Habitat use by Pileated Woodpeckers at two spatial scales in eastern Canada

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Abstract: To study the multiple spatial scale pattern of habitat use by Pileated Woodpeckers (*Dryocopus pileatus* L.), we compared the vegetation characteristics at used sites with those at unused sites at macrohabitat (154 ha radius plots) and microhabitat (ca. 0.04 ha radius plots) scales in the La Mauricie region of Québec. Used macrohabitats were those in which woodpeckers were detected at playback stations. Used microhabitats corresponded to sites showing signs of foraging (i.e., excavated cavities). Pileated Woodpeckers responded to vegetation structure at both scales sampled. Macrohabitats used by woodpeckers had relatively low percentages of mixed shade-intolerant hardwood stands, coniferous stands, and stands of relatively low stem density and tree height, but included high percentages of 51- to 90-year-old stands. Microhabitats used by woodpeckers were characterized most strongly by a high density of large snags but also by a high density of small-diameter snags and a low density of shade-intolerant hardwood trees and coniferous trees ≤30 cm diameter at breast height. The concordance between the observed and predicted use of micro- and macrohabitat plots was independent of spatial scale (logistic regression, $\chi^2_{0.05,1} = 1.8$, $P = 0.18$, $n = 429$), suggesting that habitats use by woodpeckers was influenced to a similar extent by habitat features measured at both spatial scales. Because Pileated Woodpeckers are likely to require specific habitat features at different spatial scales, forest-management guidelines intended to conserve this umbrella species should consider a multiple spatial scales approach.

Résumé : Nous avons étudié la variation spatiale de l'utilisation de l'habitat par le Grand Pic (*Dryocopus pileatus* L.) dans une forêt mixte-décidue de la Mauricie, au Québec, en comparant les caractéristiques végétales de sites utilisés et non utilisés à l'échelle du macrohabitat (parcelles de 154 ha) et du microhabitat (parcelles de 0.04 ha). Les macrohabitats utilisés correspondaient à des stations d'appel où des pics ont été repérés. Les microhabitats utilisés correspondaient à des sites avec signes d'alimentation (c.-à-d. cavités). À chacune des échelles, les pics utilisaient l'habitat principalement en fonction de variables structurales de la végétation. Les macrohabitats utilisés par les pics avaient de faibles pourcentages de peuplements mixtes à dominance de feuillus intolérants à l'ombre, de peuplements conifériens et de peuplements de densité × hauteur moyenne. Ils avaient toutefois de forts pourcentages de peuplements matures (c.-à-d. 51–90 ans). D'autre part, les microhabitats utilisés étaient caractérisés surtout par une densité élevée de chicots de grand diamètre, mais aussi par de faibles densités de feuillus intolérants à l'ombre de diamètre à hauteur de poitrine (dhp) ≤30 cm et d'essences conifériennes de dhp ≤30 cm ainsi que par une densuté élevée de chicots ≤30 cm. La concordance entre l'utilisation observée et l'utilisation prédite des parcelles de macro et microhabitats était indépendante de l'échelle spatiale (régression logistique, $\chi^2_{0.05,1} = 1.8$, $P = 0.18$, $n = 419$), ce qui suggère un degré d'influence similaire des caractéristiques végétales aux deux échelles spatiales. Étant donné que le Grand Pic peut répondre à certaines composantes végétales à différentes échelles spatiales, les aménagements forestiers pour cette espèce parapluie devraient tenir compte de plusieurs échelles spatiales.

Introduction

Heterogeneity of landscape and vegetation varies across spatial scales and may be considered hierarchically structured (Urban et al. 1987; Kotliar and Wiens 1990; Keitt et al. 1997). Multiple spatial scale (referred to here as multiscale) analyses suggest that birds respond to this hierarchical structure, as their patterns of habitat use vary across spatial scales (Addicott et al. 1987; Orians and Wittenberger 1991; Hunter et al. 1995; Jokimaki and Huhta 1996). Consequently, studies investigating the habitat-use pattern of a given species at only one spatial scale are potentially misleading if the scale of observation is arbitrarily set or does not correspond to the scale of responses (Wiens et al. 1986; Addicott et al. 1987). Thus, to understand the hierarchical response of birds to vegetation, a multiscale approach should be used that encompasses the range of spatial scales over which organisms are likely to respond to the heterogeneity of habitat and landscape components (Addicott et al. 1987).

Few species considered to be ecological indicators have been the subject of multiscale studies. Examples are the Northern Spotted Owl (*Strix occidentalis caurina* Merriam) in the Pacific Northwest region (Hunter et al. 1995) and the Sandhill Crane (*Grus canadensis* L.) in the Midwest (Baker et al. 1995). In Canada, no multiscale studies have been done on habitat use by the Pileated Woodpecker (*Dryocopus pileatus* L.), considered to be an indicator and an umbrella species in Québec (Lafleur and Larue 1992), Ontario (Naylor

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et al. 1996), Saskatchewan (Anonymous 1991),[2] Alberta (Bonar 1997),[3] and New Brunswick (Flemming et al. 1999). Studies of habitat use by Pileated Woodpeckers conducted over a single spatial scale (Bull 1987; Bull et al. 1992; Bull and Holthausen 1993; Renken and Wiggers 1993; Flemming et al. 1999) suggest that this species responds to vegetation heterogeneity at different scales. For example, at the home-range scale in Oregon, Pileated Woodpeckers are known to show a preference for mature and old-growth stands with a high and complex canopy layer and a high density of large tree snags and stumps (Bull 1987; Bull and Holthausen 1993). Furthermore, at the scale of forest stands, this species prefers live trees with a high incidence of heart-rot fungi and large snags for nesting and large fallen logs for foraging activities (Conner et al. 1975; Bull and Meslow 1977; Bull et al. 1992).

Here we describe habitat use by Pileated Woodpeckers at the microhabitat (ca. 0.04-ha variable-radius plots) and macro-habitat (ca. 154 ha radius plots) scales to determine whether woodpeckers are influenced simultaneously at two contrasting spatial scales. We compare the influence of vegetation at these two spatial scales to help determine whether a multiscale approach should be used to manage habitats for the Pileated Woodpecker.

Study area

We studied Pileated Woodpeckers' habitat use between May and July 1994 in the La Mauricie region (46°36′N, 73°31′W) of southern Québec. The 1400-km^2 study area is composed of the southern part of the Réserve Faunique Mastigouche (RFM; ≈1000 km^2) and La Mauricie National Park (LMNP; ≈400 km^2). More than 50% of the study area is composed of mixed hardwood stands (i.e., similar amounts of shade-intolerant hardwood and conifer species) with a mean canopy height of ≥22 m and canopy closure of ≥60%, whereas the remaining area is composed of lakes, recent clearcuts, and conifer plantations <30 years old (Savignac 1996). Dominant tree species include sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and balsam fir (*Abies balsamea* L. (Mill.)). Half of the area of the RFM has been subjected to selective and clear-cut logging since 1945 (Government of Québec 1990), whereas LMNP has not been logged since its creation in 1970, but was subjected to selective logging prior to this period. Dominant features across the landscape are several lakes, rivers, and 200–600 m high hills.

Methods

Choice of spatial scales

We defined macrohabitat as the scale at which woodpeckers responded to the aggregation of forest stands in the landscape. We set the maximal distance from which territorial birds could be attracted by playback calls at 700 m, as determined from previous trials during which birds were called from known distances ranging from 500 to 1000 m (C. Savignac, unpublished data). We considered the macrohabitat to be representative of the scale at which this species defends territories in southern Québec (the mean size of three home ranges during the breeding season was 268 ± 69 (SD) ha; C. Savignac, unpublished data). We regarded the

microhabitat as the aggregation of vegetation patches within the macrohabitat scale and considered it to be representative of the scale at which individuals make foraging decisions. We sampled microhabitats with plots of ca. 0.04 ha (variable radius), delimited using Bitterlich's method with a factor 2 prism (Grausenbaugh 1952). This technique consists of counting with a prism all trees within a minimum apparent diameter from the center of a plot. The number of trees is then converted to basal area and stem density by means of a simple formula (Grausenbaugh 1952).

Macrohabitat use

We located territorial woodpeckers by means of playback of calls and drumming at 75 playback stations placed, according to access, along logging roads throughout the study area. We used playback stations at locations that were similar in their forest composition (i.e., only in mature and old-growth hardwood and mixed stands) and contained ≥75% of forested area. Stations were placed >1.5 km apart to reduce the possibility of double-counting individuals during a given sampling period. All stations were located at least 500 m from lakes and recently harvested areas to reduce the effect of nonforested areas on sound propagation. Playbacks were performed with 5-W amplifiers and portable speakers and lasted 5 min with five 30-s pauses equally distributed across the playback period. Each station was monitored on five evenly spaced visits from 06:30 to 11:00 from late May to late July on days with no rain or wind <30 km/h. A playback station was considered to be used when a territorial woodpecker was detected at least once during the five visits. Since territorial and resident woodpeckers are more likely to respond to playback than nonbreeding individuals, we considered the presence of woodpeckers at playback stations during the breeding period as an indicator of site use over the year.

Microhabitat use

We characterized vegetation at living trees, snags, stumps with woodpecker feeding cavities, and microhabitats without signs of use. Used sites were ≤30 m from unused sites. We sampled only foraging sites with fresh wood chips at the base of substrata. If wood chips appeared to be lying on top of dead leaves from the previous year, we assumed that foraging cavities had been excavated after fall. Feeding cavities could be easily identified from their rectangular shape and large size (Flemming et al. 1999). Since Pileated Woodpeckers forage mainly by excavation (Conner 1981; Brawn et al. 1982; Swallow and Gutiérrez 1986), we considered feeding cavities to be good indicators of microhabitat use. A maximum of four recently used trees were sampled randomly by two observers walking ≈20 m each side of 29–650 m long transects and looking for trees with foraging sites up to 50 m from transect lines. Transects were placed systematically throughout the study area in ≥70-year-old mixed-hardwood stands that were similar in topography and logging history. Selected stands were always large enough to fully enclose a transect. An equal number of sites without cavities were sampled at ≥200-m intervals along each transect. Both used and unused microhabitats were sampled ≥50 m from roads to minimize potential edge effects. None of the sampled sites overlapped. Owing to the difficulty of aging feeding cavities with precision to a period during the year, we interpreted microhabitat use as a year-round process.

Vegetation description

At the macrohabitat scale, we described the vegetation within a 700-m radius (154 ha) of each playback station. Vegetation was

[2] Anonymous. 1991. Saskatchewan Forest Habitat Project. Unpublished report prepared by Terrestrial and Aquatic Environment Managers Ltd. and the Wildlife Branch, Saskatchewan Parks and Renewable Resources, Prince Albert.

[3] L.R. Bonar. 1997. Pileated Woodpecker (*Dryocopus pileatus*): habitat suitability index (HSI) model. *In* Habitat suitability index models for 35 wildlife species in the Foothills Model Forest. *Edited by* B. Beck, J. Beck, W. Bessie, R. Bonar, and M. Todd. Draft report, Foothills Model Forest, Hinton, Alberta. pp. 193–202.

Table 1. Habitat variables sampled at the macrohabitat and microhabitat scales in La Mauricie, 1994.

Macrohabitat variable	Microhabitat analog	Description	Range[a]
HABITAT1	HABITAT1	Mastigouche Wildlife Reserve and La Mauricie National Park	1, 2
CON	DENCON1, DENCON2	Percentage of conifer stands	0–61
INTCON	DENINT1, DENINT2	Percentage of mixed shade-intolerant hardwood stands	0–93
HARDCON	DENTOL1, DENTOL2	Percentage of mixed shade-tolerant hardwood stands	0–97
UNEVEN	—	Percentage of uneven-aged stands	0–98
NFORA	—	Percentage of nonforested area	0–41
AGE1	OVERHT	Percentage of 10- to 50-year-old stands	0–69
AGE2	OVERHT	Percentage of 51- to 90-year-old stands	0–89
AGE3	OVERHT	Percentage of >90-year-old stands	0–98
DH1	OVERC, OVERHT	Percentage of stands with height ≥17 m and density ≥60%	0–83
DH2	OVERC, OVERHT	Percentage of stands with height ≥12–17 m and density ≥60% and height ≥17 m and density 25–60%	0–73
DH3	OVERC, OVERHT	Percentage of stands with height ≥4–12 m and density 25–100%	0–83
SNAGD	DENSG1, DENSG2	Density of snags ≥35 cm dbh (snags/ha)	13–36
MICROHABITAT	MACROHABITAT ANALOG		
HABITAT1	HABITAT1	Mastigouche Wildlife reserve and La Mauricie National Park	1, 2
OVERC	DH1, DH2, DH3	Overstory density (%)	20–100
UNDERC	—	Understory density (%)	20–100
OVERHT	DH1, DH2, DH3, AGE1-3	Overstory canopy height (m)	4–28
BASLT	—	Basal area of living trees (m²/ha)	0–58
MNDBHL	—	Mean dbh of living trees (cm)	0–53
MNDBHS	—	Mean dbh of snags (cm)	0–79
DENCON1	CON	Density of coniferous trees 10 ≤ dbh ≤ 30 cm (stems/ha)	0–763
DENCON2	CON	Density of coniferous trees >30 cm dbh (stems/ha)	0–147
DENTOL1	HARDCON	Density of hardwood trees 10 ≤ dbh ≤ 30 cm (stems/ha)	0–763
DENTOL2	HARDCON	Density of hardwood trees >30 cm dbh (stems/ha)	0–147
DENINT1	INTCON	Density of shade-intolerant hardwood trees 10 ≤ dbh ≤ 30 cm (stems/ha)	0–916
DENINT2	—	Density of shade-intolerant hardwood trees >30 cm dbh (stems/ha)	0–111
DENSN1	SNAG	Density of snags 10 ≤ dbh ≤ 30 cm (snags/ha)	0–407
DENSN2	SNAG	Density of snags >30 cm dbh (snags/ha)	0–90
LOGVOL	—	Log volume (m³/0.04 ha)	0–673

[a]Values 1 and 2 represent dummy variables for each area.

characterized at the stand level using forestry inventory maps (Government of Québec 1990) that showed cover types, tree species composition, age of forest stands, perturbations, slope, and soil drainage. Around each station we recorded the percentage of the total area covered by 13 habitat variables grouped into six categories: floristic composition, nonforested area, age of forest stands, stand structure, and snag density (Table 1). Because canopy height and tree density are generally correlated, we used Lafleur and Blanchette's (1993) classification system, which combines tree density and height into three categories (DH1, DH2, DH3; Table 1). Since no information on snag density was available on forest cover maps, density of snags ≥35 cm diameter at breast height (dbh) had been previously sampled on 48 transects, each containing ten 0.04-ha plots equally spaced and distributed in the RFM according to six representative stand types (mixed shade-intolerant hardwood, mixed shade-tolerant hardwood, hardwood, shade-intolerant hardwood, coniferous, and clearcut) and two age-classes (≥70 and <70 years old) (Government of Québec, unpublished data). We counted snags in each plot and calculated the density for each stand and age-class. We then calculated a weighted average snag density for each playback station by taking into account the proportion of the sampled area covered by each stand type. We included the influence of land management within our study area (i.e., RFM and LMNP) on macrohabitat use by using a dummy variable.

At the microhabitat scale, 16 vegetation variables were recorded. We estimated overstory and understory density using four density classes: ≤40, 41–60, 61–80, and 81–100%. Canopy height was measured with a clinometer. We identified and measured the diameter at breast height of all tree species and snags ≥5 cm dbh using Bitterlich's method (Grausenbaugh 1952). We calculated the mean diameter at breast height of living trees and snags and the basal area of living trees. We measured the density of coniferous trees, deciduous trees (grouped by shade-tolerant and shade-intolerant hardwood species), and snags for two classes, 5–30 and >30 cm dbh. We estimated the volume of all logs that were partially or totally included within a 0.04-ha plot around used and unused trees using the cylinder equation with the mean of the

Table 2. Habitat predictors of Pileated Woodpecker occurrence at the microhabitat and macrohabitat scales in La Mauricie, 1994.

	Change in deviance	df	P
Macrohabitat predictor			
Percentage of shade-intolerant and coniferous stands (–)	8.4	1	0.004
Percentage of coniferous stands (–)	8.1	1	0.004
Percentage of 51- to 90-year-old stands (+)	4.6	1	0.032
Percentage of stands of moderate density–height classes (–)	3.6	1	0.060
Microhabitat predictor			
Density of snags ≥31 cm dbh (+)	17.9	1	0.000
Density of snags ≤30 cm dbh (+)	7.1	1	0.007
Density of shade-intolerant tree species ≤30 cm dbh (–)	7.3	1	0.007
Density of coniferous tree species ≤30 cm dbh (–)	2.8	1	0.091

Note: A plus sign denotes a higher value at used sites and a minus sign a higher value at unused sites. Goodness of fit (R^2) for macrohabitat and microhabitat are 0.13 and 0.25, respectively.

diameter of both ends of fallen logs. We included the influence of land management within our study area (i.e., RFM and LMNP) on microhabitat use by using a dummy variable.

Data analysis

For both scales, we used a Spearman's correlation matrix in order to eliminate statistically redundant variables with $r_s \geq 0.7$ (Savignac 1996), but kept all those that were biologically important for woodpeckers, based on the literature (Bull and Meslow 1977; Renken and Wiggers 1989, 1993; Bull and Holthausen 1993). For each scale, we used backward elimination stepwise logistic regressions (SLR) (SPSS 1997) to obtain sets of predictors of habitat use by woodpeckers. The significance of the final models and of the contribution of each variable was tested by the change in deviance (–2 log-likelihood ratio) between the saturated model (all variables included) and the models with variables of interest removed. Entry and removal probabilities for each step of the stepwise procedure were set at 0.05 and 0.1, respectively. We used Nagelkerke's R^2 (Nagelkerke 1991) as a goodness-of-fit indicator of the final models.

To determine whether the response of Pileated Woodpeckers to vegetation was scale-dependent, we used, for each spatial scale, the predictive functions of the SLR to obtain the number of vegetation plots correctly and incorrectly classified as used or unused by woodpeckers. For both scales, we classified plots as being used when the estimated probability of use was >0.5. Maximum difference in vegetation characteristics between used and unused sites would be indicated by a correct classification of 100%; whereas no differece between groups would be indicated by a classification of 50%. Similarity in sample size between groups at both scales limited the bias toward classifying vegetation into the largest group. We then tested the null hypothesis that the frequency at which sites were correctly classified did not differ significantly between spatial scales by using χ^2 analysis at $\alpha = 0.05$.

Results

Macrohabitat use

Woodpeckers were detected at least once at 41% of the 75 playback stations. Twenty-four percent of stations with

woodpecker responses had more than one response over the five visits. Responses were distributed inconsistently among the five visits. Ninety percent of all stations with responses corresponded to territorial males that showed aggressive behavior toward playback calls (i.e., agitated birds flying over or perching near a station, frequent drumming and calling).

We eliminated from the SLR analysis the percentages of uneven-aged stands, stands with canopy height ≥17 m and a density ≥60%, and >90-year-old stands because they were highly correlated ($r_s \geq 0.8$) with the percentage of mixed shade-tolerant hardwood stands. The latter variable was therefore used as a proxy for the set of four correlated variables. Although the density of snags of ≥35 cm dbh was highly correlated with the above variables, we kept it in the analysis because of its high biological significance for the Pileated Woodpecker (see Conner 1980; Bull and Holthausen 1993).

The occurrence of Pileated Woodpeckers was significantly influenced by macrohabitat vegetation structure (Table 2). Their occurrence was negatively and strongly associated with the percentages of shade-intolerant and coniferous stands and of coniferous stands (Table 2). Occurrence was, to a lesser extent, positively associated with the percentage of 51- to 90-year-old stands and negatively associated with the percentage of stands of intermediate density–height classes.

Microhabitat use

Since the density of shade-tolerant hardwood trees 10 ≤ dbh ≤ 30 cm (stems/ha) and of shade-tolerant hardwood trees >30 cm dbh (stems/ha) were highly correlated ($r_s = 0.8$), we retained the latter as a proxy for overall density of shade-tolerant trees. Of the 15 variables entered in the SLR model, 4 were retained as being significantly related to woodpecker occurrence (Table 2). Occurrence was positively and strongly associated with the density of snags ≥31 cm dbh (Table 2). Moreover, occurrence was negatively associated with density of stems of shade-intolerant hardwoods ≤30 cm dbh, positively associated with the density of snags ≤30 cm dbh, and negatively associated with the density of coniferous trees ≤30 cm dbh.

Response to vegetation across scales

Predictive functions of the SLR showed similar, but relatively low, rates of correct classification of used and unused sites at both spatial scales. Sixty-two percent of microhabitat plots were correctly classified compared with 71% at the macrohabitat scale. The proportion of sites that were correctly classified did not differ significantly between spatial scales ($\chi^2_{0.05,1} = 1.8$, $P = 0.18$, $n = 429$), indicating that habitat features measured at the macro- and micro-habitat scales affected Pileated Woodpeckers' habitat use similarly.

Discussion

Importance of spatial scale

Pileated Woodpeckers in La Mauricie responded to vegetation structure and composition at contrasting spatial scales. Although we measured analog variables that were common to both scales, woodpecker occurrence was most clearly related to different variables at different scales. In general, woodpeckers responded both to variation in forest cover at

the macrohabitat scale and to variation in snag abundance among microhabitat patches. Multiscale patterns of habitat use have been noted with other bird species (Wiens 1986; Orians and Wittenberger 1991; Bergin 1992). For example, Wiens (1986) demonstrated that several shrub-steppe bird species in the western United States use different categories of structural and floristic features of vegetation along a gradient of five spatial scales ranging from the landscape to the microhabitat scale. Similarly, VanderWerf (1993) found that foraging Elepaio (*Chasiempis sandwichensis* Gmelin) use different structural features of vegetation at three spatial scales within territories. Also, songbirds such as the Pied Flycatcher (*Fidedula hypoleuca* L.) in Finland also respond to habitat at different spatial scales by being negatively affected by the degree of fragmentation at the scale of 4-ha plots, but show no responses to habitat components at the landscape scale (i.e., 4-km^2 plot) (Jokimäki and Huhta 1996). On the other hand, some species are also known to respond to habitat components that are common to multiple scales (Sedgwick and Knopf 1992; Hall and Mannan 1999).

Patterns of habitat use by woodpeckers in southern Québec can be explained in part by the structural cues hypothesis (Smith and Shugart 1987), which suggests that structural features are better proximate cues than food density because they remain relatively constant over time, whereas actual food density may vary greatly from year to year. At the macrohabitat scale, Pileated Woodpeckers might have cued on forest mosaics dominated by mature shade-tolerant hardwood stands because they were likely to offer the greatest abundance of snags and other potential foraging substrata. At the microhabitat scale, however, woodpeckers might have cued on snags patches in order to evaluate ant-colony density more directly. Because we did not measure food availability within territories, further studies are needed to better assess differences in the influence of food density and habitat characteristics on habitat use.

From where did the most of the variation that is unexplained by our models come? Scale-dependent habitat selection might have been affected by several unmeasured biotic factors. For example, at the macrohabitat scale, habitat use might have been influenced by territory availability in the landscape. Pulliam and Danielson (1991) argue that individuals could be limited in their choice of high-quality territory by the preemptive behavior of territorial individuals in the population. Therefore, habitat-use patterns are likely to be more pronounced in lower density populations when high-quality territories are still available, as was probably the case in our study area (Savignac 1996). Another unmeasured explanatory factor that might have influenced decisions at the macrohabitat scale is the availability of nesting sites, which has been shown to greatly influence decisions related to home-range settlement by cavity-nesters (Conner and Adkisson 1976).

Other biotic factors were also likely to influence microhabitat use. For example, studies have shown that predation on Pileated Woodpeckers by raptors such as the Northern Goshawk (*Accipiter gentilis*) is relatively important during the breeding season (Bull et al. 1992). Therefore, it is reasonable to assume that the presence of predators may affect woodpeckers' habitat use within their territories at a scale similar to the microhabitat scale. Furthermore, considering the importance of snags to the foraging behavior of Pileated Woodpeckers (Bull 1987; Bull and Holthausen 1993), their spatial distribution within territories was likely to influence habitat use.

Our results suggest that Pileated Woodpeckers were equally sensitive to variation in vegetation at the two scales examined. It is unclear, however, whether they would have shown similar responses at other spatial scales. A study that looked at habitat use by Pileated Woodpeckers in northwestern Alberta suggests that Pileated Woodpeckers select patches of deciduous trees for nesting but demonstrate weak selection of nest locations within those patches (R. Bonar, unpublished data). Another study that looked at the vegetation characteristics of sites used for foraging by cavity-nesters in New York State suggests that this guild responds more strongly to vegetation near trees than to characteristics of the trees that are actually used (Swallow and Gutiérrez 1986). Furthermore, Jokimäki and Huhta (1996) found that cavity-nesters in northern Finland responded to meso- and micro-scale vegetation characteristics but not to landscape-scale heterogeneity.

Macrohabitat use

Pileated Woodpeckers in our study area avoided immature mixed shade-intolerant hardwood and coniferous macrohabitats and preferred mature mixed shade-tolerant hardwood stands for foraging. These results are in agreement with other findings from Missouri (Renken and Wiggers 1993) that indicate a positive relationship between abundance and density of Pileated Woodpeckers and the amount of hardwood bottomland forest. The negative relationship between woodpeckers' occurrence and the percentage of mixed and coniferous stands in our study might have been related in part to the low availability of higher quality substrata, particularly large yellow birch, sugar maple, and balsam fir in these stands. Large-diameter birches and maples were preferred by woodpeckers in mature and overmature mixed shade-tolerant hardwood stands, but firs were more commonly used only in immature mixed shade-intolerant stands (C. Savignac, unpublished data). In contrast with our findings, Flemming et al. (1999) found that dead and declining balsam firs are the main foraging substrata for Pileated Woodpeckers in southern New Brunswick. Those authors argue that firs are preferred by woodpeckers because they have softer wood and their bark peals off easily, hastening the decay process relative to shade-tolerant hardwood species. In our study, large firs were not preferred by woodpeckers, since they were at low density and well-decayed, large shade-tolerant hardwood snags were the most abundant foraging substratum (Savignac 1996).

Our results at the macrohabitat scale contrast with those of other studies which suggest that Pileated Woodpeckers are more likely to select their habitat on the basis of high densities of coarse woody debris (Renken and Wiggers 1989). In our study area, this apparent lack of response by woodpeckers to these features was possibly due to an overabundance of snags (Savignac 1996). Steele (1992) demonstrated a similar pattern tn Black-throated Blue Warblers (*Dendroica caerulescens* Gmelin), which select patches with high shrub density (i.e., the main habitat predictor of habitat use) within territories. Warblers prefer to nest in microhabitats with high shrub density, but do not respond to this

feature at the scale of the territory when it exceeds a certain threshold. Finally, owing to the fact that we did not collect data on stump and log volumes at the macrohabitat scale, we cannot rule out the possibility that these features would have had some effect on woodpeckers' habitat use at this scale.

Microhabitat use

A high density of small and large snags was the main habitat feature affecting Pileated Woodpecker occurrence at the microhabitat scale. As Pileated Woodpeckers mainly feed on carpenter ants (*Camponotus* spp. and *Formica* spp.) in large snags and other coarse woody debris (Beckwith and Bull 1985; Torgersen and Bull 1995), the use of patches containing high densities of these components was likely to increase food intake and thus reduce searching time among microhabitats. The greater response to snags in microhabitats relative to macrohabitats suggests that this resource is relevant to immediate foraging decisions rather than territory-placement decisions. Our results at the microhabitat scale are also in agreement with habitat-use patterns of Pileated Woodpeckers in Oregon, where the species uses microhabitats with high densities of large-diameter snags (Bull and Meslow 1977; Bull et al. 1992). At this scale, woodpeckers in our study area also use sites containing fewer small-diameter shade-intolerant hardwood and coniferous species, which accords with the fact that small-diameter stems might not provide enough opportunity for foraging (Bull and Meslow 1977; Conner 1980). In other parts of the species' range, such as Oregon and Virginia, it has been noted that other habitat features like dense canopy and ground cover are important for habitat use at the microhabitat scale (Conner 1980; Bull 1987). In view of the fact that we sampled foraging sites that were mostly in forested areas with no recent logging activity, it is likely that we sampled sites with similar percentages of canopy cover.

Our results concerning the importance of coarse woody debris other than snags contrast with those of other studies which suggest that logs and stumps are important habitat components in the foraging behavior of Pileated Woodpeckers (Bull and Meslow 1977; Bull 1987; Bull et al. 1992; Renken and Wiggers 1993). Flemming et al. (1999) point out that woodpecker excavation marks on very decayed stumps and logs could easily remain undetected or be misinterpreted by observers surveying them while walking along transects. Those authors also mention that because no direct foraging observations were made on individuals, the low use of coarse woody debris might have been an artifact of the survey method. In our case, direct observations using telemetry tracking of three individuals during the breeding season suggested that very few logs and stumps were actually used for foraging. It is unclear, however, if this response to these components was due to their low density in our study area or a greater preference for snags and dying trees by woodpeckers.

Management implications

Because of the multiscale responses of Pileated Woodpeckers to vegetation heterogeneity described for southeastern Québec, managing the species' habitat at only one scale is likely to be irrelevant if the scale is chosen arbitrarily by managers and does not capture factors that are important at other scales. Considering the increasing number of management guidelines for Pileated Woodpecker habitat (see Conner et al. 1975; Bull and Holthausen 1993; Naylor et al. 1996), management of this and companion species' habitat must be done on a multiscale basis in order to maintain the multiscale habitat requirements of these species. Prior to multiscale analysis, managers should have a clear idea of the life history of the target species in order to select relevant scales. If little information exists for a given species, making comparisons of habitat use that consider a series of circular plots of different diameters around locations where a given species is active (i.e., nest or foraging sites) and around random sites can be a valuable technique for determining relevant scales (see Baker et al. 1995; Hunter et al. 1995). On the other hand, if a large data base of telemetry locations exists, appropriate scales could be determined by looking at aggregation patterns of locations for a specific area and period within a species' life cycle.

The pattern of habitat use by Pileated Woodpeckers at both spatial scales suggest that habitats displaying vegetation features characteristic of mature forest were the most important factors in determining their habitat use. To improve habitat management for Pileated Woodpeckers, information obtained at the macrohabitat scale can easily be used for managing the species at the stand level (the current scale of management for most wildlife species). For example, to maintain adequate tree-species composition and high snag density, sensitive logging practices such as selective cutting could be implemented in stands considered high quality for Pileated Woodpeckers. Moreover, to provide foraging and nesting habitat for Pileated Woodpeckers within managed stands, management at the microhabitat scale should focus on retaining "wildlife trees" that include a large amount of coarse woody debris. If retention of wildlife trees is not possible during operations, owing to high risk for forest workers, creation of wildlife trees by retaining intentionally killed trees can be a valuable alternative (Bull and Partridge 1986).

References

Addicott, J.F., Abo, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., and Soluk, D.A. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos, **49**: 340–346.

Baker, B.W., Cade, B.S., Mangus, W.L., and McMillen, J.L. 1995. Spatial analysis of Sandhill Crane nesting habitat. J. Wildl. Manage. **59**: 752–758.

Beckwith, R.C., and Bull, E.L. 1985. Scat analysis of the arthropod component of Pileated Woodpecker diet. Murrelet, **66**: 90–92.

Bergin, T.M. 1992. Habitat selection by the western kingbird in western Nebraska: a hierarchical analysis. Condor, **94**: 903–911.

Brawn, J.D., Elder, W.H., and Evans, K.E. 1982. Winter foraging by cavity nesting birds in an oak–hickory forest. Wildl. Soc. Bull. **10**: 271–275.

Bull, E.L. 1987. Ecology of the Pileated Woodpecker in northeastern Oregon. J. Wildl. Manage. **51**: 472–481.

Bull, E.L., and Holthausen, R.S. 1993. Habitat use management of Pileated Woodpecker in northeastern Oregon. J. Wildl. Manage. **57**: 335–345.

Bull, E.L., and Meslow, E.C. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. J. For. **75**: 335–337.

Bull, E.L., and Partridge, A.D. 1986. Methods of killing trees for use by cavity nesters. Wildl. Soc. Bull. **14**: 142–146.

Bull, E.L., Holthausen, R.S., and Henjum, M.G. 1992. Roost trees used by Pileated Woodpeckers in northeastern Oregon. J. Wildl. Manage. **56**: 786–793.

Conner, R.N. 1980. Foraging habitats of woodpecker in south western Virginia. J. Field Ornithol. **51**: 119–127.

Conner, R.N. 1981. Seasonal changes in woodpecker foraging patterns. Auk, **98**: 562–570.

Conner, R.N., and Adkisson, S. 1976. Discriminant function analysis: a possible aid in determining the impact of forest management on woodpecker nesting habitat. For. Sci. **22**: 122–127.

Conner, R.N., Hooper, R.G., Crawford, H.S., and Mosby, H.S. 1975. Woodpecker nesting habitat in cut and uncut woodland in Virginia. J. Wildl. Manage. **39**: 144–50.

Flemming, S.P., Holloway, G.L., Watts, E.J., and Lawrance, P.S. 1999. Characteristics of foraging trees selected by pileated woodpeckers in New Brunswick. J. Wildl. Manage. **63**: 461–469.

Government of Québec. 1990. Carte écoforestière. Ministère de l'énergie et des ressources, Service des inventaires forestiers. Ste-Foy, Québec.

Grausenbaugh, L.R. 1952. Plotless timber estimates. New, Fast, Easy. J. For. **50**: 32–37.

Hall, L.S., and Mannan, R.W. 1999. Multiscaled habitat selection by the elegant trogon in southeastern Arizona. J. Wildl. Manage. **63**: 451–460.

Hunter, J.E., Gutiérrez, R.J., and Franklin, A.B. 1995. Habitat configuration around Spotted Owl sites in northwestern California. Condor, **97**: 684–693.

Jokimäki, J., and Huhta, E. 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. Ornis Fenn. **73**: 97–113.

Keitt, T.H. Urban, D.L., and Milne, B.T.M. 1997. Detecting critical scale in fragmented landscapes. Conserv. Ecol. **1**: 4.

Kotliar, N.B., and Wiens, J.A. 1990. Multiple scales of patchiness patch structure: a hierarchical framework for the study of heterogeneity. Oikos, **59**: 253–260.

Lafleur, P.-É., and Larue, P. 1992. La sélection d'espèces fauniques représentatives des rèserves Mastigouche et des Laurentides :

cadre général d'analyse et proposition d'une liste d'espèces-cibles. Gestion intégrée des ressources, Direction générale de la ressource faunique, Ministère du Loisir, de la chasse et de la pêche, Gouvernement du Québec, document technique 91/7.

Lafleur, P.-É., and Blanchette, P. 1993. Développement d'un indice de qualité de l'habitat pour le Grand Pic (*Dryocopus pileatus*) au Québec. Gestion intégrée des ressources, Direction générale de la ressource faunique, Ministère du Loisir, de la chasse et de la pêche, Gouvernement du Québec, document technique 93/3.

Nagelkerke, N.J.D. 1991. A note on general definition of the coefficient of determination. Biometrika, **78**: 691–692.

Naylor, B.J., Baker, J.A., Hogg, D.M., McNicol, J.G., and Watt, W.R. 1996. Forest management guidelines for the provision of Pileated Woodpecker habitat, version 1.0. Forest Management Branch, Ontario Ministry of Natural Resources, Sault Ste. Marie.

Orians, G.H., and Wittenberger, J.F. 1991. Spatial temporal scales in habitat selection. Am. Nat. **137**: S29–S49.

Pulliam, H.R., and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. **137**: S50–S66.

Renken, R.B., and Wiggers, E.P. 1989. Forest characteristics related to Pileated Woodpecker territory size in Missouri. Condor, **91**: 642–652.

Renken, R.B., and Wiggers, E.P. 1993. Habitat characteristics related to Pileated Woodpecker densities in Missouri, Wilson. Bull. **105**: 77–83.

Savignac, C. 1996. Sélection de l'habitat par le Grand Pic (*Dryocopus pileatus*) à différentes échelles spatiales dans la Mauricie, Québec. M.Sc. thesis, Université Laval, Ste-Foy, Qué.

Sedgwick, J.E., and Knopf, F.L. 1992. Describing willow flycatcher habitats: scale perspectives and gender differences. Condor, **94**: 720–733.

Smith, T.M., and Shugart, H.H. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology, **68**: 695–704.

SPSS. 1997. SPSS/PC+, version 8.0.0. SPSS, Chicago.

Steele, B.B. 1992. Habitat selection by breeding black-throated blue warblers at two spatial scales. Ornis Scand. **23**: 33–42.

Swallow, S.K., and Gutiérrez, R.J. 1986. Primary cavity-site selection by birds. J. Wildl. Manage. **50**: 576–583.

Torgersen, T.R., and Bull, E.L. 1995. Down logs as habitat for forest-dwelling ants: the primary prey of Pileated Woodpecker in Oregon. Northwest. Sci. **69**: 294–303.

Urban, D.L., O'Neill, R.V., and Shugart, H.H., Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial pattern. BioScience, **37**: 120–127.

VanderWerf, E.A. 1993. Scales of habitat selection by foraging Elepaio in undisturbed human-altered forests in Hawaii. Condor, **95**: 980–989.

Wiens, J.A. 1986. Spatial scale temporal variation in studies of shrubsteppe birds. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper and Row, New York. pp. 154–172.

Wiens, J.A., Addicott, J., Case, T., and Diamond, J. 1986. Overview: the importance of spatial and temporal scale in ecological investigation. *In* Community ecology. *Edited by* J. Diamond and T.J. Case. Harper and Row, New York. pp. 145–153.