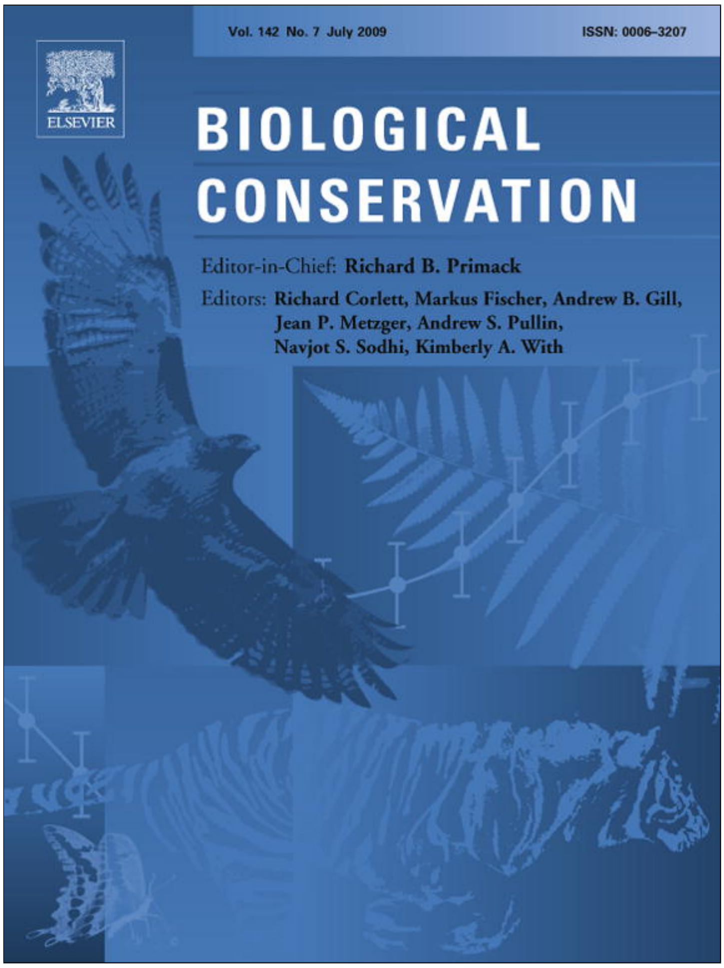
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Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: Are burns source habitats?

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ABSTRACT

The black-backed woodpecker (*Picoides arcticus*) is considered a fire specialist throughout its breeding range. Given its high abundance in recent burns, it has been hypothesized that post-fire forests are source habitats for this species. We conducted a 3-year post-fire study to evaluate the temporal occupancy and reproductive success of black-backed woodpeckers in high-severity burned black spruce forests of central Quebec, Canada. We examined how reproductive success varied temporally and spatially within a burned landscape and investigated the potential source or sink status of this woodpecker population over time. Woodpecker nest density was high in the year after fire but declined significantly over the 3-year period. Based on 106 nests, nest success declined from 84% the first year after fire to 73% and 25%, respectively, for the second and third years after fire. Nest density and reproductive success were higher in areas with high proportions of burned mature forests than in areas dominated by burned young forests. Reproductive success was also higher in proximity to unburned forests. Comparison of annual productivity with a range of survival estimates indicated that these burned forests likely functioned as source habitats for the first 2 years following fire, although this status varied as a function of pre-fire forest age. Our results suggest that post-fire forests may contribute significantly to population levels in fire-prone ecosystems. Forest management practices that reduce the amount of mature and over-mature forests can affect the quality of post-fire habitats important to the black-backed woodpecker and other fire-associated species.

1. Introduction

Wildfire is a major natural disturbance of many North American forest ecosystems, and is increasingly recognized as an important determinant of forest biodiversity (Saab and Powell, 2005; Noss and Lindenmayer, 2006). Beyond its role in forest dynamics (Bergeron, 2000; Brown and Smith, 2000; Kuuluvainen, 2002), fire also creates short-term habitat conditions that are suitable and sometimes critical to many plant and animal species. In the boreal forest for instance, many plants, invertebrates and vertebrates are found either exclusively or at higher abundances in post-fire habitats than in other natural or managed forest types (Nguyen-Xuan et al., 2000; Saint-Germain et al., 2004a; Hannon and Drapeau, 2005; Buddle et al., 2006; Schieck and Song, 2006). Burned forests are particularly important as they provide abundant high-quality snags for many deadwood-dependent species such as saproxylic insects (Jonsell et al., 1998; Wikars, 2002; Saint-Germain et al., 2004b,c) and cavity-nesting vertebrates (Drapeau et al., 2002; Hannon and Drapeau, 2005; Saab and Powell, 2005).

Because fire-associated species (i.e. species found in higher abundance in post-fire habitats) evolved in a context where wildfires have long been the primary process driving forest dynamics, it is hypothesized that fires play an important role in the abundance and the long-term maintenance of regional populations (Berg et al., 1994; Hutto, 1995; Murphy and Lehnhausen, 1998). This hypothesis has important implications for conservation because alteration of fire regimes and post-fire logging may pose a serious threat to the persistence of post-fire forest habitats and their associated biodiversity (Lindenmayer et al., 2004; Noss and Lindenmayer, 2006). Although many studies have provided valuable information on the response (e.g. presence and abundance) of forest species to fire, much less information is available on the demography (e.g. birth and mortality) of fire-associated species in post-fire habitats (Saab and Powell, 2005). Because abundance is not necessarily an adequate indicator of habitat quality (Van Horne, 1983; Vickery et al., 1992; Saab et al., 2007; but see Bock and Jones, 2004), it is essential to measure critical demographic parameters such as reproductive success to assess the ecological role of burned forests in the population dynamics of fire-associated species, and ultimately to the persistence of their regional populations. Moreover,

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recent studies have shown that species responses to fire are sensitive to heterogeneity (i.e. fire severity, pre-fire forest composition and structure) and temporal changes in post-fire conditions (Smucker et al., 2005; Kotliar et al., 2007; Saab et al., 2007; Vierling et al., 2008). Understanding how these factors influence reproductive success may help determine when and which portions of a burn are most suitable for fire associates and, thus, should be maintained during post-fire forest logging (Lindenmayer et al., 2008).

The black-backed woodpecker (*Picoides arcticus*) has a breeding distribution that coincides closely with the range of boreal and mountainous conifer forests in North-America and is considered a fire-specialist throughout its breeding range (Dixon and Saab, 2000; Hannon and Drapeau, 2005; Saab and Powell, 2005). This species responds positively to beetle concentrations (in particular Cerambycidae beetles) following large-scale disturbances, especially in high-severity burned forests where woodpecker densities are typically higher than in other forest types (Hutto, 1995, 2008; Murphy and Lehnhausen, 1998; Nappi, 2000; Hoyt and Hannon, 2002; Koivula and Schmiegelow, 2007). Higher abundance of black-backed woodpeckers in burns led Hutto (1995) to suggest that populations of this species are maintained by a patchwork of recently burned forests across the landscape. In other words, burned forests would act as source habitats from which birds emigrate once post-fire conditions become unsuitable, thereby helping maintain sink populations in unburned forests (Hutto, 1995; Murphy and Lehnhausen, 1998). Although large numbers of black-backed woodpeckers in recently burned forests suggests these forests are high-quality habitats, little information exists on the species reproductive success (e.g. often based on small numbers of nests) and on the factors that influence this reproductive success in burns (but see Saab et al., 2007; Vierling et al., 2008).

In 1999, a fire burned ~4500 ha of coniferous forest in the Parc national des Grands-Jardins in central Quebec, Canada. Because logging was not allowed within the park and because accessible burned forests are promptly salvage logged in Quebec (Nappi et al., 2004), this fire provided a unique opportunity to study black-backed woodpecker population dynamics in unsalvaged post-fire forests. In this paper, we examine the occupancy and reproductive success of a black-backed woodpecker population over 3 years following a stand-replacing wildfire in black spruce forests of eastern Canada. Specifically, we sought to answer the following: (1) how long are these burned forests used for nesting, (2) what is the reproductive success of this species in this habitat and how does it change in relation to time since fire and to within-burn variability in forest conditions, and (3) are these burned forests likely to be source or sink habitats for this species and how does this status change over time and with post-fire forest conditions?

2. Methods

2.1. Study area

This study took place in the Parc national des Grands-Jardins (310 km^2), a provincial park located in the Charlevoix Highlands approximately 120 km north-east of Quebec City in Quebec, Canada (47°44′ N; 70°46′ W; Fig. 1). Elevation at our study sites ranges from 600 m to 900 m. Mean annual temperature is 0 °C and total annual precipitation averages 1405 mm, with 407 mm falling as snow (Boisclair, 1990). While vegetation is typical of the spruce-moss bioclimatic domain, the park also contains the southernmost lichen woodland stands in eastern Canada (Payette et al., 2000a). Black spruce (*Picea mariana*) is the dominant tree species, with lesser abundances of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Fire has been the main natural disturbance with 13 fires burning about 40% of the total park area 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).

Between 30 May and 25 June 1999, a fire burned 4546 ha of conifer-dominated forest mostly within the park limits (Société de protection des forêts contre le feu, 2000; Fig. 1). This fire was generally severe with most of the stands being totally burned. 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 a 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). We obtained a similar burn severity estimate with field measures taken at random burned sites (3.14-ha plots, $n = 32$); mean percentage of burned crown cover at these sites was 98.3 ± 4.0%.

Although forests were relatively homogeneous in their pre-fire composition (black spruce dominance), the history of natural and anthropogenic disturbances had created a mosaic of stand ages. Stand age largely determines tree diameter, one of the most important factors for foraging and nest snag selection by black-backed woodpeckers (Nappi et al., 2003). As we expected this to influence the quality of post-fire habitat for black-backed woodpeckers, we used tree height as a surrogate for tree diameter to classify stands as mature (canopy height >7 m) or young (canopy height <7 m) based on pre-fire digital forest inventory maps. Given the overall high severity of the burn, no difference in burn severity was observed between burned mature and young stands. Based on field measures of burn severity, mean percentage of burned crown cover at burned mature stands was 99.0 ± 1.7% whereas it was 97.8 ± 4.7% at burned young stands (Mann–Whitney test, $Z = -0.128$, $P = 0.899$).

The north-western portion of the burned landscape originated from a 1922 fire (Payette et al., 2000b) and was dominated by mature stands (approximately 80-year old stands); this area is hereafter referred to as the "burned mature landscape" (Fig. 1). The remaining burned matrix was dominated by young stands that originated from previous logging that occurred in the late 1950s and early 1960s, therefore averaging 40 years of age (Payette et al., 2000b), and was interspersed with mature stands left undisturbed at the time of previous logging; this area is hereafter referred to as the "burned young landscape".

2.2. Nest search and nest density estimation

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 total burned forest landscape): 305 ha in the burned mature landscape and 880 ha in the burned young landscape. Nest searching methods were similar to the ones described in Dudley and Saab (2003). Within these delineated portions of the burn, nests were searched along transects separated by 200 m and which spanned the entire delineated areas. All transects were walked three times and nest searching effort was standardized among these delineated areas. Transects were walked during morning hours (05h00–12h00) and nests were located by searching for cavities, by listening for nest excavation or begging nestlings or by following adults to their cavity. To increase our chance of locating nests and to confirm the presence or absence of potential nesting pairs in a given area, birds were attracted

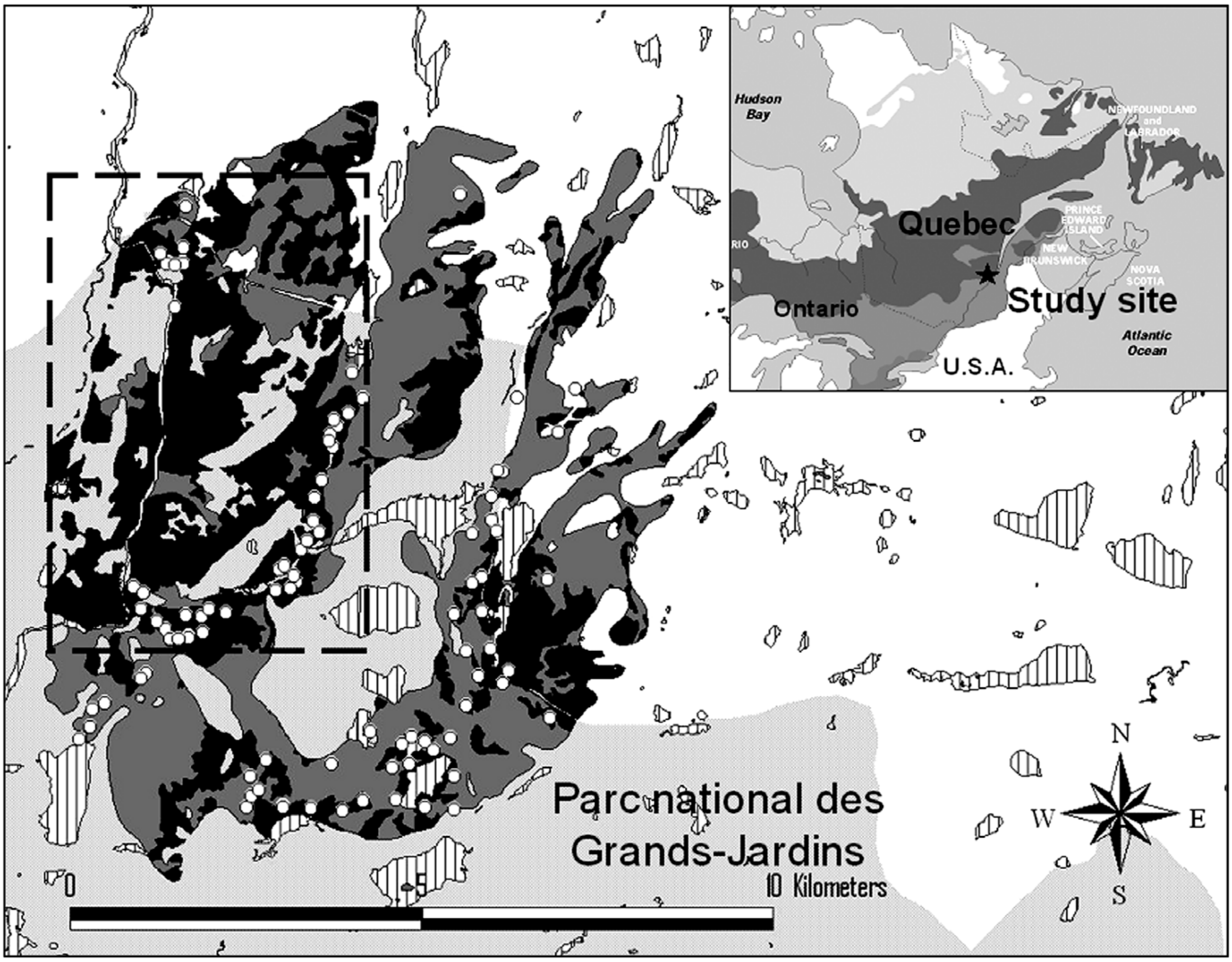

Fig. 1. Location of the Parc national des Grands-Jardins (Quebec, Canada) and the 1999 fire. Forest stands within the burned landscape were classified according to their development stages prior to fire: black = burned mature stands, dark grey = burned young stands (park is in light grey; water bodies are hatched). The north-western portion of the burn (rectangle) was dominated by burned mature stands: this area is referred to as the "burned mature landscape". Other portions of the burn were dominated by young burned stands and referred to as the "burned young landscape". Nests monitored over the 3-year study are indicated by white dots.

using 5-min playbacks at sampling stations 200 m apart along these transects. These surveys were distributed from early May to early July in order to cover the peak of the breeding season in our area (median day for start of incubation = 30 May, $n = 111$ nests) and to increase our chance of detecting nests when birds are more likely to respond to playback (outside the incubation stage). Additional visits in potentially occupied areas (e.g. where a pair was observed) were made until nests were located. We considered nests to be active when egg-laying was completed and incubation initiated. The same delineated areas were sampled each year with an equivalent sampling effort. Nest density was estimated each year based on the number of active nests within the surveyed areas. These estimates were made separately for the burned mature and young landscapes. Some additional nests were found opportunistically outside these surveyed areas and were included in reproductive success analyses (see below).

2.3. Reproductive success

We monitored each nest every 3–6 days until fledging or nest failure. Nest cavities excavated by black-backed woodpeckers were particularly low (Table 1). All cavities but two were easily accessible. We were therefore able to make direct observations of nest content (number of eggs or nestlings) using a small mirror and a flashlight (Fayt, 2003). A nest was considered to fail if evidence of predation or abandonment was observed during the nesting period or if it was no longer occupied by at least one young before the potential fledge interval (<80% of the average nesting cycle; Saab and Vierling, 2001). Predation included cases with signs of predation (e.g. nest destroyed), loss of eggs, and loss of nestlings or usurpation by another species prior to potential fledge interval. Abandonment included cases where eggs or nestlings were left unattended for more than two visits. We estimated length of the nesting period based on our own data set using nests with known nesting chronologies (incubation period = 11 days ($n = 38$), nestling period = 24 days ($n = 11$), total nesting period = 35 days ($n = 29$)). We assumed egg-laying to be asynchronous and incubation to start with the last egg, based on our own observations and on information reported for the closely-related species *Picoides tridactylus* (Leonard, 2001). Using a 35-day nesting period, the start of the potential fledge interval corresponded at 28 days after the onset of incubation.

Nest success was calculated using Johnson's (1979) method which takes into account unequal periods of nest observation (Mayfield, 1961, 1975) and produces standard errors of estimates. For each year, we computed daily nest mortality rate as the total number of nest failures divided by the total number of observation days (for all nests pooled within a year) and then derived the daily

Table 1
Summary of explanatory variables used in regression models to predict daily nest mortality or nest productivity of black-backed woodpeckers (based on all 111 nests monitored).

Variables	Mean (SD)	Min	Max
Temporal			
Years since fire	Class: second year is compared with year one; third year is compared with year one		
Nest tree level			
Nest height (m)	2.23 (1.10)	0.55	5.39
Tree diameter at nest height (cm)	20.9 (3.9)	13.5	33.5
Diameter of cavity entrance (cm)	4.8 (0.4)	4.2	6.8
Cavity depth (cm)	30 (4)	20	41
Cavity orientation	Dummy: four orientations (N, E, S, W)		
Nest site level			
Snag density (no./ha)			
>10 cm dbh	1182 (587)	89	2844
>15 cm dbh	485 (255)	44	1200
>20 cm dbh	151 (132)	1	622
Burned mature forest (%)			
Radius 100 m	51.0 (38.0)	0	100
Radius 250 m	45.0 (29.5)	0	96.6
Radius 500 m	38.5 (21.3)	0	79.5
Landscape context	Dummy: "burned mature" (1) vs "burned young" (0) landscape		
Unburned forests (%)			
Radius 100 m	6.9 (18.1)	0	100
Radius 250 m	9.6 (15.2)	0	76.6
Radius 500 m	14.9 (15.2)	0	61.8
Distance to unburned forest (m)	Dummy: less (1) or more (0) than a given distance to unburned forest (100, 200, 300, 400, 500 m)		
Elevation (m)	750 (41)	655	900

nest survival rate (1-daily mortality rate). Nest success was then calculated as daily survival rate raised to the exponent corresponding to the length of the total nesting cycle (35 days). Nest success estimates give the probability of a nest surviving its whole nesting cycle and successfully fledging at least one young. The first day of observation corresponded to the first day the nest containing eggs or nestlings was found or the first day of incubation when the nest was discovered prior to incubation. For the last day of observation, we used midpoint between last active day (a visit with at least one young at nest) and last check for nests that failed, whereas we used the last active day for successful nests or nests with uncertain fate ("Last Active-A" approach of Manolis et al., 2000). Productivity of successful nests was based on the number of young observed near the time of fledging (>80% of nesting cycle or higher count of last two active visits).

2.4. Data analyses

Differences in nest densities among years were assessed for the burned mature and young landscapes using Goodness-of-fit tests. We investigated the effect of temporal, nest tree and nest site variables on reproductive success by selecting variables considered to have a potential effect on the breeding performance of woodpeckers based on a literature review and our own experience of the area and species under study. We first tested the effect of these explanatory variables on daily nest mortality rate using Mayfield logistic regression (Aebischer, 1999; Hazler, 2004). With this modeling approach, each nest represents multiple binomial trials (failure/success) and number of trials corresponds to the number of days the nest was under observation (observation days). This method reduces the bias associated with unequal periods of observation (Mayfield, 1961, 1975) while allowing the inclusion of individual explanatory variables into the analysis (Hazler, 2004). Three different categories of "failure" were considered as the dependent variable: (1) all failures (including both predated and abandoned nests), (2) predation only (abandoned nests were excluded from the data set) and (3) abandonment only (predated nests were excluded). We also examined the effect of these same explanatory variables on individual nest productivity by analyzing clutch size and fledgling number using cumulative logit models (Allison, 1999). Modeling of clutch size included all nests for which incubation had been initiated. When modeling fledgling number, we excluded nests that had been predated and we considered abandoned nests as zeros in terms of productivity; therefore we assumed the same factors were involved in abandonment and in the productivity of successful nests and that these factors were different than the ones involved in predation.

Explanatory variables were divided into three groups (Table 1). We first tested the effect of time since fire given that we expected habitat quality (i.e. abundance of Cerambycidae beetles) to decline with years elapsed since fire (Murphy and Lehnhausen, 1998; Covert-Bratland et al., 2006). A second group included variables at the nest tree level that likely influence reproductive success of cavity nesters: nest height, tree diameter at nest height, diameter of cavity entrance, cavity depth and cavity orientation (Conner, 1975; Nilsson, 1984; Rendell and Robertson, 1989; Wiebe, 2001). The last group included site variables indicative of habitat quality for woodpeckers. Snag density was measured using 225 m^2 plots centred on each nest and estimates were produced for different diameters at breast height (dbh; >10, >15 and >20 cm). Proportion of burned mature forest surrounding nests was estimated for different radii (100, 250 and 500 m) from the combination of digital pre- and post-fire forest inventory maps. Each nest was also assigned to one of the two landscape classes described in the study area section (burned mature vs. burned young landscapes). We also tested the effect of nest proximity to burn edges on reproductive success as we expected nest predation to be highest close to unburned forest (Saab and Vierling, 2001). Conversely, we hypothesized that productivity per nest would be higher for nests closer to unburned forest as these portions of the burn may represent higher-quality foraging habitats for woodpeckers (Murphy and Lehnhausen, 1998; Saint-Germain et al., 2004b). Proximity to unburned forest was measured with two variables based on digital post-fire forest inventory maps: (1) proportion of unburned forest surrounding nests (within 100, 250 and 500 m radii) and (2) shortest distance to unburned forest (>1 ha) using different distances (more or less than 100, 200, 300, 400 or 500 m). Because elevation may also affect the density of wood-boring beetles (Saint-Germain et al., 2004b), this was also included as an explanatory variable and was measured using a global positioning system and topographic maps.

Mayfield logistic and cumulative logit regression models were performed in two steps. We first conducted regressions on each group of variables separately using stepwise selection to select significant variables in each set ($p < 0.05$). Variables that came out as significant in each set were then entered concurrently using stepwise selection in a final regression model. Daily nest mortality and nest productivity models predict opposite responses in terms of reproductive success. A positive relationship of a given variable with daily nest mortality (e.g. predation) indicates a negative influence on reproductive success. Conversely, a positive relationship with productivity (e.g. no. of fledglings) indicates a positive influence on reproductive success. Models were evaluated for overdispersion by estimating the variance inflation factor $\hat{c}$ (Deviance/DF) and standard errors were adjusted when $\hat{c}$ was >1 using the deviance statistic (Allison, 1999; Hazler, 2004). All regressions were performed using proc Logistic in SAS (SAS Institute Inc., 2004).

We assessed whether burned forests represented potential source habitats for the black-backed woodpecker during the three post-fire breeding seasons. This assessment was made separately for the burned mature and young landscapes. Three demographic parameters are necessary to estimate the source-sink status of a population: productivity, juvenile survivorship and adult survivorship (Pulliam, 1988). The source-sink status was calculated each year by comparing annual productivity to a source-sink threshold that corresponds to the minimal annual productivity necessary to maintain a viable population. This source-sink threshold was calculated according to the following equation (Trine, 1998; Bourque and Villard, 2001):

$$\text{Source} - \text{sink threshold} = 2 \times \text{adult mortality}/(1 - \text{juvenile mortality})$$

We calculated annual productivity from our data and used estimates of adult and juvenile survival rates from the literature. Annual productivity was calculated for each year and each landscape as the product of the mean number of fledglings per successful nest and nest success (Donovan et al., 1995). Secondary nesting and brooding were not incorporated in the calculations since less than 2% of all nesting events were second nesting attempts in our study and black-backed woodpeckers raise only one brood per year (Dixon and Saab, 2000). The population was considered a source in a given year if annual productivity was high enough to compensate for adult and juvenile mortality (source-sink threshold). Conversely, a population was considered a sink if annual productivity was insufficient to compensate for adult and juvenile mortality.

Estimates of survival rates are often limited for woodpeckers (Pasinelli, 2006; Wiebe, 2006), and no estimate is available for the black-backed woodpecker. We used survival rate estimates for other woodpecker species in other study areas and derived a range of survival estimates that could be used to assess the potential source or sink status of our population (Saab and Vierling, 2001). Wiebe (2006) reviewed the literature for survival rates of adult North American and European woodpecker species and reported an average survival rate for all species combined of 0.58. Mean survival rates for individual *Picoides* species varied between 0.48 and 0.82 for stable populations. Therefore, we assumed that adult survival rate of black-backed woodpeckers was within these values and used three rates representative of this range (low: 0.50; medium: 0.65; high: 0.80). Rates of juvenile survival are even less documented and many authors have used a range of 30–50% of adult survival rates in models of population dynamics of migratory bird species (Donovan et al., 1995; Trine, 1998). Given that the black-backed woodpecker is a resident species, we used 50% of adult survival rate as a reference to determine a range of juvenile survival rates (low: 0.25; medium: 0.33; high: 0.40). We computed the source-sink thresholds under these nine different scenarios. According to the intermediate scenario, productivity higher than 2.1 offspring per nest per year would indicate the population is a source. Productivity thresholds for the lowest and highest survivorship scenarios were, respectively, 4.0 and 1.0 offspring per nest per year.

2.5. Prey identification

In order to identify black-backed woodpecker's main prey, we collected stomach contents of two adults nesting in different sites in June 2001. Birds were forced to regurgitate by orally administrating a 1.5% solution of antimony potassium tartrate (according to the methods described by Poulin et al. (1994)). We also collected a fecal sample from one of these birds. The samples were conserved in a 70% ethanol solution and items were later identified by M. Saint-Germain (Université du Québec à Montréal).

3. Results

3.1. Woodpecker nest density

We observed a significant decline in nest density of black-backed woodpeckers for both the burned mature ($\chi^2 = 30.0$, df = 2, $p < 0.001$) and young landscapes ($\chi^2 = 38.1$, df = 2, $p < 0.001$). The decline of nest density was constant and densities observed by the second year were about half the densities observed the first year post-fire (Fig. 2). Nesting activity in year 3 was marginal compared to the first 2 years post-fire. Nest density in the burned mature landscape area was more than twice the density observed in the burned young landscape, a difference that was maintained through time.

3.2. Reproductive success and source-sink status

We found 111 active nests over the 3-year study from which 106 could be used to estimate nest success (i.e. >1 observation day; Table 2). Nest success declined from 84% the first year post-fire to 73% and 25% the second and third year following fire

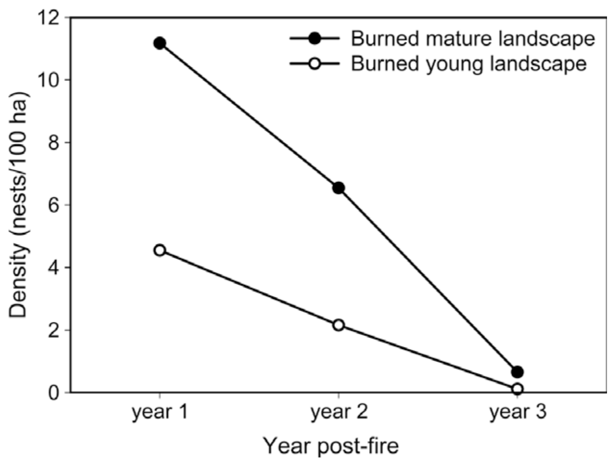

Fig. 2. Nest density of black-backed woodpeckers in the first 3 years following the 1999 fire in the Parc national des Grands-Jardins, Quebec, Canada. Nest densities were estimated separately for two portions of the burned landscape: burned mature and burned young landscapes (see Section 2 for details).

Table 2
Reproductive success of black-backed woodpeckers in the first 3 years following the 1999 fire in the Parc national des Grands-Jardins, Quebec, Canada.

Time since fire	*n*[a]	Observation days	Daily survival rate	Nest success	No. of young per successful nest	Productivity per nest[b]
1 year	61	1564	0.995 ± 0.002	0.84 ± 0.05	3.09 ± 0.10	2.59 ± 0.25
2 year	41	1024	0.991 ± 0.003	0.73 ± 0.08	3.00 ± 0.12	2.20 ± 0.31
3 year	4	52	0.962 ± 0.027	0.25 ± 0.25	3.00[c]	0.76 ± 0.74

[a] Number of nests with more than one observation day.
[b] Nest success * mean number of young per successful nest.
[c] Based on one nest only.

(Table 2). A total of 19 nest failures occurred over the 3 year study of which 47% (9) were attributed to predation and 53% (10) to abandonment. Both predation and abandonment rates were low but increased with time since fire. The relative importance of each cause of failures (predation and abandonment) remained similar each year. Observed predation cases during the study included one nest destruction by a black bear (*Ursus americanus*) and one nest usurpation by an eastern bluebird (*Sialia sialis*). Other potential nest predators in our study area included the red squirrel (*Tamiasciurus hudsonicus*), the american marten (*Martes americana*) and weasels (*Mustela* spp.). Mean number of young produced by a successful nest averaged 3 young per nest, a value that remained constant over the 3 year period.

Both years since fire and nest site variables significantly influenced reproductive success of black-backed woodpeckers. Years since fire had a positive effect on daily nest mortality, although this result was significant only for the regression that included all failures regardless of cause (Table 3). Conversely, years since fire influenced clutch size negatively. Nest site conditions had a similar influence on clutch size and number of fledglings although different variables were involved in the models (Table 3). Nesting pairs located in the burned mature landscape had larger clutch sizes than those nesting in the burned young landscape. Similarly, nests that were surrounded by a higher proportion of burned mature forest within a 100 m radius tend to fledge more young (Table 3, Fig. 3). In addition, nests in proximity to unburned forest were more productive than nests located further inside the burn (Table 3, Fig. 3).

In both the burned mature and young landscapes, annual productivity of black-backed woodpeckers in the first year post-fire was sufficient to compensate for adult and juvenile mortality in six of the nine source-sink threshold scenarios, including the intermediate scenario (Fig. 4). This status remained similar for the burned mature landscape in the second year post-fire (six of nine scenarios). For the burned young landscape however, annual productivity in year 2 was below the intermediate source-sink threshold scenario and was likely to offset mortality for only four of the nine scenarios examined. Active nests were rare by year 3, which precluded precise estimation of annual productivity. However, these few active nests had low nest success and, consequently, mean productivity of nests fell below all scenarios.

3.3. Woodpecker prey

Diet of the two examined nesting birds consisted mainly of Cerambycidae larvae. Stomach contents of one bird consisted of six head capsules of *Monochamus scutellatus* and three complete *M. scutellatus* larvae. Stomach content of the other bird was two *Acmaeops proteus* larvae, three other Cerambycidae larvae (probably *M. Scutellatus*) and Lepidoptera cocoon remnants. The fecal sample of the latter contained seven head capsules of *Monochamus* sp. and one large Lycosidae spider.

4. Discussion

Burned forests are considered important habitat for the black-backed woodpecker, a status largely based on the higher abundance of this species in burns as compared to other habitat types (Hutto, 1995, 2008; Hannon and Drapeau, 2005; Saab et al., 2005). The high nest density and reproductive success of black-backed woodpeckers observed in this study suggest that severely burned spruce forests may indeed represent a high-quality nesting

Table 3
Variables that influence daily nest mortality (Mayfield logistic regressions) and nest productivity (cumulative logit regressions) of black-backed woodpeckers.

Model	*n*[a]	Explanatory variables								
		Temporal			Nest tree			Nest site		
		Variable[b]	Relation[c]	*P*[d]	Variable[b]	Relation[c]	*P*[d]	Variable[b]	Relation[c]	*P*[d]
Daily nest mortality										
All failures	106	**Year**	+	**0.0369**				D200	–	
								UB500	+	
Predation	106	n.s.			n.s.			n.s.		
Abandonment	106	n.s.			n.s.			n.s.		
Nest productivity										
Clutch size	85	**Year**	–	**0.0008**	N	–		**Land_M**	+	**0.0113**
								D100	+	**0.0377**
Number of fledglings	97	n.s.			n.s			**BM100**	+	**0.0309**
								D200	+	**0.0102**

[a] Sample sizes differed among models according to data availability.
[b] Significant predictors for each individual group of variables are listed (with relation signs). Variables that came out as significant in the final model are indicated in bold with their significance levels: Year = years since fire; N = north-oriented cavity; UB500 = % of unburned forests within 500-m radius; Land_M = burned mature landscape; BM100 = % of burned mature forest within 100-m radius; D100 = less than 100 m from unburned forest edges; D200 = less than 200 m from unburned forest edges.
[c] Daily nest mortality models: a positive relationship indicates lower reproductive success; nest productivity models: a positive relationship indicates higher reproductive success.
[d] Significance at last step.

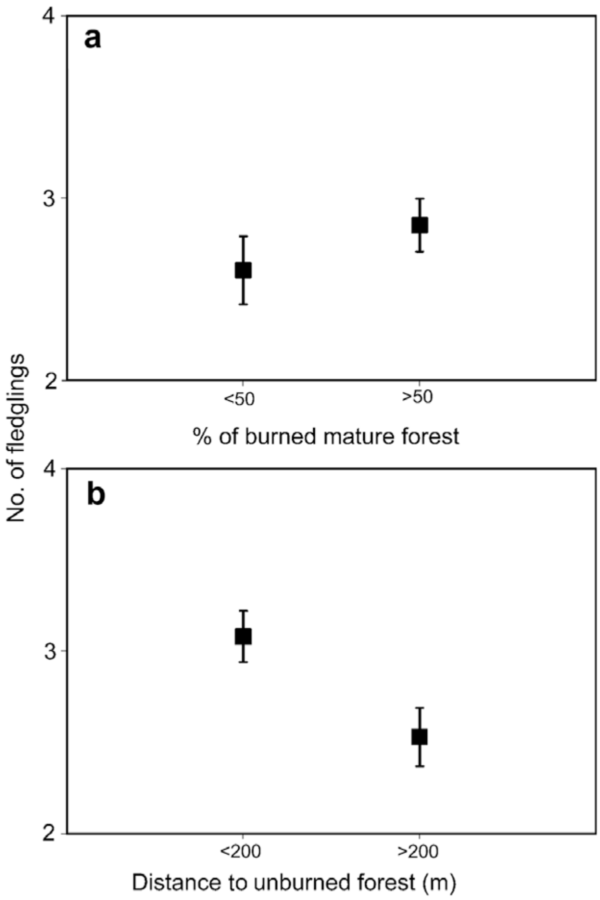

Fig. 3. Relationship between nest productivity (mean no. of fledglings ±SE) and (a) percentage of burned mature forest surrounding nests (within 100 m radius) and (b) distance to unburned forest (< or >200 m).

habitat for this species. Nest density was as high as 0.11 nests/ha in our study area, among the highest densities of nesting pairs reported for this species across its range (Dixon and Saab, 2000; Saab et al., 2007; Vierling et al., 2008). Our comparison of woodpeckers' annual productivity with a range of survival estimates suggests that these burned forests likely functioned as a source habitat for

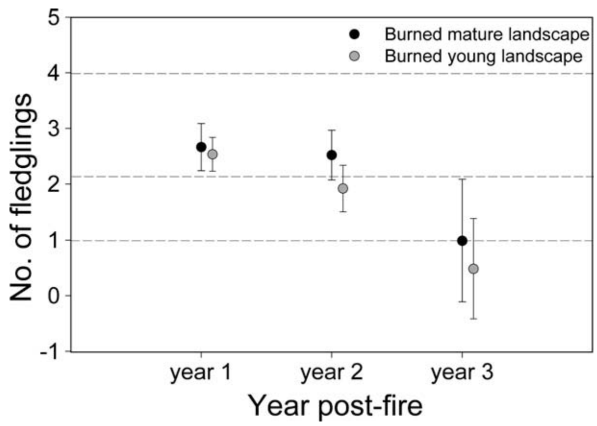

Fig. 4. Comparison of nest productivity (mean no. of fledglings ±SE) with source-sink thresholds. Dotted lines represent the number of young per nest necessary to compensate for mortality rates based on the highest threshold scenario (lowest adult and juvenile survival rate values), the intermediate threshold scenario (intermediate adult and juvenile survival rate values) and the lowest threshold scenario (highest adult and juvenile survival rate values). Productivity above a given line indicates that the population likely functions as a source.

this species (Hutto, 1995; Murphy and Lehnhausen, 1998). Yet, results on nest density and reproductive success also indicated that habitat quality of these post-fire forests was temporally limited and varied within our burned landscape.

4.1. Effect of time since fire

Temporal occupancy patterns of cavity-nesting birds after fire differ depending on species-specific habitat requirements. Whereas aerial and ground foragers may occupy burns for more than a decade after fire, bark-foraging *Picoides* woodpeckers (black-backed, American three-toed *Picoides dorsalis* and hairy *Picoides villosus* woodpeckers) are typically restricted to the first few years following fire (Murphy and Lehnhausen, 1998; Covert-Bratland et al., 2006; Saab et al., 2007). In our study, nesting activity of black-backed woodpeckers declined sharply with time since fire, with woodpeckers being nearly absent by the third year following fire. This short occupancy pattern is mainly linked to the ephemeral availability of bark and wood-boring beetles, *Picoides* woodpeckers' main prey, that typically colonize these snag forests soon after disturbance (Murphy and Lehnhausen, 1998; Saint-Germain et al., 2004c; Boulanger and Sirois, 2007). Wood-feeding insects that colonize spruce snags are typically limited to the early stages of degradation since most of these species reproduce only in heavily stressed or recently dead trees (Saint-Germain et al., 2007). Because severe stand-replacing fires create a pulse of snags in more or less the same initial post-fire stage, foraging opportunities for *Picoides* woodpeckers are temporally constrained by the life cycles of these saproxylic insects in snags.

In spruce forests of Alaska, Murphy and Lehnhausen (1998) observed a similar 3-year decline in black-backed woodpecker abundance which they attributed to the decrease of *M. scutellatus*, the woodpecker's main prey in their study. This deep-boring cerambycid is well-known for colonizing stands soon after disturbance and larvae of this species remain in the wood for 1–3 years before emerging as adults (Rose, 1957). *M. scutellatus* was the most common cerambycid species in burned spruce trees of our study area (Saint-Germain et al., 2004c) and stomach contents of two nesting birds suggests that larvae of this wood-borer were the woodpecker's main prey as well. Rearing experiments at our sites indicate that *M. scutellatus* adults of the 1999 cohort emerged primarily 2 years after fire (11% in 2000; 89% in 2001; 0% in 2002; C. Hébert, unpublished data). Few wood-borers were still found in our burned landscape after the first 2 years (C. Hébert, personal communication). The observed decline in woodpecker nest density is thus likely to have reflected changes in prey availability over the course of our study.

Annual productivity of black-backed woodpeckers also decreased significantly over the 3-year period. Given that the number of young produced per successful nest remained relatively constant over the 3-year period, the decrease in the annual productivity was mainly linked to the decrease in nest success. Part of this decrease in nest success was caused by an increased level of predation. Although few nests were predated, predation rate was two times higher the second than the first year post-fire. This increase in predation rate might have been caused by partial recolonization of these burned areas by mammalian predators (e.g. red squirrels), although this effect seems to be limited in the first years following fire (Saab and Vierling, 2001; Fisher and Wilkinson, 2005; Vierling et al., 2008). The other cause of this decrease in nest success was the increase in nest abandonment. As food availability is a crucial determinant of breeding performance in birds (Martin, 1987), the observed pattern in nest abandonment may have been caused by a decrease in the availability of food resources (wood-boring beetles). Lower food availability would also explain the observed decrease in mean clutch size with time since fire, although no significant effect was detected for the number of young produced per nest. The similarities in occupancy patterns found in this and in another study conducted in Alaska (Murphy and Lehnhausen, 1998), together with our results on reproductive success, suggest burned forests represent important breeding habitats for the black-backed woodpecker in the first 2 years following fire in northern spruce forests.

4.2. Effect of within-burn variability in forest conditions

Spatial variability of post-fire conditions within burns can greatly influence occupancy patterns of fire-associated species (Kashian and Barnes, 2000; Saint-Germain et al., 2004b; Smucker et al., 2005; Kotliar et al., 2007). For species that depend on dead wood, pre-fire forest conditions directly determine species, diameter and degradation stage of burned snags and thereby influence the quality of burned forests for these species. Tree diameter is of particular importance for woodpeckers as large trees are required for nesting and provide high concentrations of saproxylic insects (Nappi et al., 2003; Saint-Germain et al., 2004c). Because of its effect on tree size, forest age may influence post-fire habitat quality, especially in northern conifer boreal forests where trees may take a long time to reach adequate sizes for woodpeckers. Although the burned landscape we studied was dominated by pure black spruce stands, previous natural and anthropogenic disturbances have generated stands of varying age.

Our results show that pre-fire differences in forest age influenced both nest density and productivity of black-backed woodpeckers. Nest density in the burned mature landscape was more than two times the density observed in the burned young landscape, a difference that likely reflected the concentration of food resources. We also found that the proportion of burned mature forests surrounding nests had a positive influence on productivity (no. of fledged young). These results indicate that forest conditions (density of large trees) at the moment of fire have an important influence on the quality of post-fire habitats for black-backed woodpeckers. In our study area, burned mature forests that were at least 80 years old likely represented higher quality habitats for the black-backed woodpecker than 40-year-old stands.

The distance of a nest to unburned forest edges also influenced black-backed woodpecker reproductive success. Murphy and Lehnhausen (1998) noted woodpeckers concentrate at the burn periphery where spruce trees were less heavily scorched. Although woodpecker nests in our study were found up to 1 km inside the burn, the proximity of nests to unburned forest edges had a positive effect on woodpecker productivity. These forest-burn ecotones may provide better foraging opportunities, as snags close to unburned edges are generally less severely burned and thus more likely to support high densities of wood-boring beetles (Saint-Germain et al., 2004c). Saint-Germain et al. (2004b) showed proximity of burned forests to unburned areas, after controlling for fire severity, had a positive effect on *M. scutellatus* densities, a pattern that is probably linked to the feeding requirements of wood-borer adults. Contrary to our expectations, nests close to unburned forests were not more likely to be predated, a pattern that is partly explained by the overall low predation pressure in these burned forests. Because of its influence on nest density and reproductive success, within-burn heterogeneity caused by pre-fire forest conditions (e.g. forest age) and fire severity patterns (e.g. distance to unburned forest) may together be an important determinant of the quality of burned forest habitat for the black-backed woodpecker.

4.3. Burned forests as source habitats

Hutto (1995) proposed that burned forests could function as source habitats for the black-backed woodpecker and that populations in unburned forests could represent sink populations maintained through emigration from burns after conditions become less suitable (see also Murphy and Lehnhausen, 1998). Our productivity data show that the burned forests we studied likely functioned as source habitats for the black-backed woodpecker. However, our results also emphasize that this source status varied both temporally and spatially within the burn. Our comparison of annual productivity with survival estimates suggests burned forests were more likely to represent source habitats in the first 2 years after fire. Only a few nests were active by year three and productivity, although based on a small sample, was much lower than in the first 2 years. In addition, we observed that pre-fire forest conditions had an important effect on reproductive success and, thus, on the source-sink status. Burned mature forests were more likely to represent source habitats than burned young forests in the second year post-fire.

Several other factors including pre-fire forest composition, fire characteristics (e.g. severity, size, season), saproxylic insect assemblage (e.g. species, abundance) and woodpecker population density at a regional scale may influence temporal occupancy pattern, density and reproductive success of the black-backed woodpecker in burns. Indeed, other studies have reported longer temporal use of burns by black-backed woodpeckers (>2 years, Hoyt and Hannon, 2002; Saab et al., 2007) or high nest success many years following fire (Saab et al., 2007). Also, both woodpecker abundance and reproductive success have been shown to be influenced positively by fire severity (Koivula and Schmiegelow, 2007; Vierling et al., 2008). The burned forests we studied were relatively homogeneous in their pre-fire forest composition and burn severity, being dominated by severely burned black spruce stands. Although this study does not cover all post-fire conditions, the results we obtained for these severely burned spruce forests are probably representative of many burned forests used by the black-backed woodpecker. Indeed, spruce forests of the Boreal Shield ecozone represent an important portion of the black-backed woodpecker's distribution and these forests are largely shaped by severe stand-replacing fires, those with which black-backed woodpeckers are generally associated (Hutto, 2008).

Despite the inherent variability in post-fire forest conditions, burned forests likely represent high-quality habitats for the black-backed woodpecker. Indeed, the high reproductive success observed in our study in the first 2 years following fire (73–84%) is consistent with previous results reported in other burned forests (87%: Saab and Dudley, 1998; 100%: Dixon and Saab, 2000). Vierling et al. (2008) also found nest success of black-backed woodpeckers to increase with higher fire severity and reported a 80% nest success in high-severity *Pinus ponderosa* burned stands. Although black-backed woodpeckers occupy unburned forests as well (Bent, 1939; Weinhagen, 1998; Setterington et al., 2000), few estimates of reproductive success are available to compare with post-fire habitats. Yet, results of studies conducted following pine beetle outbreaks suggest that nest success of the black-backed woodpecker in beetle-affected forests is generally less than what is observed in burned forests (63%: Goggans et al., 1989; 44–78%: Bonnot et al., 2008). This higher nest success in burned than unburned forests is consistent with what has been reported for other cavity nesting birds. For instance, Saab et al. (2005) reviewed available data on reproductive success of six cavity-nesting bird species (including the black-backed woodpecker) between burned and unburned forests of the Rocky Mountains and found nest success was typically higher in burned than unburned habitats. The relative higher nest success in burns does not mean that other forest types are unsuitable for breeding black-backed woodpeckers (see also Bonnot et al., 2008). Rather, these results emphasize that burned forests provide highly favourable conditions that are less likely to be found at similar levels in unburned forests.

Two factors are likely responsible for this relatively higher reproductive success in burns. First, nests in burns may be less susceptible to predation, which is often the major cause of nesting failure in birds (Nilsson, 1984; Martin, 1992). For instance, Saab and Vierling (2001) found higher nest success of Lewis woodpecker (*Melanerpes lewis*) in burned than in unburned forests, a result mainly caused by higher predation levels in unburned forests. Given that recolonization of burned forests by nest predators associated with unburned forests may take several years (Saab and Vierling, 2001; Gentry and Vierling, 2007), predation may thus have a limited effect on black-backed woodpecker nest success considering the short-term occupancy of this species in burns. Second, recent burns provide high concentrations of high-quality foraging substrates that are otherwise scarce or patchily distributed in other forest types (Imbeau and Desrochers, 2002; Pedlar et al., 2002; Saint-Germain et al., 2004c). Because nest predation by mammalian predators is likely to decrease with increasing fire severity (i.e. less protection cover and forage for mammal species) whereas foraging opportunities (i.e. snag density) typically increase, nest success is likely to be highest in high-severity burned forests such as the ones we studied (see also Vierling et al., 2008).

We observed considerable variation in the reproductive success of woodpeckers within our burned landscape, even though our stands were relatively similar in pre-fire forest composition and burn severity. This underscores the importance of estimating reproductive success in a wide variety of burn conditions and with a large number of nests. Also, this suggests that estimating reproductive success in unburned forests would be even more problematic as forest conditions may be much more variable than what is observed in burned forests. For instance, dead wood quality and availability in unburned forests may be highly variable due to factors operating at different scales (from individual snag recruitment to larger-scale disturbances). Given that differences in habitat conditions affected the reproductive success of woodpeckers within our burned landscape, a similar effect may occur in unburned forests (e.g. higher reproductive success where density of foraging snags is higher) and it is likely that reproductive success would vary much more than in post-fire habitats.

The high reproductive success observed in this and previous studies suggests that burned forests may contribute significantly to population levels of the black-backed woodpecker, especially in regions where the fire cycle is short. Although fire is recognized as the main natural stand-replacing disturbance in the Canadian boreal forest, fire cycle (the time required to burn an area equal in size to the reference area) has been shown to vary widely among regions (e.g. 50 to over 500 years; Van Wagner, 1978; Foster, 1983; Bergeron et al., 2004, 2006). This variability inevitably affects the availability of post-fire habitats for the black-backed woodpecker. In regions where the fire cycle is short, recent burns may cover an important proportion of the area. Because fire cycle also influences forest age structure, the proportion of mature and old-growth forests – which can represent alternative habitat for black-backed woodpeckers (Weinhagen, 1998; Setterington et al., 2000) – will tend to decrease with a shorter fire cycle. Given that burned forests generally support much higher densities of woodpeckers (Hutto, 1995; Hoyt and Hannon, 2002), an important proportion of black-backed woodpeckers may be recruited in burns on an annual basis in regions with short fire cycle.

The source-sink dynamic proposed by Hutto (1995) for the black-backed woodpecker entails that the net surplus of individuals produced in source (burned) habitats would compensate for the net loss of individuals in sink (unburned) habitats (Pulliam, 1988). This equilibrium in a closed population (no emigration, no immigration) depends both on population growth in each habitat ($\lambda > 1$ in sources, $\lambda < 1$ in sinks) and on the relative proportion of the population in these habitats (Pulliam, 1988). In regions with a short fire cycle, this source-sink dynamic is plausible given that recent burns would support an important proportion of the population and thus compensate for potential deficits in unburned habitats. However, in regions where the fire cycle is longer, potential habitats for black-backed woodpecker consist mainly of mature and old-growth forests. The net surplus generated by burned forests in these regions is unlikely to compensate for deficits generated in unburned habitats (given the high proportion of these areas) if indeed the mean productivity in these habitats is less than population replacement levels. It is thus likely that bird productivity in at least some of these unburned habitats (e.g. some old-growth forests) is high enough to allow population persistence. A non-mutually exclusive alternative would be that regions with short fire cycles serve as regional sources from which surplus individuals disperse into forest regions with long fire cycles (regional sinks).

4.4. Conservation implications

Alteration of fire regimes and forest management practices in North American boreal forests may have important impacts on the availability of wildfire-created habitats. Fire suppression may considerably reduce the availability of this habitat in historically fire-mediated forest ecosystems. In Fennoscandian boreal forests for instance, fire suppression has efficiently controlled the extent of wildfires, which is thought to have contributed to the decline of many fire-associated species (Ahnlund and Lindhe, 1992; Angelstam and Mikusiński, 1994; Berg et al., 1994; Jonsell et al., 1998). In Canadian boreal forests, wildfires are still relatively common although comparisons of historical and current burn rates indicate a decrease in the extent of fires in most regions (Bergeron et al., 2004). Yet, post-fire logging ("salvage logging") in boreal burned forests is becoming an important economic activity that may reduce both the quantity and quality of burned habitats for fire-associated species (Nappi et al., 2004; Schmiegelow et al., 2006). A major impact of this management practice is the removal of burned trees of commercial size that are also the most valuable to deadwood-dependent species such as saproxylic insects and bark-foraging woodpeckers. Our results clearly indicate that burned conifer forests represent important nesting habitats for the black-backed woodpecker, as for other cavity-nesting birds (Saab et al., 2005). Conservation of post-fire habitats may thus play a key role in the persistence of black-backed woodpecker populations and many other fire-specialists in managed forest landscapes. Large continuous tracks of unsalvaged stands of commercial value (i.e. large diameter snags) and located close to unburned forests should therefore be maintained as black-backed woodpecker nesting habitat.

Even-aged management in the boreal forest is likely to induce large-scale changes in the age structure of forest stands, a change that may also affect populations of the black-backed woodpecker (Imbeau et al., 2001). Indeed, this management approach will inevitably reduce the availability of mature and old-growth forests (Bergeron et al., 2007; Drapeau et al., 2009), an important alternative habitat for the black-backed woodpecker (Setterington et al., 2000). This practice may also indirectly affect the quality of post-fire forest habitats. As the abundance and extent of over-mature forests decrease, fire is more likely to burn younger stands, which, in turn, are less likely to support the required densities of larger trees suitable for foraging and nesting. Indeed, our data show that burned forests that were younger at the time of fire supported lower densities of nesting pairs and lower levels of productivity than older forests. Therefore, current management practices in the boreal forest that produce younger forest mosaics may interfere with stand-replacing fires and create post-fire habitats that are less suitable for the black-backed woodpecker and other fire-associated species.

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