat quality for this keystone species.

**Résumé :** Nous avons analysé l'influence relative des caractéristiques des substrats d'alimentation sur leur probabilité d'utilisation par le grand pic (*Dryocopus pileatus* L.) et nous avons déterminé des valeurs seuils pour les variables significatives. Nous avons échantillonné les substrats utilisés et disponibles autour de 126 stations distribuées dans une forêt acadienne sous aménagement intensif, dans le nord-ouest du Nouveau-Brunswick, au Canada. Nous avons développé une fonction de sélection des ressources (FSR), validée par une procédure de rééchantillonnage, et comparé les ratios de sélection des variables significatives. Le diamètre à hauteur de poitrine (DHP) des arbres et des chicots était la variable la plus significative, reflétant probablement la sélection des substrats de nidification de sa principale proie, les fourmis charpentières (*Camponotus* spp.). Le grand pic préférait les feuillus avec un de DHP > 35 cm et les conifères avec un DHP > 30 cm. Parmi les feuillus, il préférait les chicots plutôt que les arbres vivants alors que cette préférence n'a pas été notée chez les conifères. Le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) était clairement préféré par rapport aux autres espèces d'arbres. La FSR que nous avons développée et les seuils que nous avons obtenus devraient aider les décideurs en matière d'aménagement et de conservation à évaluer la qualité de l'habitat pour cette espèce-clé dans cette région forestière ou des régions similaires.

## Introduction

The pileated woodpecker (*Dryocopus pileatus* L.) has frequently been used as a focal species when guidelines for sustainable forest management are designed, in both Canada and the United States. It is considered an indicator species of mature and old forest conditions (Bull et al. 1992; Bull and Holthausen 1993; Lafleur and Blanchette 1993; Savignac et al. 2000). Its indicator status reflects the fact that the pileated woodpecker (1) nests and roosts in large snags or dying trees

(Bull et al. 1992; Bull and Holthausen 1993; McClelland and McClelland 1999); (2) mainly forages on large woody substrate, including trees, snags, stumps, and logs (Bull and Holthausen 1993; Flemming et al. 1999); (3) is the largest primary cavity excavator in North America, creating nesting and roosting sites for a wide variety of secondary cavity nesters (Martin and Eadie 1999; Bonar 2000); and (4) is considered an umbrella species, owing to its large home range (mean home range in published studies, 360 ha; range, 53–1056 ha) (Renken and Wiggers 1989; Mellen et al. 1992; Bull and Holthausen 1993; Savignac et al. 2000). In contrast, the black woodpecker (*Dryocopus martius* L.) occupies a similar niche in Eurasia but seems to adapt better to fragmentation of its habitat by agriculture (Tjernberg et al. 1993) and to moderate-intensity forestry (Rolstad et al. 1998).

Whereas the pileated woodpecker requires about one nesting substrate per year and around seven roosting substrates per year (Bull and Jackson 1993), it uses many more foraging substrates to meet its energetic requirements. This is especially the case in portions of its range where winters are severe and access to foraging substrates is restricted by short

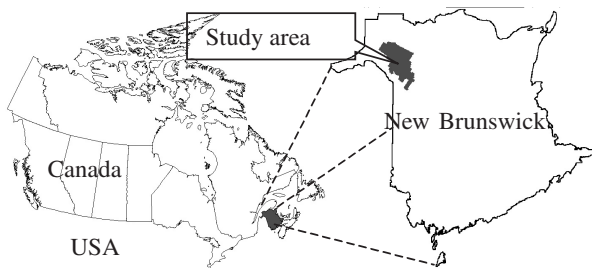
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**Fig. 1.** Location of the study area, a 190 000 ha forest district owned by J.D. Irving Ltd.



day length and snow cover. Yet, to our knowledge, foraging substrate use by the pileated woodpecker has been the focus of only one study in northeastern North America (Flemming et al. 1999), although it has been fairly well documented in Oregon (Bull and Meslow 1977; Bull and Holthausen 1993). However, none of those studies was designed to determine the relative influence of foraging substrate characteristics as predictors of the probability of use by the woodpecker. This information is crucial for developing conservation strategies that reflect the ecological requirements of the species.

In this study, we analyzed pileated woodpecker foraging patterns to determine substrate characteristics best predicting their use. Then we focused on each predictor to refine our knowledge of pileated woodpecker foraging preferences and identified thresholds for significant predictors, which can then be used for designing management and conservation strategies.

## Materials and methods

### Study area

This study was conducted in the Black Brook District, a 190 000-ha forest in northwestern New Brunswick, Canada (47°23'N, 67°40'W; Fig. 1). The landscape is among the most intensively managed ones in Canada, with extensive conifer plantation (mean area, 25 ha) beginning in the late 1950s. In 2002, young plantations ( $\leq 35$  years old) accounted for 34% of the district. More recently, single-tree selection and patch cutting have been applied in deciduous and mixedwood stands.

The study area is characterized by rolling hills and valleys, with elevations averaging 250 m a.s.l. and reaching a maximum of 495 m a.s.l. Mean annual temperature is 3.2 °C, and precipitation averages 1122 mm annually. Mean snow depth is 21 cm from November to April, with a maximum of 77 cm in February (Environment Canada 2003). Shade-tolerant deciduous tree species dominate hilltops (32%), and coniferous species dominate valleys (51%). The remaining 17% of the district's forest is represented by mixedwood stands. In the forest stands we surveyed, total basal area of trees  $\geq 8$  cm diameter at breast height (DBH) was composed of 32.2% sugar maple (*Acer saccharum* Marsh.), 14.5% black spruce, red spruce, and white spruce (*Picea* spp.), 14.2% balsam fir (*Abies balsamea* (L.) Mill.), 13.5% yellow birch (*Betula alleghaniensis* Britt.), 9.4% American beech (*Fagus grandifolia* Ehrh.), 8.2% eastern white-cedar (*Thuja occidentalis* L.), 2.6% red maple (*Acer rubrum* L.), 1.5% white birch (*Betula papyrifera* Marsh.), 1.3% trembling aspen (*Populus tremuloides* Michx.),

**Table 1.** Distribution of sampling stations among forest stand types and silvicultural treatments.

| Treatment       | Stand composition |           |           | Total |
|-----------------|-------------------|-----------|-----------|-------|
|                 | Coniferous        | Mixedwood | Deciduous |       |
| No treatment    | 15                | 12        | 23        | 50    |
| Retention patch | 3                 | 1         | na        | 4     |
| Partial cut     | 7                 | 2         | na        | 9     |
| Selection cut   | 5                 | 12        | 19        | 36    |
| Patch cut       | na                | 6         | 21        | 27    |
| Total           | 30                | 33        | 63        | 126   |

**Note:** na, silvicultural treatment is not applied in the corresponding stand composition.

0.6% tamarack (*Larix laricina* (Du Roi) K. Koch), and 2% other tree species.

At the time of the study, 83% of the district was managed under some form of silvicultural system, 9% was in riparian buffer strips (where low-intensity harvesting was permitted under certain conditions), 4% was protected as deer yards, 3% was set aside as scientific reserves, and 1% comprised 31 unique sites (i.e., areas protected for their unique biodiversity, geology, water bodies, or cultural, spiritual, or aesthetic value).

### Sampling design

From 10 May to 16 July 2002, we recorded the presence of recent foraging excavations by pileated woodpecker on all woody substrates at 126 stations distributed across the Black Brook District. We stratified our sampling to survey the main combinations of stand composition and silvicultural treatments (Table 1). Stations were located at least 100 m from the nearest road; the mean distance between adjacent stations was  $483 \pm 55$  m (range, 363–652 m). We used a type I sampling design (Manly et al. 1993), that is, we surveyed substrates available and used by pileated woodpeckers, without distinguishing individual birds.

### Use of foraging substrates

Pileated woodpecker foraging excavations can be reliably distinguished from those of other woodpecker species by their larger size and vertical rectangular shape (Bull and Jackson 1995). However, to reduce the risk of confounding this woodpecker's excavations with those of the hairy woodpecker (*Picoides villosus* L.), we considered in the analyses only foraging excavations at least 5 cm wide  $\times$  5 cm long  $\times$  5 cm deep. This method also reduced the risk of failing to detect small cavities excavated high above the ground. Pileated woodpecker foraging excavations are easily distinguished from its nesting and roosting excavations, because the latter have well-defined entrance holes that are deeper and more circular. We considered a substrate to have been excavated between October and April where we found wood chips at the surface of the leaf litter. We did not consider other foraging techniques (gleaning, pecking, and scaling) because (1) the pileated woodpecker uses excavation techniques in 53%–77% of foraging time (Bull and Holthausen 1993; Bull and Jackson 1995); (2) we did not record signs of scaling in our study area; and (3) sampling substrate use for gleaning and pecking would have required direct observation of foraging

individuals, which we did not conduct. Focusing on indirect foraging evidence allowed us to survey a more extensive area and a broader variety of stand types.

We visually scanned all woody substrates along four transects, 10 m × 100 m, running to the north, south, east, and west of each station (0.4 ha per station). As we found only two recently excavated logs and no recently excavated stumps, we focused on recently excavated trees and snags (hereafter referred to as “used substrate”). For all used substrate, we recorded the species, DBH, crown condition (totally broken or not), and decay class (modified from those of Maser et al. (1979) as follows: 1, healthy tree (with all its branches); 2, dying tree (presence of dead limbs); 3, recent snag (dead tree with a physical structure similar to that of a living tree); 4, snag (dead tree with some bark remaining and most branches broken); 5, very decayed snag (dead tree without bark and, generally, with a broken crown).

### Sampling of available foraging substrates

At each station, we recorded the species, DBH, and type (tree or snag) of all standing substrates with DBH ≥ 8 cm in 4-m bands along three 80-m transects running north, south-east, and southwest (0.096 ha per station). We recorded substrates if at least half the trunk overlapped the transect belt. We also recorded decay class and crown condition of available substrates at 61 of the 126 stations.

### Prediction of foraging substrate use

To compare significant predictors of pileated woodpecker substrate selection and to compare their relative influence, we used a resource selection function (RSF) (Manly et al. 1993). We coded available substrates as “0” and used substrates as “1”, and we adjusted the RSF to consider the bias associated with this false binary variable (Manly et al. 1993). In fact, the intercept  $\beta_0$  of the standard logistic regression equation was replaced by  $\ln(P_u/P_a) + \beta'_0$ , where  $P_u$  is the sampling proportion of used substrates and  $P_a$  that of available substrates:

$$[1] \quad w^*(x) = \frac{\exp(\ln(P_u/P_a) + \beta_0 + \beta'_0 + \beta_1x_1 + \dots + \beta_ix_i)}{1 + \exp(\ln(P_u/P_a) + \beta_0 + \beta'_0 + \beta_1x_1 + \dots + \beta_ix_i)}$$

where  $w^*(x)$  represents the resource selection probability function (RSPF); and  $\beta_i$  represents the coefficients of regression. To resolve the equation  $\beta_0 = \ln(P_u/P_a) + \beta'_0$ , the exact proportions of used and available substrates sampled must be known, which is virtually impossible for  $P_u$ . For this reason, we could not estimate  $\beta_0$ , and we were unable to estimate an RSPF, which would allow us to give a probability of use for each substrate (range [0; 1]). However, we could estimate an RSF, which is less practical because its range is [0; +∞]. For this purpose, we conducted standard multivariate logistic regressions, including  $\beta_0$  in the calculation, but we removed  $\beta_0$  once the model evaluation process was completed (see Manly et al. 1993). Therefore, the RSF is

$$[2] \quad w(x) = \exp(\beta_1x_1 + \dots + \beta_ix_i)$$

where  $w(x)$  represents the RSF.

We used Nagelkerke  $R^2$  and receiver operating characteristic (ROC) analysis to assess the significance of interactions and the overall fit of the final models (Fielding and Bell

1997; Hosmer and Lemeshow 2000; Manel et al. 2001; Guénette and Villard 2005). We assessed model performance using the area under the ROC curve (AUC): AUC = 0.5 indicates a poor model; AUC = 1.0, a perfect fit. An AUC ≥ 0.7 is considered to indicate good model fit (Hosmer and Lemeshow 2000). For the tree species variable, we labelled all unused tree species and those with fewer than five used stems as “others”. For a subset of 61 stations, we tested the predictive power of decay class and crown condition, in addition to that of DBH and tree species. By comparing this RSF with the original one (predictors tested: DBH, tree species, substrate type), we found that decay class and crown condition were not significantly better predictors than substrate type alone. Hence, we omitted these two variables from further analyses.

Finally, we built another RSF to account for possible pseudoreplication. Indeed, several adjacent stations could have sampled a single individual's home range (Hurlbert 1984; Johnson 2002). Estimates of pileated woodpecker home range size on the basis of telemetry vary greatly: 87 ± 32 ha (range: 58–160 ha;  $n = 11$ ) in Missouri (Renken and Wiggers 1989); 268 ± 69 ha ( $n = 3$ ) in southern Quebec (Savignac et al. 2000); 437 ha (range: 321–689 ha;  $n = 22$ ) in northeastern Oregon (Bull and Holthausen 1993); and 478 ± 219 ha (range: 267–1056 ha;  $n = 11$ ) in western Oregon (Mellen et al. 1992). As the mean distance between adjacent stations in our study sites was generally shorter (483 ± 55 m) than the mean radius of home ranges reported above (approximately 1 km), we might have considered used substrates as independent when, in fact, they had been excavated by the same individual. Therefore, we randomly resampled our data set 1000 times, excluding stations <1 km apart, and we built a RSF for each of the 1000 subsamples, hereafter referred to as the “randomized RSF”. We grouped tree species by substrate type, that is, by snags and trees, to simplify these RSFs for testing if the original RSF was biased owing to pseudoreplication, rather than explaining the foraging patterns of the pileated woodpecker. To allow the randomized RSF to converge, we could consider only three categories for the tree species–substrate type variable, namely: American beech snags, American beech trees, and others. We then compared the medians of the coefficients obtained from the 1000 randomized RSFs with those obtained from an RSF having the same predictors as the randomized RSFs but built with the original 126 stations, hereafter referred to as the “validation RSF”.

### Analysis of foraging patterns

We estimated the selection ratios for predictors, which added significance to the original RSF, and compared used substrates with those available (Manly et al. 1993). The following equation allowed us to determine the preference of the pileated woodpecker for a particular category of substrate:

$$[3] \quad \hat{w} = \frac{o_i}{\hat{\pi}_i}$$

where  $\hat{w}$  is the selection ratio for category  $i$ ; and  $o_i$  and  $\hat{\pi}_i$  are proportions of used and available substrates in category  $i$ , respectively. The preference threshold is 1. If the 95%

**Table 2.** Resource selection function predicting foraging substrate use by the pileated woodpecker in a managed Acadian forest.

| Variable                    | $\beta$ | SE ( $\beta$ ) | Wald <i>P</i> | Odds ratio (95% CI) |
|-----------------------------|---------|----------------|---------------|---------------------|
| DBH                         | 0.10    | 0.01           | <0.001        | 1.10 (1.09–1.12)    |
| Substrate type              | 0.97    | 0.27           | <0.001        | 2.63 (1.55–4.44)    |
| Tree species* (balsam fir)  | -0.77   | 0.32           | 0.018         | 0.46 (0.25–0.88)    |
| Tree species* (sugar maple) | -2.94   | 0.41           | <0.001        | 0.05 (0.02–0.12)    |
| Tree species* (white-cedar) | -1.67   | 0.51           | 0.001         | 0.19 (0.07–0.51)    |
| Tree species* (others)      | -3.17   | 0.46           | <0.001        | 0.04 (0.02–0.10)    |

**Note:** Nagelkerke  $R^2 = 0.320$ ; area under the ROC curve (95% CI) = 0.927 (0.900–0.954);  $n = 126$  stations.

\*The tree species of reference is American beech.

**Table 3.** Randomized and validation resource selection functions (RSFs), validating the use of the original RSF (see Table 2).

| Variable  | Randomized RSF |                                   | Validation RSF |               |
|---|----------------|-----------------------------------|----------------|---------------|
|   | $\beta_{1000}$ | SE( $\beta_{1000}$ ) <sup>†</sup> | $\beta$        | SE( $\beta$ ) |
| DBH   | 0.06           | 0.05                              | 0.06           | 0.02          |
| Tree species – substrate type* (American beech trees)     | -4.09          | 2.40                              | -4.31          | 1.34          |
| Tree species – substrate type* (others)                   | -3.58          | 1.85                              | -3.71          | 1.02          |
| DBH tree species – substrate type* (American beech trees) | 0.07           | 0.06                              | 0.08           | 0.03          |
| DBH tree species – substrate type* (others)               | 0.01           | 0.05                              | 0.01           | 0.03          |

**Note:** Randomized RSFs were obtained by subsampling the data set 1000 times, excluding stations <1 km apart. The validation RSF was built with the original 126 stations but with the same predictors as the randomized RSF.

\*The category of reference is American beech snags.

<sup>†</sup>Medians of the regression coefficients, calculated from the randomized RSF (1000 subsamples).

confidence interval (CI) of a selection ratio for the category  $i$  is  $>1$ , the category is “preferred”; if the 95% CI of a selection ratio for the category  $i$  is  $<1$ , the category is “avoided”; and if the 95% CI of a selection ratio for the category  $i$  includes 1, the category is used as a function of its availability.

For each predictor, we compared selection ratios using Bonferroni-corrected  $\chi^2$  tests for multiple comparisons ( $\alpha = 0.05$ ). We grouped categories where observed frequencies were  $<5$ , to respect assumptions of the  $\chi^2$  test (Manly et al. 1993) and to minimize spurious relationships resulting from bias of observer perception of availability (Johnson 1980).

## Results

We found 77 recently excavated substrates, including 12 living trees, 35 dying trees, and 30 snags. Of the trees and snags used, 27 were coniferous and 50 were deciduous.

The best predictor of substrate use was DBH, followed by substrate type and tree species (Table 2). We found a significant interaction between DBH and species, but we omitted it from the RSF because it added very little predictive power to the main effects model (Nagelkerke  $R^2 = 0.326$ , rather than 0.320; AUC (95% CI) = 0.930 (0.906–0.954), rather than 0.927 (0.900–0.954)).

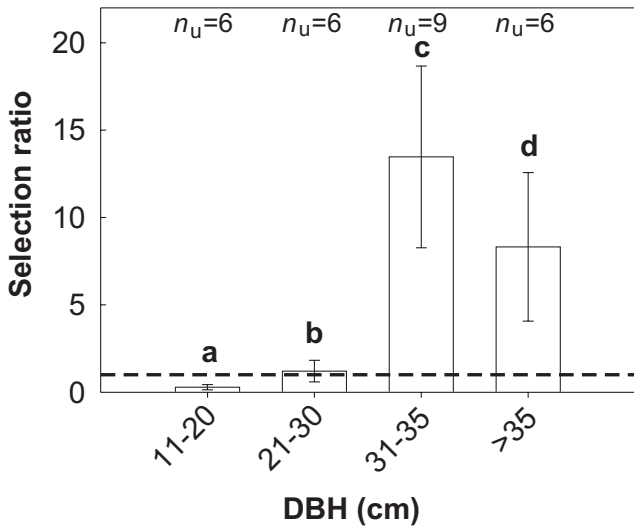
The median regression coefficients of the randomized RSF were very similar to those of the validation RSF (Table 3), suggesting that the original RSF was not affected by possible pseudoreplication. However, SE ( $\beta$ ) tended to be higher in the randomized RSF than in the validation RSF, suggesting that the original RSF tended to underestimate standard errors around regression coefficients.

The pileated woodpecker used coniferous substrates, in proportion to their availability, with DBH from 21 to 30 cm, and it preferred substrates with DBH  $>30$  cm (Fig. 2;  $\chi^2 = 148.7$ ,  $df = 3$ ,  $P < 0.001$ ). It also showed a preference for deciduous substrates with DBH  $>35$  cm (Fig. 3;  $\chi^2 = 250.9$ ,  $df = 5$ ,  $P < 0.001$ ). American beech was strongly preferred over all other tree species (Fig. 4;  $\chi^2 \geq 165.7$ ,  $df = 1$ ,  $\alpha/n = 0.005$ ,  $P < 0.001$ ). Balsam fir, sugar maple, and white-cedar were used in proportion to their availability. American beech was not among the largest tree species in the study area, but it tended to have more recent snags than other used species (Fig. 5; multiple  $\chi^2$  test comparisons,  $\alpha/n = 0.002$ ). The pileated woodpecker strongly preferred, for deciduous substrates, snags over trees (Fig. 6;  $\chi^2 \geq 179.0$ ,  $df = 1$ ,  $\alpha/n = 0.025$ ,  $P < 0.001$ ).

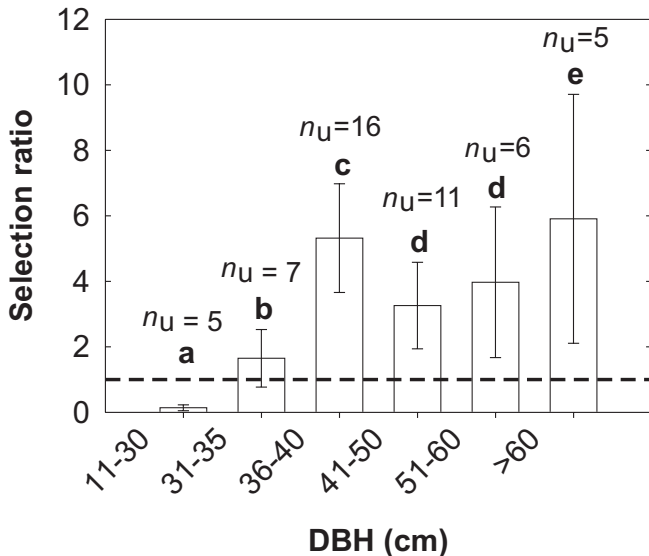
## Discussion

Our results show that DBH is the best predictor of foraging substrate use by the pileated woodpecker. Given the fact that the pileated woodpecker is a powerful excavator, its strong selection for large-diameter foraging substrates should mainly reflect the substrate selection patterns of its main prey, carpenter ants. These ants select large-diameter substrates to reduce the risk of nest destruction by blowdown when the colony grows and when gallery density increases, thus decreasing substrate resistance (Hansen and Akre 1985). In coniferous forests of Ontario, Sanders (1970) found that carpenter ants did not nest in substrates with DBH  $>20$  cm. Indeed, the pileated woodpecker did not use coniferous substrates  $\leq 20$  cm in our study area, which is consistent with its dietary specialization.

**Fig. 2.** Selection ratios and their 95% confidence intervals for DBH classes of coniferous trees and snags used by the pileated woodpecker. Shared lower-case letters indicate no significant difference in selection ratios among DBH classes (Bonferroni-corrected  $\chi^2$  tests). The dashed line indicates the preference threshold (see Methods), and  $n_u$  indicates the number of used substrates in the corresponding category.

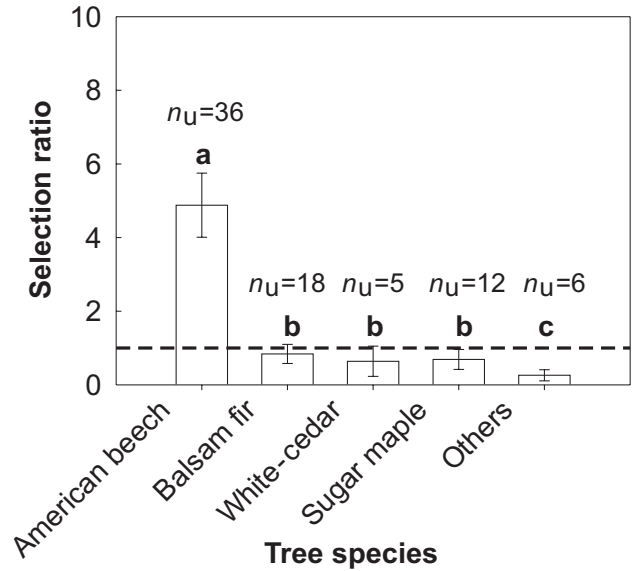


**Fig. 3.** Selection ratios and their 95% confidence intervals for DBH classes of deciduous trees and snags used by the pileated woodpecker. Shared lower-case letters indicate no significant difference in selection ratios among DBH classes (Bonferroni-corrected  $\chi^2$  tests). The dashed line indicates the preference threshold (see Methods), and  $n_u$  indicates the number of used substrates in the corresponding category.



A major consequence of intensive forest management is the suppression of large trees and snags over the long term, owing to short harvest rotations. In the future, this might force carpenter ants to use smaller nesting substrates, allowing them to grow smaller colonies (Hansen and Akre 1985). In that case, the pileated woodpecker would have to find and to excavate more substrates to satisfy its energetic require-

**Fig. 4.** Selection ratios and their 95% confidence intervals for tree species used for foraging by the pileated woodpecker. Shared lower-case letters indicate no significant difference in selection ratios among DBH classes (Bonferroni-corrected  $\chi^2$  tests). Category “others” includes aspen ( $n = 2$ ), tamarack ( $n = 1$ ), and spruces ( $n = 3$ ). The dashed line indicates the preference threshold (see Methods), and  $n_u$  indicates the number of used substrates in the corresponding category.

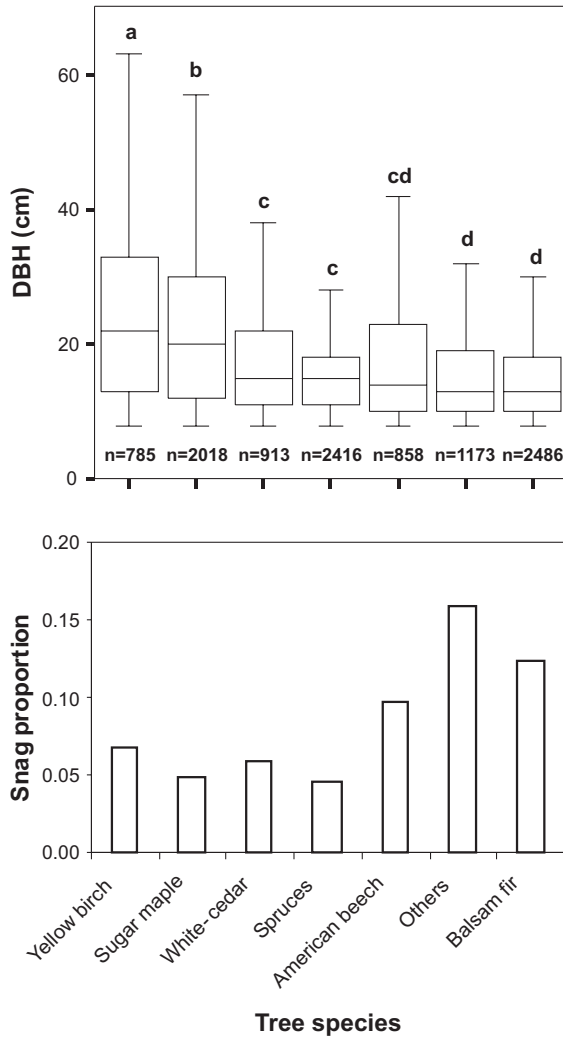


ments. Alternatively, individuals might become less specialized on carpenter ants to survive, and populations in altered habitat might evolve more opportunistic foraging behaviours.

Tree species was also a significant predictor of substrate use by the pileated woodpecker. In our study area, the pileated woodpecker exhibited a strong preference for American beech. Preferences for certain tree species as foraging substrates have already been reported elsewhere, although both preferred and available species vary greatly among study regions. In northeastern Oregon, the pileated woodpecker preferred Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western larch (*Larix occidentalis* Nutt.) (Bull and Meslow 1977; Bull and Holthausen 1993). In southeastern New Brunswick, the most frequently used species were red spruce (*Picea rubens* Sarg.) and balsam fir (Flemming et al. 1999). In west-central Alberta, Bonar (2001) found that tree species preference varied among seasons, white spruce (*Picea glauca* (Moench) Voss) being preferred in winter, trembling aspen in spring, and balsam poplar (*Populus balsamifera* L.) in summer. Flemming et al. (1999) suggested that apparent tree species preferences might reflect pileated woodpecker response to underlying characteristics that make certain tree species easier than others to excavate, or more likely to be colonized by insects than other species. Our results show that American beech preference is not an epiphenomenon associated with its larger DBH, but rather it reflects a greater proportion of beech snags in the study region. However, large yellow birch snags, for example, were never used by the pileated woodpecker, suggesting that tree species is indeed an important predictor.

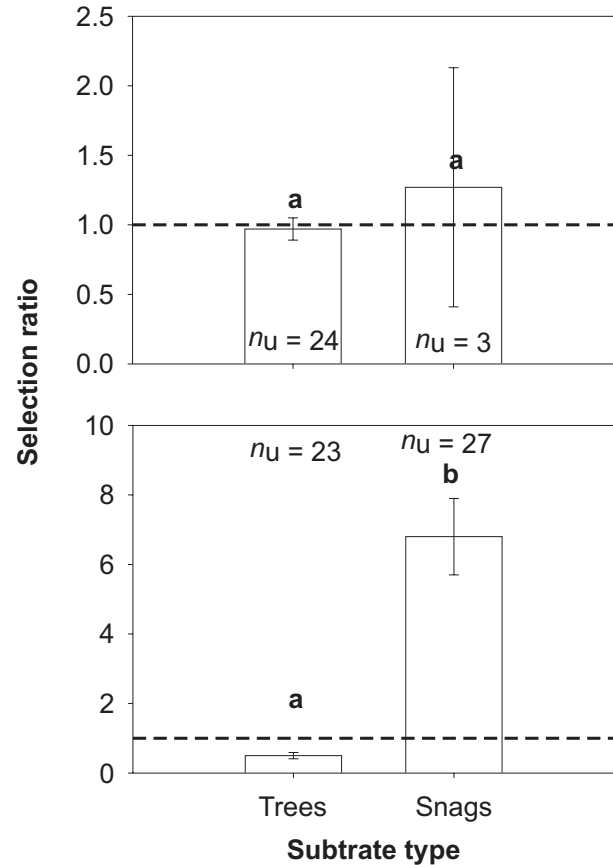
Therefore, conservation strategies that use the pileated woodpecker as a focal species should not only emphasize

**Fig. 5.** Box plot of DBH (top) and snag proportion (bottom) for the main tree species available (DBH ≥ 8 cm), that is, with a frequency >5%. In the top figure, horizontal lines within boxes are medians; boxes include 50% of the values around the median, and terminal bars include 75%; shared lower-case letters among species indicate no significant difference in DBH (Bonferroni-corrected *U* tests).



the protection and recruitment of large-diameter trees but also consider the dynamics in tree species. In our study region, selection systems are designed in part to suppress American beech in favour of more commercially valuable tree species (e.g., sugar maple, yellow birch) (Bohn and Nyland 2003). Because American beech was clearly preferred by the foraging pileated woodpecker, harvest prescriptions should ensure that enough large beech snags are maintained and recruited postharvest (snags with DBH >35 cm for immediate use, dying trees with DBH >35 cm for short- to mid-term use, and healthy trees for future use). Preference for American beech might be a temporary phenomenon reflecting the current ravages of beech bark disease, which appeared in the study area in the 1960s (Houston 1994). However, this study is not the first report of a positive association between beech species and woodpeckers (e.g., the black woodpecker and common beech (*Fagus sylvatica* L.) in central Germany (Pavlik 1996); the black woodpecker and the white-backed wood-

**Fig. 6.** Selection ratios and their 95% confidence intervals for coniferous (top) and deciduous (bottom) substrate types used for foraging by the pileated woodpecker. Category trees include both healthy and dying trees. Shared lower-case letters indicate no significant difference in selection ratios among DBH classes (Bonferroni-corrected  $\chi^2$  tests). The dashed line indicates the preference threshold (see Methods), and  $n_u$  indicates the number of used substrates in the corresponding category.



pecker (*Dendrocopos leucotos* Bechst.) with the same beech species in northern Spain (Fernandez and Azkona 1996)).

Flemming et al. (1999) found that the proportion of excavated deciduous substrates was greater in a fragmented forest than in a contiguous conifer-dominated forest nearby. In our intensively managed study area, the pileated woodpecker also preferred a deciduous species. Flemming et al. (1999) argued that for preferred species of coniferous substrates, the physical characteristics were less suitable than those of deciduous substrates in a fragmented landscape; that is, the conifers were not large enough or decayed enough. This hypothesis seems to hold in our study area because, until recently, harvesting took place mainly in coniferous stands, so most currently available coniferous substrates are less suitable than deciduous ones because they are too young for carpenter ants to invade their boles.

The RSF we developed can be used by managers in this or similar forest regions as a tool for assessing foraging habitat quality in stands or in forest landscapes as a whole. However, adaptive forest management requires proper monitoring to periodically reassess the effectiveness of this RSF over space and time and to update it on the basis of new findings.

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