Pre-fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: the case of the black-backed woodpecker

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Abstract: Burned forests represent high-quality habitats for many deadwood-dependent species. Yet, post-fire conditions may vary greatly within and among burns and thereby may affect habitat suitability for these species. We studied habitat selection of nesting black-backed woodpeckers (*Picoides arcticus* Swainson) in recently burned spruce-dominated boreal forests. Our objectives were to (*i*) identify factors involved in snag selection for both nesting and foraging and (*ii*) examine selection of nest sites within the burned landscape. A total of 92 nests and 1612 foraging observations were used to investigate snag selection. Our results show that both pre-fire forest conditions and fire severity are important in determining the quality of burned forests for black-backed woodpeckers. This species selected large snags for both nesting (>20 cm DBH) and foraging (>15 cm DBH). Woodpeckers selected deciduous and degraded "pre-fire" snags for nesting whereas black spruce snags that had been created by fire and that were moderately burned were preferred for foraging. Nest sites were concentrated in burned mature stands and supported higher densities of large snags (e.g., >15 cm DBH). Our results suggest that burned forest patches of at least 20 ha and composed mainly of burned mature and old-growth forests should be maintained during post-fire harvesting. The decrease in the amount of late seral stands in managed forest landscapes raises concerns about the future availability of high-quality burned forests for this species.

Résumé : Les forêts brûlées constituent des habitats de grande qualité pour plusieurs espèces qui dépendent du bois mort. Cependant, l'état de la forêt après feu peut varier grandement, ce qui peut affecter la qualité de cet habitat. Nous avons étudié la sélection d'habitat par les pics à dos noir nicheurs (*Picoides arcticus* Swainson) dans des pessières noires boréales récemment brûlées. Nos objectifs consistaient à (*i*) identifier les facteurs impliqués dans la sélection d'arbres morts pour la nidification et l'alimentation et (*ii*) examiner la sélection des sites de nidification à l'intérieur du paysage brûlé. Un total de 92 nids et 1 612 observations d'alimentation ont été utilisés pour étudier la sélection des chicots. Nos résultats montrent que l'état de la forêt avant un feu et la sévérité du feu sont deux éléments qui déterminent la qualité d'habitat pour le pic à dos noir. Cette espèce sélectionnait les chicots de gros diamètre pour la nidification (>20 cm au DHP) ainsi que pour l'alimentation (>15 cm au DHP). Les pics sélectionnaient les chicots d'essences feuillues et ceux plus décomposés (arbres morts avant le feu) pour la nidification. À l'inverse, ils préféraient s'alimenter sur des épinettes noires tuées par le feu et modérément brûlées. Les nids étaient surtout localisés dans des peuplements matures brûlés qui supportaient une forte densité de gros chicots (par ex. >15 cm au DHP). Nos résultats suggèrent que des blocs d'au moins 20 ha de forêts résineuses matures et vieilles brûlées devraient être conservés lors de la récolte du bois brûlé. Le rajeunissement de la matrice forestière en forêt boréale aménagée soulève des inquiétudes quant à la disponibilité à long terme de forêts brûlées de haute qualité pour l'espèce.

Introduction

Burned forests typically represent high-quality habitats for many plant and animal species (Saab and Powell 2005; Hutto 2006; Lindenmayer et al. 2008). In the boreal as in many other forest ecosystems worldwide, many species have been identified as fire associated, fire specialized, fire favoured, or fire dependent (e.g., Jonsell et al. 1998; Wikars 2002; Hannon and Drapeau 2005; Saab and Powell 2005). Indeed, fire creates short-term habitat conditions that are often scarce or patchily distributed in unburned or managed forests (Lindenmayer et al. 2008). In particular, fires provide high densities of snags and may thus be an important source of deadwood at the regional scale. In forest landscapes where fire is a major natural disturbance, it may contribute to the persistence of populations of deadwood-dependent species such as many saproxylic insects (Wikars 2002; Saint-Germain et al. 2004*a*, 2004*b*) and cavity-nesting birds (Hutto 1995; Saab and Powell 2005; Nappi and Drapeau 2009).

Post-fire forest conditions are markedly different from

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those present in unburned forest types. However, these conditions can also vary greatly within and among burns. Part of this heterogeneity is caused by variability in fire severity. In the boreal forest, where fires have been historically described as severe stand-replacing disturbances, recent studies have shown that wildfires may leave a large proportion of stands unburned or partially burned (Bergeron et al. 2002; Schmiegelow et al. 2006). In addition, forest conditions present at the time of fire (such as tree species composition, stand age, and stand structure) may vary as well and, consequently, greatly influence post-fire conditions (Hutto 2008; Vierling et al. 2008). The resulting variability in post-fire conditions may affect habitat resources for fire-associated species (Wikars and Schimmel 2001; Purdon et al. 2004; Smucker et al. 2005). For deadwood-dependent species, this variability in post-fire conditions may be particularly important, as it will determine the quantity and the characteristics of snags present in burned forests and thus the suitability of these habitats for feeding and breeding activities (Saint-Germain et al. 2004*b*; Koivula and Schmiegelow 2007).

Forest management may influence both the abundance and the suitability of habitats created by wildfire. In North American boreal forests, for instance, harvesting of post-fire forests ("salvage logging") has become an important management activity in recent years that reduces the availability of post-fire habitats (Nappi et al. 2004; Schmiegelow et al. 2006). Because salvage logging operations may target specific tree characteristics (i.e., specific tree size, species, or fire damage class), remaining burned stands may not be representative of natural post-fire conditions and may not be suitable for deadwood associates (Hutto 2008). In parallel, pre-fire management may also influence age, structure, and composition of forest stands at the landscape scale. This indirectly influences the characteristics of burned forests and thus their suitability for deadwood-associated species. Understanding habitat requirements of the most demanding species should be used to generate appropriate management guidelines that will maintain key habitats and processes in forest ecosystems (the "focal species approach"; Lambeck 1997). In the boreal forest where fire is a major natural disturbance (Bergeron et al. 2002, 2004), species whose populations are limited by fire and (or) species that depend on critical resources such as deadwood in burns are important indicator species that can be used to gauge the efficacy of post-wildfire management.

We conducted habitat selection analyses at two different scales to investigate habitat requirements of black-backed woodpeckers (*Picoides arcticus* Swainson) in burned boreal black spruce (*Picea mariana* (Mill.) BSP) forests. Our first objective was to identify factors involved in the selection of snags for both nesting and foraging. Our second objective was to examine nest site selection within the burned landscape based on pre-fire forest age and snag density. We used the black-backed woodpecker as our focal species because it is a deadwood-dependent (Nappi 2009; Tremblay et al. 2010) and a well-known fire-associated species that responds strongly and positively to the high abundance of snags in recently burned forests throughout its range (Murphy and Lehnhausen 1998; Hoyt and Hannon 2002; Hutto 2008). Recent studies have shown that this species is highly specialized on severely burned forests (Hutto 2008) and that reproductive success is high in recent burns of the boreal forest (Nappi and Drapeau 2009). As with other woodpecker species (e.g., Martikainen et al. 1998; Conner et al. 2001; Virkkala 2006), the black-backed woodpecker may also serve as an umbrella species (given that other fire associates such as many saproxylic insects may benefit from the same post-fire conditions) or a keystone species (given that they provide cavities for other cavity nesters) in post-fire forests.

Methods

Study area

This study was conducted in the parc national des Grands-Jardins (310 km^2), a provincial park located approximately 120 km northeast of Quebec city, Canada (47°44′N, 70°46′W) (Fig. 1). The park is located on the Laurentian Highlands (elevation from 600 to 900 m). Vegetation typically reflects the southern boreal forest zone (Saucier et al. 2003) and includes the southernmost lichen woodlands in eastern Canada (Payette et al. 2000). Mean annual temperature is 0 °C and total annual precipitation averages 1405 mm, with 407 mm falling as snow (Boisclair 1990). Wildfires have profoundly shaped the land, with 13 fires burning about 40% of the park during the 20th century (Payette and Delwaide 2003). In addition, 39% of the area was logged between 1940 and the creation of the park in 1981 (Payette and Delwaide 2003). No logging has occurred since the park was created.

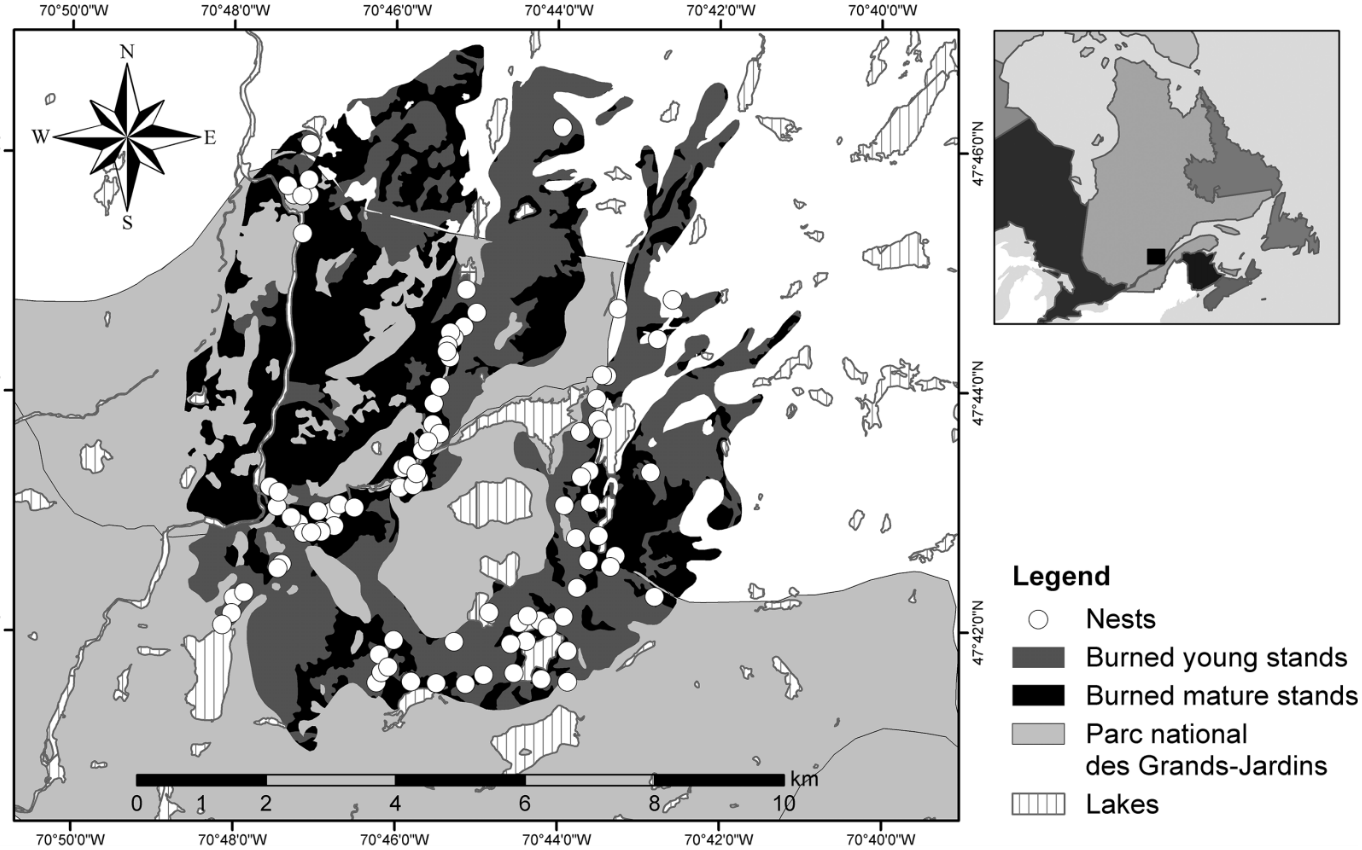
In 1999, between 30 May and 25 June, a fire burned 4500 ha of conifer-dominated forest mostly within the park boundaries (Fig. 1). The burned landscape was dominated by black spruce with scattered balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Burn severity was evaluated by the Quebec Ministry of Natural Resources and Wildlife based on the percentage of the crown cover that had been burned (based on Landsat imagery at a 30 m × 30 m pixel resolution). Based on this evaluation, 96% of the area affected by the fire was composed of high-severity burned stands (stands with >90% of the crown cover burned) whereas 4% consisted of low-severity burned stands (dominance of unburned crown cover).

Because of the history of natural and anthropogenic disturbances, the fire burned a mosaic of stand ages (Fig. 1). Mature stands originated from a fire in 1922 or from stands undisturbed by either fire or harvesting in the last century; therefore, mature stands were >77 years old. Young stands mostly originated from previous logging in the late 1950s and early 1960s, therefore averaging 40 years of age. We used tree height as a surrogate for stand age to classify stands as mature (canopy height >7 m) or young (canopy height <7 m) based on digital pre-fire forest inventory maps. About half of the burned landscape was composed of mature stands (47%) with the rest composed of young stands (53%). No salvage logging occurred within the burned landscape.

Snag selection for nesting

We searched for black-backed woodpecker nests during the first three breeding seasons following fire (2000–2002). Active nests were located by systematic searching in delineated portions of the burn that were accessible (e.g., road access). Overall, 1185 ha of burned forest was surveyed (26% of the

Fig. 1. Location of the parc national des Grands-Jardins (Quebec, Canada), of the 1999 fire, and of black-backed woodpecker nests (*Picoides arcticus*) found during the 3-year study. Forest stands within the burned landscape were classified according to their development stages prior to fire (burned mature or burned young stands).



total burned forest landscape), which covered both burned young and burned mature forests (Fig. 1) (see also Nappi and Drapeau 2009). Within these delineated portions of the burn, nests were searched along transects separated by 200 m and that spanned the entire delineated areas. All transects were walked three times and nest searching effort was standardized among these delineated areas. The same delineated areas were sampled each year with an equivalent sampling effort. Transects were walked during morning hours (05:00 to 12:00) and nests were located by searching for cavities, by listening for nest excavation or begging nestlings, or by following adults to their cavity. Playbacks were also used along these transects to increase our chance of locating individuals and nests. These surveys were distributed from early May to early July to cover the peak of the breeding season in our area. We considered nests to be active when egg-laying was completed and incubation initiated. Some additional nests were found opportunistically outside these surveyed areas and were included in the nest tree selection analysis (see below).

At each nest site, we measured characteristics of the nest tree and unused trees within a 225 m^2 plot centred on the nest. All nests were located in severely burned stands; therefore, all nest and surrounding unused trees were snags. We noted species, diameter at breast height (DBH), and degradation stage for each snag larger than 15 cm. These three variables are known to potentially influence nest tree use (e.g., Raphael and White 1984; Saab and Dudley 1998; Schepps et al. 1999; Martin et al. 2004). We measured only snags larger than 15 cm DBH because this corresponded to the smallest DBH value used by nesting black-backed woodpeckers in this study. Degradation stage was assessed with an index used to differentiate trees that died after the fire ("fire-created snags", Deg1) from those that were dead prior to the fire ("pre-fire snags", Deg2 and Deg3). Decisions were based on several criteria, including visual appearance, quantity of bark and branches, and treetop condition. This latter criterion was used to separate pre-fire snags with an intact top (Deg2) from snags with broken tops (Deg3).

Using the set of nest and unused trees, we conducted logistic regressions to determine the effects of these variables (DBH, degradation, and species) on nest tree selection. We used Akaike's information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002) to assess the relative strength of eight candidate models (models with one variable, models with two variables, a model with the intercept only, and the full model). This approach uses the model log-likelihood (which reflects the overall fit of the model) while penalizing for the addition of parameters. Each model was ranked according to its AIC_c weight so that models with the highest values were the most parsimonious. Because trees are clustered within each plot, our observations were not independent. To adjust for this possible autocorrelation, models were built using generalized estimating equations (GEE) available through the GENMOD procedure in SAS and by invoking the REPEATED statement (Allison 1999). This method takes into account the clustered structure of data and produces standard errors that are adjusted for autocorrelation. In addition, we statistically weighted the number of trees per plot so that each plot contributed to 1 degree of freedom in the model (Nappi et al. 2003). Degradation was treated as a class variable using the Deg3 as the omitted category. For tree species, black spruce was the omitted category; therefore, coefficients of other tree species are comparisons between each of these values and the black spruce value (Allison 1999). All regressions were performed using SAS (SAS Institute Inc. 2004).

Snag selection for foraging

To investigate selection of foraging trees, we monitored a subsample of 10 individuals (six males and four females) from seven nesting pairs during the second breeding season. Nests were selected from northern, central, and southern portions of the burn so that these were representative of the population that we studied. Our data are based on focal surveys of foraging birds that were conducted during the nestling stage, a period where males and females make frequent visits to the nest to feed nestlings. Each "observation bout" started at the nest and the bird was followed until it was lost or until it returned to its cavity. During each observation bout, we recorded locations with a global positioning system (precision 5–10 m) and marked trees on which woodpeckers foraged for at least 10 s or where they were seen extracting prey. Because observations are correlated within each observation bout, we focused on maximizing the number of observation bouts per individual rather than the number of foraging locations. Foraging observations were made during morning hours (05:00–12:00) between 11 June and 6 July 2001.

Our goal was to compare used and available foraging trees within a home range of a nesting bird (i.e., third-order selection; sensu Johnson 1980). We thus used woodpecker foraging locations to delineate foraging areas (hereafter "core foraging areas") and then compared characteristics of used and available trees within these core foraging areas. These were estimated and delineated using the minimum convex polygon method using all foraging locations. Incremental plots (based on one random location per observation bout) were used to assess whether the number of observation bouts was high enough to reach an asymptote in area estimation (Kenward 2001). Asymptotes were generally obtained by 40–50 observation bouts. Although we obtained stable estimates for all birds, our method, as compared with standard radio-tracking, may underestimate the total home range of a bird given that more peripheral locations could be left unrecorded. Hence, we consider these core foraging areas as areas where nesting woodpeckers concentrate most of their foraging effort during the nestling stage.

"Available" trees were sampled in four 225 m^2 plots randomly selected (i.e., random bearing, 50 m from nest) within each core foraging area (samples were then merged for each core foraging area). Foraging and available trees were characterized by DBH, tree species, fire severity, and degradation stage. However, tree species and degradation stage variables were not retained for the analysis: black spruce fire-created snags represented 93.7% of the total available trees and were selected in the same proportion (93.3%) as their availability. Our analysis therefore compares use and availability based on the combination of DBH and fire severity classes. Fire severity, at the tree level, was based on percentage of the trunk surface burned: moderate = trunk partially charred and severe = trunk completely charred. Comparisons of use and availability data were made using the compositional analysis method (Aebischer et al. 1993). In essence, this approach ranks habitat components based on log-ratio differences between use and available proportions, thereby overcoming the potential problems of nonindependence of proportional data. This approach also uses the animal instead of each observation as the sample unit to avoid problems of pseudoreplication. No habitat category had a 0% utilization value (Bingham and Brennan 2004). The analysis was performed with Compos Analysis version 5.1 (Smith 2003).

Nest site selection

We assessed nest site selection within the burned landscape based on stand age prior to fire (burned mature versus burned young stands) and on snag density. First, we investigated whether woodpecker nest sites (i.e., area that includes the nest and foraging areas) were located in areas with higher proportions of burned mature forests as compared with their availability in the landscape. For this purpose, proportions of burned mature forests surrounding nests were compared with proportions calculated from random locations (Potvin et al. 2000). Because some portions of the landscape were composed of burned mature forests only, we restricted our analysis to a 700 ha portion of the landscape that consisted of a mosaic of burned young and mature stands. For all nests (n = 41) and an equivalent number of random locations, we measured the proportion of burned mature forest within a 250 m radius from the nest using digital pre-fire forest inventory maps. This radius was chosen because the area covered (19.6 ha) was similar to mean core foraging areas of nesting pairs in this study. Proportions of burned mature forest were compared between nest and random locations using a nonparametric Mann–Whitney U test. To investigate the relationship between forest age and snag density, we compared snag densities between burned mature and burned young stands using 225 m^2 random plots (n = 49) at least 300 m apart sampled during a simultaneous study on bird communities (P. Drapeau, unpublished data). Comparisons were conducted for DBH >10, >15, and, >20 cm using nonparametric Mann–Whitney U tests.

Second, we investigated differences in snag density among nest tree sites, foraging sites, and random sites using 225 m^2 plots. Nest tree plots (n = 92) were centred on the nest and corresponded to the same plots used for nest tree selection analysis. Foraging plots (n = 66) consisted of plots sampled in proximity to nests (50 m from the nest, random azimuths) and were therefore considered as part of each bird's potential core foraging area. Random plots (n = 49) corresponded to the ones described above. Comparisons were conducted separately for DBH >10, >15, and >20 cm using nonparametric Kruskal–Wallis tests.

Results

Nest trees

Ninety-two nest trees were located during the 3-year study and used to assess nest tree selection. Although some nests were reused in a subsequent year, we considered these reused nests as single nest trees. Tree DBH, species, and degradation were predictors of nest tree selection: the best model included the main effects of these three variables (Fig. 2). Akaike weight (which indicates the probability that the model is the best among the whole set of candidate models) was 0.47, indicating that this model had a 47% chance of being the best one among the set of candidate logistic regression models considered.

Despite considering only trees >15 cm DBH, diameter was still an important criterion in nest tree selection (Fig. 2*a*). Mean DBH was 22 cm, with roughly 70% of nest trees being >20 cm DBH (although these only represented 30% of the available trees within nest plots). Black-backed woodpeckers tended to select trembling aspen and paper birch over black spruce (which represented most coniferous trees) for nest excavation (Fig. 2*b*). About half of the nests were excavated in deciduous trees (36% for trembling aspen and 15% for paper birch), a proportion much higher than the relative availability of these tree species (12% for trembling aspen and 4% for paper birch). Conversely, black-backed woodpeckers used black spruce in lower proportion than its availability (37% of nest trees versus 72% of available trees). Nests were occasionally excavated in other coniferous trees (8% balsam fir, 3% jack pine, and 1% tamarack) in about the same proportions as their relative availabilities in nest plots (8% balsam fir, 2% jack pine, and 2% tamarack). Although most nests were in fire-created snags (Deg1), black-backed woodpeckers selected pre-fire snags (Deg2 and Deg3) in higher proportion than their availability (Fig. 2*c*).

Foraging trees

Black-backed woodpecker foraging was recorded on 1723 trees during 570 observation bouts and 46 days of monitoring. This represents an average of 172 foraging trees, 57 observation bouts, and 5 days of monitoring per bird (Table 1). Foraging occurred within core foraging areas that surrounded nests and that covered 6.9–16.7 ha (Table 1). Selection of foraging trees by these 10 individuals was assessed for fire-created black spruce snags based on the combination of two variables (DBH and fire severity) and using a total of 1612 foraging trees and 1265 available trees. Although only 10 birds were monitored, black-backed woodpeckers showed consistent patterns in their selection of foraging trees based on DBH and fire severity (Wilks' $\lambda = 0.047$, $P < 0.01$, df = 5) (Fig. 3). Larger trees were selected over smaller ones for foraging. Woodpeckers showed a strong preference for snags >15 cm DBH: these were used in much higher proportion than their availability. Fire severity was also important in the selection of foraging trees: within each DBH class, moderately charred trees were preferred over severely charred ones.

Nest sites

Woodpeckers' nest sites were concentrated in burned mature forests within the burned landscape. Indeed, nest sites (i.e., large area that includes the nest and foraging sites) contained higher proportions of burned mature forest than random sites, although this result was only marginally significant ($Z = -1.809$, $P = 0.071$). Mature stands typically supported higher densities of large snags than burned young stands. This pattern was significant for snags >10 cm DBH ($Z = -2.092$, $P = 0.036$) and marginally significant for snags >15 cm DBH ($Z = -1.887$, $P = 0.059$). Snags >20 cm DBH were scarce and no significant difference was observed between stand types ($Z = -1.107$, $P = 0.268$).

Snag densities were highest in nest tree plots, lowest in random plots, and intermediate in foraging plots, a result consistent across all DBH levels (all Kruskal–Wallis tests: $P < 0.05$) (Fig. 4). For instance, density of snags >15 cm

Fig. 2. Relative proportion of available trees and nest trees for each of the three variables involved in nest tree selection: (*a*) diameter at breast height (DBH), (*b*) tree species, and (*c*) degradation. DBH is presented in three classes for illustration. Tree species includes only the three most frequently used species: PM, *Picea mariana*; PT, *Populus tremuloides*; BP, *Betula papyrifera*. Degradation classes: Deg1, fire-created snag; Deg2, pre-fire snag with intact top; Deg3, pre-fire snag with broken top.

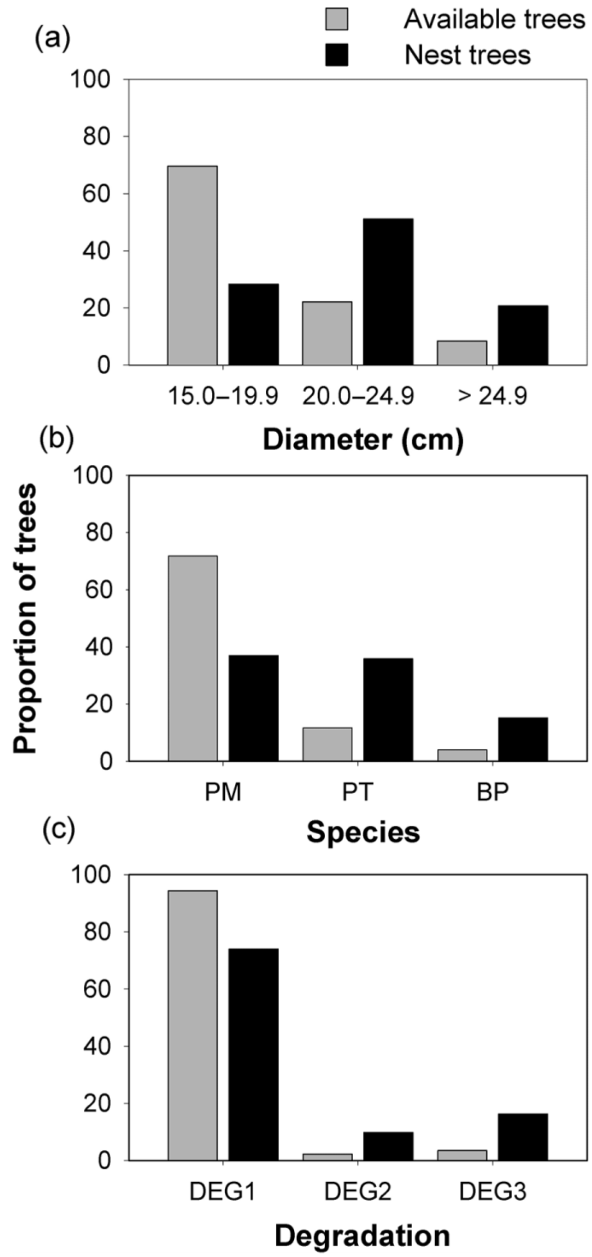


Table 1. Sample sizes of foraging observations (number of sampling days, observation bouts, and foraging trees) and core foraging area estimates for 10 nesting black-backed woodpeckers (*Picoides arcticus*) 2 years after fire.

Nest	Sex	Days	Bouts	Trees	Area (ha)*
1	F	4	54	180	8.0
2	M	5	56	162	14.9
3	M	4	50	221	6.9
4	M	4	83	105	10.6
5	F	4	45	127	10.2
5	M	4	60	283	13.1
6	F	5	61	236	16.7
6	M	4	30	71	10.3
7	F	6	64	186	11.6
7	M	6	67	152	13.8
Mean per individual		5	57	172	11.6

*Estimations are based on minimum convex polygons, including 100% locations.

Fig. 3. Relative proportion of available trees and foraging trees for different diameter at breast height (DBH) (cm) and fire severity classes (M, moderate; S, severe). Bars represent mean relative proportions (+1 SE) of each class (based on the 10 individuals). Ranking values indicate preferences of foraging black-backed woodpeckers (*Picoides arcticus*) for the different DBH and fire severity classes based on compositional analysis results; a highest rank indicates highest preference.

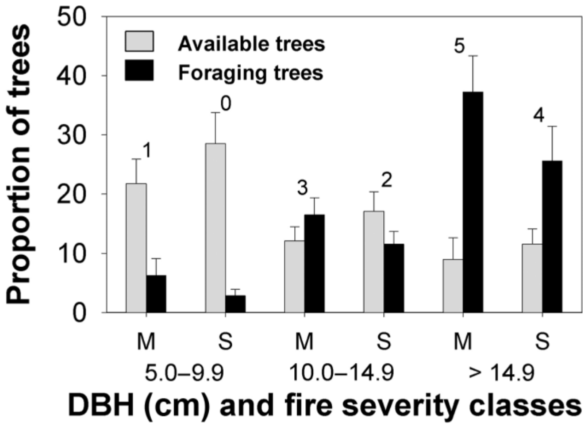
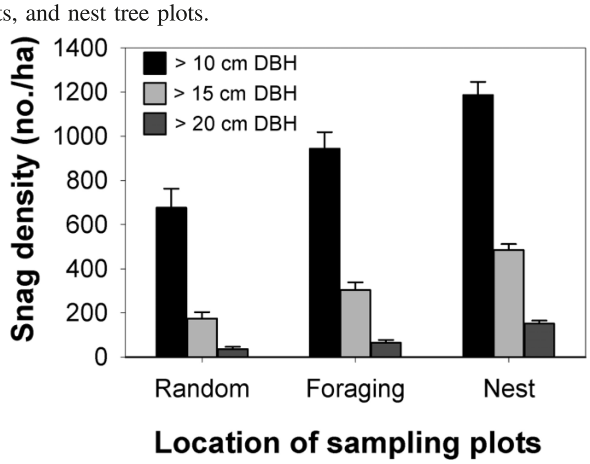


Fig. 4. Mean density of snags (+1 SE) in random plots, foraging plots, and nest tree plots.



DBH was about three times higher in nest tree than in random plots.

Discussion

Although recently burned forests typically represent high-quality habitats for many plant and animal species, the suitability of such habitats may vary greatly (e.g., Purdon et al. 2004; Saint-Germain et al. 2004*b*; Smucker et al. 2005; Vierling et al. 2008). Our results for the black-backed woodpecker show that post-fire habitat quality is influenced by the combined effect of pre-fire forest conditions, i.e., tree species, diameter, and degradation stage, and fire severity (at the tree scale). Yet, our study also indicates that conditions preferred by this species may differ markedly between nesting and foraging, therefore emphasizing the importance of considering both nesting and foraging requirements in habitat selection.

Importance of pre-fire tree characteristics

Forest conditions present at the time of fire directly influence characteristics of trees available thereafter for dead-wood-dependent species. Our results show that diameter, species, and degradation stage of trees are characteristics that are of crucial importance in determining the quality of nesting and foraging substrates for the black-backed woodpecker. Tree diameter is particularly important for nest tree selection, as it directly influences potential cavity size and thickness of the insulating and protective wood wall (Schepps et al. 1999). In post-fire forests, as in other forest types, use or selection of large trees for nest excavation by primary cavity-nesting birds is well documented (e.g., Raphael and White 1984; Saab and Dudley 1998; Martin et al. 2004). Although previous observations reported the use of relatively small-diameter trees by nesting black-backed woodpeckers as compared with other species (Saab and Dudley 1998; Vierling et al. 2008; Saab et al. 2009), our results underscore the importance of tree size for the black-backed woodpecker, especially in the boreal forest where trees are of relatively small diameter. Minimum and mean diameters of selected trees in our study represented the smallest values recorded for this species throughout its range (e.g., Goggans et al. 1989; Saab and Dudley 1998; Weinhagen 1998). Given that the internal diameter of black-backed woodpecker nest cavities averages 11 cm (Raphael and White 1984; Martin et al. 2004), many of the nest trees in this study are close to the minimum diameter threshold required for nest excavation. This suggests that large trees may have been limited in our burned landscape.

As for nesting, tree diameter was an important factor in foraging tree selection. Larger trees, which typically contain higher densities of wood-boring insect larvae, were higher quality foraging substrates (Nappi et al. 2003; Saint-Germain et al. 2004*b*, 2004*c*). The cerambycid *Monochamus scutellatus* (Say) was among the most abundant saproxylic species in these burned spruce trees (Saint-Germain et al. 2004*b*) and represented the main prey of the black-backed woodpecker (Nappi and Drapeau 2009). Preference for large snags by such deep wood-boring insects can be attributed to the requirements of late-instar larvae, which excavate deep galleries into sapwood and heartwood (Gardiner 1957; Cerezke 1977). Tree diameter is also correlated with bark and phloem thickness, two attributes that enhance microhabitat conditions for these insects: thicker bark increases protection of subcortical tissues from excessive desiccation and phloem is of higher nutritional quality for larvae that feed extensively on cambium and phloem tissues during first-instar stages (Gardiner 1957; Rose 1957; Saint-Germain et al. 2004*b*).

Black-backed woodpeckers showed clear preferences for some tree species and degradation stages. Our results show that deciduous trees were clearly preferred over coniferous trees by black-backed woodpeckers for nesting. This finding emphasizes the importance of deciduous trees, in particular aspen, as key nesting substrates for cavity nesters (e.g., Li and Martin 1991; Martin et al. 2004). In our study, aspen may have been preferred in part because of its relatively high diameter compared with conifers. High aspen use may also be related to its susceptibility to heartwood decay, which provides a soft substrate for excavation while providing a sound sapwood shell (Basham 1991; Losin et al. 2006).

Based on broad classes of tree degradation, our results show that woodpeckers tend to select trees for nesting that were already dead or in an advanced stage of decay at the time of fire. Interaction effects between tree species and degradation classes were not assessed in our models because of small sample sizes, but woodpecker preference for pre-fire snags was principally for white birch and black spruce. When alive, white birch is much less affected by heartwood rot than trembling aspen, although birches decay rapidly after death (Basham 1991). Among eastern boreal conifers, black spruce is less affected by trunk decay, irrespective of tree age, and is mainly affected by root rot and butt decay (Basham 1991). Trees not previously invaded by heart-rot fungi provide little immediate opportunity for woodpecker excavation at the time of tree death. For these two tree species, pre-fire snags already affected by trunk decay (such as broken top snags) provide easily excavated nesting substrates in the first years after fire, a period when most snags are still relatively intact. Selection of softer trees by cavity excavators is known to vary among species (Schepps et al. 1999). Selection of softer substrates by black-backed woodpeckers is of particular interest given that this species has one of the strongest excavator morphologies among American woodpeckers (Spring 1965; Kirby 1980) and has been shown to nest in relatively hard snags as compared with other species (Saab and Dudley 1998). Our results therefore emphasize the importance of pre-fire snags (especially with broken tops) as nest trees even for strong excavators such as the black-backed woodpecker.

Preferences for tree species and degradation stage for foraging contrasted sharply with preferences for nesting. Foraging of black-backed woodpeckers occurred almost exclusively on fire-killed spruce snags that dominated the burned landscape. Burned conifers represent high-quality substrates for wood-feeding beetles (Cerambycidae, Buprestidae, and the subfamily Scolytinae (family Curculionidae)) in the first years after fire (Saint-Germain et al. 2004*b*; Boulanger and Sirois 2007). Therefore, these recent conifer snags represented an abundant foraging resource for black-backed woodpeckers (Nappi et al. 2003). Trees that were already dead or weakened before fire (pre-fire snags) were rarely used by woodpeckers as foraging substrates. These more degraded snags had probably little or no recent phloem, a critical nutritional condition for wood-boring insects (Saint-Germain et al. 2004*b*).

Importance of pre-fire forest age

Because of its direct effect on tree diameter, forest age at the time of fire is a critical determinant of habitat quality for the black-backed woodpecker. This is especially important in northern coniferous boreal forests where trees can take a long time to reach adequate sizes for woodpeckers. In our study, differences in pre-fire forest age within the burned landscape caused important variability in habitat suitability. Not surprisingly, burned mature forests (>77 years old when burned) supported higher densities of large snags (i.e., DBH >15 cm) than burned young forests (~40 years old when burned). Because of the high number of trees required for foraging, the black-backed woodpecker is typically found in burned stands with high snag densities (Saab and Dudley 1998; Hutto 2008). Our results clearly show that black-backed woodpeckers established their nest sites (nest tree sites and foraging sites) (Fig. 4) in portions of the burned landscape with higher densities of large snags; large snag density was particularly high surrounding nest trees (~500 snags >15 cm DBH/ha). Because most mature stands originated from the 1922 fire, these also supported the scattered presence of large aspens as well as old trees that escaped the 1922 fire and have persisted to create the decayed pre-fire snags present following the 1999 fire. Results from a companion study showed that nest density and reproductive success were higher in areas with high proportions of burned mature forests than in areas dominated by burned young forests (Nappi and Drapeau 2009).

Importance of fire severity

Deadwood-dependent species may be affected by fire severity at two different scales (Saint-Germain et al. 2004*b*; Schmiegelow et al. 2006; Koivula and Schmiegelow 2007; Nappi et al. 2010). First, variability in fire severity may occur at the stand scale as reflected by the variable percentage of trees killed or damaged by fire, which influence the availability of snags for deadwood users. Second, fire severity may vary at the tree scale (e.g., percentage of bark charred) and thereby influence the microhabitat conditions suitable for foraging or breeding activities. Because the black-backed woodpecker relies on recently dead trees for foraging, it typically responds positively to burn severity at the stand scale (percentage of snags: Koivula and Schmiegelow 2007; Hutto 2008). In our study, most burned stands showed high levels of tree mortality (often close to 100%) and the transition at burned–unburned forest edges was generally sharp. Yet, our results clearly show that variation in fire severity was present at the tree level within these severely burned stands and that this variability likely influenced habitat suitability for woodpeckers.

At the tree level, fire severity was an important factor in foraging tree selection, as woodpeckers tended to select moderately charred trees over more severely charred ones. Although our results are based on 10 individuals only and are limited to the second post-fire breeding season, the pattern that we observed is consistent with the results obtained by Nappi et al. (2003) 1 year after fire in similar burned spruce forests. This preference for moderately charred trees was likely linked to the abundance of wood-boring beetles. Higher fire severity has been shown to negatively affect wood-borer densities in our study sites (Saint-Germain et al. 2004*b*, 2004*c*). It has been hypothesized that this effect of fire severity is more pronounced for spruce than for pine species because the former are less protected from desiccation by their thinner bark (Saint-Germain et al. 2004*b*). We observed that moderately burned trees preferred by foraging woodpeckers were often concentrated at burned–unburned forest edges: this further supports the idea that burned forest edges may represent high-quality sites for many saproxylic insects and woodpeckers (Murphy and Lehnhausen 1998; Werner 2002; Saint-Germain et al. 2004*c*; Nappi and Drapeau 2009).

Management implications

Pre-fire forest conditions and fire severity are factors that should be considered when planning the conservation of burned forests for the maintenance of biodiversity and key ecological functions among species (i.e., nest webs and food webs). These two factors are important in determining the suitability of fire-killed trees for the black-backed woodpecker, both for nesting and for foraging. Although only a few scattered potential nest trees per hectare are necessary for nesting purposes, foraging activities require a much higher concentration of suitable trees, to the order of several hundred per hectare as suggested by our study. Based on our size estimates of core foraging areas, burned forest patches of at least 20 ha composed mainly of mature and old-growth stands should be maintained in burned spruce boreal forests when salvage logged. These forests are likely to support the large snags required for foraging (>15 cm DBH) and for nesting (>20 cm DBH), and they are also more likely to contain the more decayed pre-fire snags preferred as nest trees. Although black-backed woodpeckers use severely burned stands (high percentage of dead trees), their preference for moderately charred trees suggests that burned–unburned forest edges as well as less severely burned stands should also be maintained when planning post-fire salvage logging.

While much of the recent conservation literature has been devoted to the impacts of salvage logging in burns (e.g., Lindenmayer et al. 2008), our study illustrates that conditions created by forest management prior to fire are at least equally important for the determination of post-fire conditions adequate for black-backed woodpeckers. Current forest management may lead to an important decrease in the abundance and extent of mature and old-growth forests in many North American eastern boreal forest landscapes (Bergeron 2004; Cyr et al. 2009). Because fire suppression in this biome has had only limited effects until now (Hannon and Drapeau 2005), fire will burn increasingly younger forests. This indirect effect of forest management, in addition to salvage logging and fire suppression, will likely reduce the extent and quality of post-fire habitat for the black-backed woodpecker and many other deadwood-dependent species. Maintaining mature and old-growth forest attributes through the use of partial cutting, longer forest rotation, and a well-dispersed network of old-growth forest conservation areas can help offset the reduction in pre-fire structural attributes important for these species.

Using the black-backed woodpecker's nesting and foraging habitat requirements in the planning of permanent retention areas in burns wherein some salvage logging occurs could highly contribute to the maintenance of key food webs and nest webs in post-fire seral stages of the boreal forest. Indeed, other deadwood-dependent species such as many saproxylic insects have similar habitat requirements. In our study, more than 15 species of Coleoptera emerged from burned spruce trees and these were affected similarly by tree diameter and fire severity variables (Saint-Germain et al. 2004*b*, 2004*c*). In addition, the black-backed woodpecker, which is often the most abundant woodpecker species in the first years following fire in the boreal forest (Koivula and Schmiegelow 2007; Nappi and Drapeau 2009), may provide numerous cavities for secondary cavity nesters (Saab et al. 2004). Because of its specific habitat requirements, its high specialization on recently burned forests, and its role in food webs and nest webs, this species should be considered a "focal" species (sensu Lambeck 1997) for post-fire management in North American boreal forests.

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