# Effects of commercial thinning on site occupancy and habitat use by spruce grouse in boreal Quebec

**Ambroise Lycke, Louis Imbeau, and Pierre Drapeau**

**Abstract:** Partial cuts are increasingly proposed to maintain habitats for species negatively affected by clearcutting, even if their benefits on nonpasserine birds and large mammals are still poorly documented. Our main objective was to evaluate effects of commercial thinning (CT) on spruce grouse (*Falcipennis canadensis* L.), a game bird of the boreal forest. Because this species is known to be associated with a dense vegetation cover, we hypothesized that habitat use would be lower in treated sites. In spring 2006, we evaluated site occupancy in 94 forest stands (50 CT and 44 uncut stands) in Quebec by visiting each on three occasions during the breeding season (March–May). Additionally, during the molting period (May–July), we used radiotelemetry to monitor habitat use by 19 males. As compared with uncut stands, results show that a lower proportion of CTs were used in spring (39% versus 60%, after accounting for detection). During the molting period, CTs were also used less than expected according to their availability. The significant reduction of lateral and vertical forest cover in CT may explain these results. We conclude that even if CT is perceived beneficial for wildlife, it does not completely fulfill the needs of species associated with dense understory vegetation, such as spruce grouse.

**Résumé :** Les coupes partielles sont de plus en plus souvent proposées pour de maintenir l'habitat pour des espèces défavorisées par les coupes totales, et ce même si leurs avantages sont peu connus pour les grands mammifères et pour plusieurs autres groupes, à l'exception des passereaux. Notre principal objectif visait à évaluer l'influence de l'éclaircie commerciale (EC) sur l'habitat du tétras du Canada (*Falcipennis canadensis* L.), un gibier à plume des forêts boréales. En raison du fait que cette espèce est associée aux sites ayant un fort couvert végétal, nous avons émis l'hypothèse que l'utilisation des habitats serait moins élevée dans les sites traités. Au printemps 2006, l'occupation des sites a été évaluée dans 94 peuplements (50 EC et 44 peuplements non récoltés) au Québec. Chaque peuplement a été visité trois fois durant la période de reproduction (mars à mai). Durant la période de mue (mai à juillet), nous avons utilisé la télémétrie pour évaluer l'utilisation de l'habitat de 19 tétras mâles. Comparativement aux peuplements non récoltés, les résultats montrent qu'une plus faible proportion de sites ont été utilisés dans les EC au printemps (39 % versus 60 %, après avoir corrigé pour la détection). Durant la période de mue, les sites EC ont également été moins utilisés que ce qui était attendu compte tenu de leur disponibilité. La diminution importante du couvert forestier latéral et vertical dans les sites EC pourrait être à l'origine de ces résultats. Bien que comparativement aux coupes totales, l'EC puisse être perçue comme une mesure d'atténuation pour la faune, nous concluons qu'elle ne répond pas complètement aux besoins d'espèces associées aux milieux fermés ayant une végétation dense, telles que le tétras du Canada.

## Introduction

Clearcut logging is still the most prevalent logging practice in the boreal forest of Canada, and many studies have shown that this harvesting technique has important negative effects on species belonging to different wildlife groups, including game species (Dussault et al. 1998; Ferron et al. 1998; Turcotte et al. 2000). To maintain high-quality habitats for species negatively affected by clearcutting, such as those associated with late-successional forests, some authors have suggested that the proportion of partial cuts be increased in boreal forests as an alternative to clearcut logging (Bergeron et al. 2007; Vanderwel et al. 2009). However, partial cuts vary widely in size and harvesting intensity, which may have variable effects, positive as well as negative, on wildlife. Indeed, even if partial cutting is currently being proposed as an alternative to clearcutting, knowledge of its effects on some wildlife groups, and particularly on nonpasserine birds as well as large mammals, is still limited (Vanderwel et al. 2009).

Spruce grouse (*Falcipennis canadensis* L.) is the main nonpasserine game bird species found in coniferous forests in Canada and the northern United States (Szuba 1989; Boag and Schroeder 1992). In eastern Canada, spruce grouse is generally associated with stands dominated by black spruce (*Picea mariana* (Mill.) BSP) (Lemay et al. 1998;

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Turcotte et al. 1993; Potvin and Courtois 2006) where it is associated with dense habitats by actively selecting dense understory vegetation cover (Szuba and Bendell 1982; Schroeder and Boag 1991; Lemay et al. 1998). This habitat association is highly relevant to studying the effects of partial cutting on wildlife, considering the fact that many partial cut techniques, including commercial thinning (CT), may considerably reduce understory vegetation cover.

Previous studies have shown that spruce grouse move from recent clearcut areas to nearby residual forests (Turcotte et al. 1994, 2000; Potvin and Courtois 2006) and that even gap harvesting (from 0.1 to 10 ha) negatively affects habitat use (Huggard 2003). However, to the best of our knowledge, the effect of partial cutting on this game species is still poorly documented. Therefore, the main objective of our study was to evaluate the use of partially cut stands by spruce grouse. Specifically, we determined whether such stands met the specific needs of this species during different critical periods of its life cycle: display and egg laying periods in the spring as well as the molting period in summer. We hypothesized that site use in spring and habitat use in summer would be significantly reduced in partially cut stands as compared with untreated stands where lateral and vertical cover would be more appropriated for spruce grouse.

## Methods

### Study area

Our study area, covering 8700 km$^2$, was located in the Abitibi–Temiscamingue region of northwestern Quebec (49°17′N to 48°38′N and 77°31′W to 78°42′W) (Fig. 1). This boreal forest occurs in the balsam fir (*Abies balsamea* (L.) Mill.) – white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Thibault and Hotte 1985). Strongly exploited by timber and pulp companies, 10% of commercial treatments within this region were made by partial cuts defined as CT, which is the most frequently used partial cut method in Quebec's boreal forests (Ministère des Ressources naturelles et de la Faune 2005). More specifically, this practice consists of harvesting commercial-sized trees (diameter at breast height ≥9 cm) in a premature stand that has regular structure and that has not reached an exploitable age with the goal of accelerating diameter growth of residual trees. This harvest is done on 25%–35% of the initial basal area, which includes the trees cut in the harvesting trails. These trails are normally parallel to one another, are roughly 30 m apart, and have a maximum width of 3.5 m. Approximately 15 years after CT has taken place, residual trees are harvested according to clearcut standards (Ministère des Ressources naturelles, de la Faune et des Parcs 2003).

We selected a total of 94 independent sites (minimum of 1 km between them) in our occupancy study: 50 black spruce dominated CTs, which had been conducted between the years 1991 and 2006, and 44 unharvested (control) black spruce stands, which had the characteristics of stands eligible for CT according to Quebec regulatory requirements (Fig. 1). We located all CT and control sites using ecoforestry maps from the Quebec Ministry of Natural Resources and Wildlife (Létourneau 1999), which were updated with information from all of the forest products companies present in the area. These maps, although they have been shown to have some weaknesses relative to stand height estimates and tree composition for some mixedwood types on upland sites (Potvin et al. 1999; Dussault et al. 2001), could nevertheless be considered as state-of-the-art, particularly the third-generation maps that we used (maps redone by the Quebec Ministry of Natural Resources and Wildlife at 10-year intervals). However, we checked each site to validate the accuracy of the data, such as dominant and subdominant tree species, height, age, and density of the stand.

### Spruce grouse and vegetation surveys

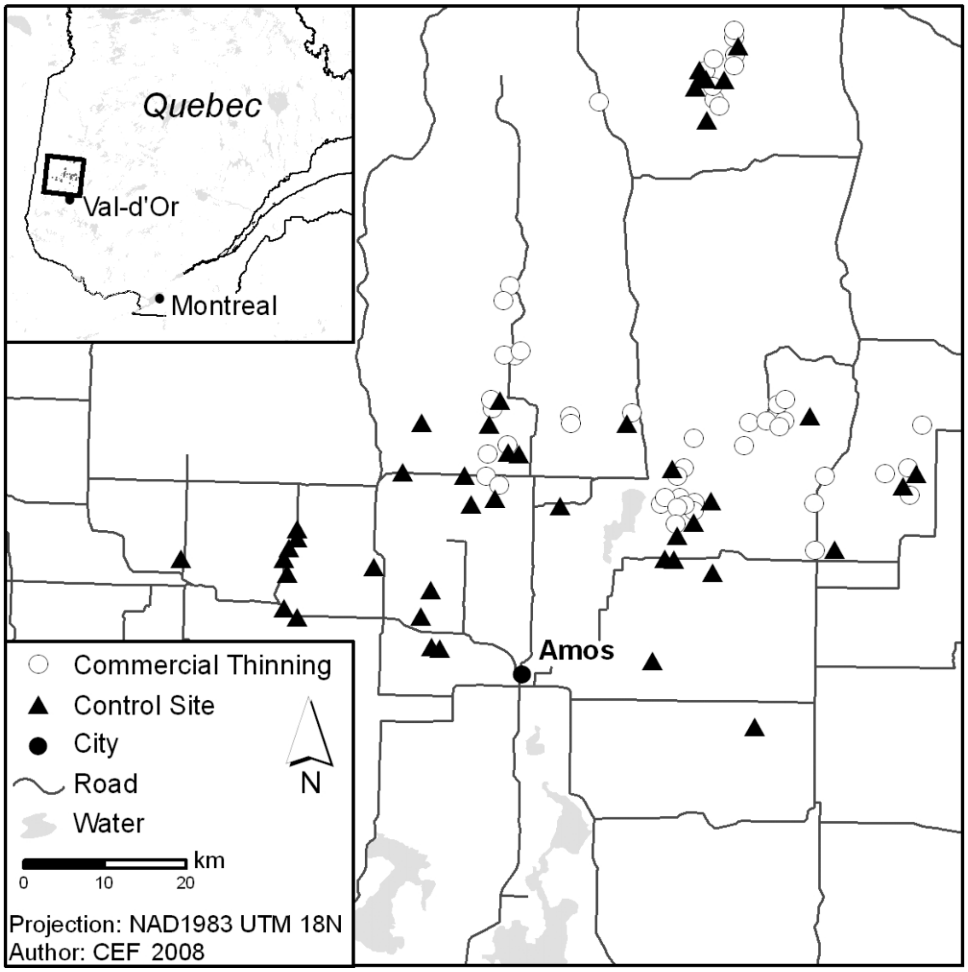
We used playbacks of female territorial calls to census birds and build detection histories at CT and control sites (Lemay and Ferron 1987; Schroeder and Boag 1989; Potvin and Courtois 2006). We visited each site on three occasions between 31 March and 18 May 2006 and played female calls, between 30 min before sunrise and noon, from the center of the site for a period of 15 min using portable amplifiers (model No. 7-100; Pignose industries, Gardena, California). Surveys were done by two-person crews, with each observer located 15–20 m from the amplifier in opposite directions to detect incoming birds. We recorded whether the species was detected (calls and (or) visual sightings of both sexes) for each visit at a given site to build our detection histories. Although we estimated that recordings could be heard within 100–150 m from the amplifier, we followed Potvin and Courtois (2006) and used number of males detected per 10 stations rather than exact densities.

To compare vegetation characteristics between CT and control sites, we used a two-factor BAF prism at each calling station to determine basal area (square metres per hectare) of selected stands. We determined diameter at breast height and species of each tree selected using the prism. We evaluated horizontal visual obstruction of the understory vegetation by using a vegetation profile board at 15 m distance on both sides of the calling station in a north–south axis (Nudds 1977). On this same north–south axis, we evaluated vertical vegetation cover every 3 m to obtain 10 cover measurements that we classified as open or closed. We considered vertical vegetation cover as open when an area with a 15 cm radius above the observer was free of vegetation (branches and leaves, living or dead). We made this measurement at a height of between 1.5 and 4 m as well as >4 m (Bertrand and Potvin 2003). We measured two additional lateral and vertical cover points 50 m east and west of the calling station. We also made a prism measurement of basal area at these two additional points.

### Radiotelemetry

We captured 19 male spruce grouse using female territorial calls and a 5 m telescopic pole equipped with a nylon snare at its end (Zwickel and Bendell 1967). We captured males in or at the border of commercially thinned stands and equipped them with a radiotransmitter (model R1-2B-M; Holohil Systems Ltd., Carp, Ontario) that weighed 14 g and was attached as a backpack with a Kevlar harness (Turcotte et al. 1993, 1994, 2000). We restricted our telemetric monitoring to males, as they are the most susceptible to avoiding open stands during the molting period, which also allowed us to circumvent the variability of territorial use due

**Fig. 1.** Distribution of commercial thinnings and control sites in the study area of site occupancy by spruce grouse (*Falcipennis canadensis*) in Abitibi, Quebec, Canada, spring 2006.




to gender (Boag and Schroeder 1992). Moreover, if partial cuts are prescribed to maintain viable wildlife habitats for spruce grouse, which is known to avoid recent clearcuts, they must retain sufficient cover for the most vulnerable gender at this critical period of its life cycle. During capture, we collected and measured the first primary feather to determine age (adult or yearling; Szuba et al. 1987). We located radiotagged birds twice a week from 17 May to 27 July 2006, and each bird was located at least 18 times during this period. We used homing when possible (Kenward 2001), with only 17% of locations determined via triangulation. We conducted this work according to an animal utilization protocol approved by the animal care committee of the Université du Quebec en Abitibi–Temiscamingue, which operates under the auspices of the Canadian Council on Animal Care.

### Statistical analysis

We used single season site-occupancy models to assess whether spruce grouse occupancy of CT and control sites differ after accounting for the probability of detection (MacKenzie et al. 2006). Because the home range of spruce grouse is larger than the size of the sampled stations, the occupancy estimator is therefore best considered as the proportion of used rather than occupied sites (sensu MacKenzie et al. 2006, pp. 104–108). We considered a set of five site-occupancy models consisting of one variable associated with occupancy (treatment, a dummy variable for CT (1) or control (0) sites), and four variables associated with detection (Julian day and Julian day squared, time after sunrise, and treatment). In a first model, we used Julian day of the survey (squared) to correct for variation in response related to peak activity of the mating season. Because male spruce grouse seem to be more active in the morning (Schroeder and Boag 1989), we also included time after sunrise of each survey. Female territorial calls are sung spontaneously when light intensities are low at dawn and dusk (Boag and Schroeder 1992), but they can be stimulated at any time during the day (Lemay and Ferron 1987; Boag and Schroeder 1992). Even if some authors presume that grouse may respond all day long to this call at a similar intensity, to the best of our knowledge, this assertion has never been quantitatively verified. In a second model linked to detection, we included only treatment because we hypothesized a priori that observers might be more successful in detecting birds in CT, where vegetation is more open, than in control sites. A third model included a treatment effect in occupancy, as we expected lower site use of CT as compared with controls. Finally, a global model (all expected effects in occupancy and detection) and a null model completed our list of candidate models.

We conducted site-occupancy analyses with the program PRESENCE 2.0 (MacKenzie et al. 2003). We standardized all continuous variables by subtracting the mean from each value and dividing by the standard deviation. Collinearity diagnostics did not reveal any confounding effects among independent variables. Based on a parametric bootstrap approach, the estimated *c*-hat value of the global site-occupancy model was close to 1 and did not suggest overdispersion or lack of fit (Burnham and Anderson 2002; MacKenzie and Bailey 2004). We ranked each site-occupancy model based on the second-order Akaike information criterion ($AIC_c$) and we computed $\Delta AIC_c$ and Akaike weights to determine the strength of evidence for each model (Burnham and Anderson 2002). We then performed model averaging to obtain estimates and associated standard errors for each parameter of interest (Burnham and Anderson 2002). We estimated occupancy and detection in CT and control sites using the delta method, accounting for all candidate models (Williams et al. 2002). We determined standard errors on these estimates using model averaging. Finally, we compared vegetation parameters between CT and control sites using *t* tests.

For each bird followed by radiotelemetry, we defined availability as the area contained within the home range and an area in its immediate surroundings. To do this, we first delineated the home range of each animal based on the minimum convex polygon method using 95% of locations (Kenward 2001). We then determined an area equivalent to the radius of the average home range of all of the birds as determined by radiotelemetry (269 m radius for a mean home range of 22.7 ha) around each bird's home range. We used ecoforestry maps to define five habitat types: (1) forest ≥30 years old, (2) regenerating forest from 10 to 30 years old, (3) wetlands (including alder swamps), (4) CTs, and (5) clearcuts (<10 years old). We determined proportion of habitat types within defined availability using ArcGIS 9.1 (Environmental Systems Research Institute 2005). Although the compositional analysis proposed by Aebischer et al. (1993) has been used widely in habitat selection studies, we did not use this technique because our data set included habitat categories with low use. In fact, the application of this technique can result in misclassified errors when available habitat categories that have gone unused by all animals (zero in use) are included in the resource selection analysis (Thomas and Taylor 2006; Bingham et al. 2007). We therefore compared the proportion of bird locations in each habitat type (use) with the proportion of habitats defined as available with a Friedman test following Alldredge and Ratti (1992). In such cases, the hypothesis tested by the Friedman method is that the ranks of the differences in use and availability are the same for all habitats. We then used nonparametric Tukey comparisons (Zar 1984) to determine which habitats were different in terms of selection versus availability. As our treated and control sites differed in size and shape, we preferred such a classification-based approach over distance-based analyses of habitat use (Dussault et al. 2005). Finally, we compared home range size between adults and yearlings with a *t* test.

**Table 1.** Detection histories of spruce grouse (*Falcipennis canadensis*) (presence (1) or absence (0) of spruce grouse on three consecutive visits) in commercial thinning (CT) and control sites in Abitibi, Quebec, Canada, spring 2006.

| | No. of sites | |
|---|---|---|
| Detection histories | CT | Controls |
| 0–0–0 | 44 | 28 |
| 1–0–0 | 3 | 6 |
| 0–1–0 | 1 | 5 |
| 1–1–0 | 1 | 2 |
| 0–0–1 | 1 | 1 |
| 0–1–1 | 0 | 1 |
| 1–1–1 | 0 | 1 |
| Total | 50 | 44 |

## Results

### Occupancy and vegetation characteristics

We detected spruce grouse in 23.4% of the 94 sites, resulting in uncorrected estimates of site use of 36% for controls and only 12% for CT (see Table 1 for complete detection histories per treatment). Mean number of males per 10 stations based on three visits was also almost three times higher in controls (1.44 ± 0.12, mean ± SE) than in CT (0.53 ± 0.04). All models containing treatment in detection or occupancy had a $\Delta AIC_c < 4$ (Table 2). Model averaging revealed that CT had a negative effect on occupancy as well as on detection, but none of the other variables selected a priori had a strong influence on detectability (zero included within a 95% unconditional confidence interval for Julian day and hour of surveys) (Table 3). Site-occupancy models, accounting for detectability, suggested that 60.1% ± 19.7% (model-averaged estimate ± 1 unconditional SE) of control sites were used by spruce grouse, with a detection rate of 25.2% ± 8.5%. In CT, models suggested that 38.9% ± 22.1% of the sites were used, with a detection rate of 16.2% ± 10.4%.

Vegetation parameters observed in CT and control sites are shown in Table 4. In terms of vegetation cover, average lateral cover was 21.1% lower and average vertical cover was 15.8% lower in CT. All measures of cover, exept high vertical cover, were significantly ($P < 0.004$ after Bonferroni correction) lower in CT compared with the controls.

### Radiotelemetry

We excluded one grouse due to death by predation, leaving 18 males for analyses. Out of 331 radio-tracked points (minimum of 18 locations per bird to get stable home range estimates, mean ± SD = 18.4 ± 0.6), only two birds were located once within a CT. Home ranges were quite variable between individuals, ranging from 3 to 117 ha, with an average of 22.7 ha for the 18 birds. The home range of the 9 yearlings (mean ± SD = 30.9 ± 35.7 ha) was twice as large ($P < 0.05$) as that of the nine adults (16.1 ± 16.8 ha).

Available habitat types in these home ranges and their buffer zones were composed, on average, of 10% clearcuts <10 years old, 27% mature forest, 12% regenerating forest, 28% wetlands, and 24% CT. The Friedman analysis re-

**Table 2.** Occupancy models of spruce grouse (*Falcipennis canadensis*) accounting for detectability in commercial thinning (CT) and control sites in Abitibi, Quebec, Canada, spring 2006.

| Model | Rank | No. of parameters | $\Delta AIC_c$ | Akaike weight |
|---|---|---|---|---|
| $\psi$(treat), $p(\cdot)$ | 1 | 3 | 0.00 | 0.4472 |
| $\psi(\cdot)$, $p$(treat) | 2 | 3 | 0.03 | 0.4410 |
| $\psi$(treat), $p$(Julian + Julian$^2$ + hour + treat) | 3 | 7 | 3.79 | 0.0671 |
| $\psi(\cdot)$, $p(\cdot)$ | 4 | 2 | 5.78 | 0.0248 |
| $\psi(\cdot)$, $p$(Julian + Julian$^2$ + hour) | 5 | 5 | 6.22 | 0.0200 |

**Note:** $\psi$, probability of occupancy; $p$, probability of detection; treat, dummy variable for CT (1) or control (0) sites; Julian, Julian day of the survey; hour, hour of the survey. All continuous variables were standardized by subtracting the mean from each value and dividing by the standard deviation.

**Table 3.** Model-averaged estimates for parameters of the site-occupancy models of spruce grouse (*Falcipennis canadensis*) in commercial thinning (CT) and control sites in Abitibi, Quebec, Canada, spring 2006.

| | | | | 95% confidence interval | |
|---|---|---|---|---|---|
| Parameter | Probability of occupancy or detection | Estimate | SE | Upper | Lower |
| Treatment | Detection | –1.32 | 0.64 | –0.06 | –2.58 |
| Julian day$^2$ | Detection | –1.36 | 3.89 | 6.27 | –8.98 |
| Hour | Detection | 0.16 | 0.29 | 0.74 | –0.41 |
| Treatment | Occupancy | –1.86 | 0.95 | –0.01 | –3.72 |

**Table 4.** Vegetation comparison between commercial thinning (CT) ($n$ = 50) and control sites ($n$ = 44), Abitibi, Quebec, Canada, 2006.

| | CT | | Control | | | | |
|---|---|---|---|---|---|---|---|
| Criterion | Estimate (%) | SD (%) | Estimate (%) | SD (%) | Mean difference (%) | SE of difference (%) | *P* |
| Proportion of black spruce | 73.6 | 15.8 | 80.6 | 13.9 | –7.1 | 3.1 | 0.025 |
| Proportion of jack pine | 15.4 | 13.2 | 6.8 | 11.2 | 8.6 | 2.5 | **0.001** |
| Proportion of snags | 6.8 | 6.6 | 10.1 | 9.3 | –3.3 | 1.7 | 0.047 |
| Basal area (m$^2$/ha) | 37.3 | 8.1 | 41.3 | 11.2 | –4.0 | 2.0 | 0.048 |
| Average vertical cover | 48.9 | 12.8 | 64.7 | 11.6 | –15.8 | 2.5 | **0.000** |
| Vertical cover (1.5–4 m) | 34.3 | 17.6 | 58.6 | 17.0 | –24.3 | 3.6 | **0.000** |
| Vertical cover (4+ m) | 63.4 | 15.5 | 70.7 | 15.3 | –7.3 | 3.2 | 0.024 |
| Average lateral cover | 46.9 | 16.4 | 68.3 | 14.8 | –21.3 | 3.2 | **0.000** |
| Lateral cover (0–50 cm) | 82.0 | 16.8 | 93.8 | 7.3 | –11.8 | 2.7 | **0.000** |
| Lateral cover (50–100 cm) | 47.9 | 21.4 | 68.6 | 18.4 | –20.7 | 4.1 | **0.000** |
| Lateral cover (100–150 cm) | 30.8 | 20.0 | 57.0 | 20.2 | –26.2 | 4.2 | **0.000** |
| Lateral cover (150–200 cm) | 27.0 | 18.3 | 53.6 | 19.2 | –26.6 | 3.9 | **0.000** |

**Note:** A *t* test was used to compare CT and control sites (df = 92). Bold values indicate significant differences after Bonferonni correction.

vealed a significant difference in selection among the five habitat groups ($\chi^2$ = 33, df = 4, $P < 0.001$). The average ranking of habitats, from most to least selected, was the following: forests >30 years old, regenerating forests, wetlands, CT, and clearcuts. Tukey multiple comparisons indicated two significantly different groups (Fig. 2). We found that regenerating and older forests were significantly more frequently used than wetlands, CT, and clearcuts.

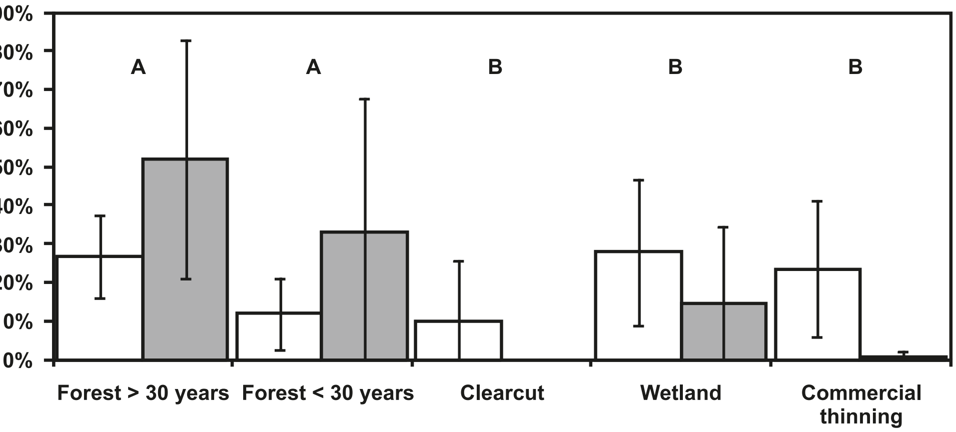
## Discussion

### Site use and vegetation characteristics of sampled sites

Although we expected greater detectability in CT than in control sites given that observers' ability to see is higher in open sites, detection probability was shown to be higher in control sites. However, even if accounting for detectability reducing the gap in the proportion of site use between CT and controls as compared with naïve estimates (from approximately one third to two thirds of control levels), treatment was still shown to have, as expected, a negative effect on site use in spring. Although exact grouse densities are difficult to compare between studies, as different amplifiers may attract individuals within variable radius from surveyed sites, our numbers of males per 10 stations (0.53–1.44 males per 10 stations) was similar or greater than those obtained by Potvin and Courtois (2006) in similar untreated spruce stands (0.23–1.04 males per 10 stations).

Regarding other detection parameters, we had not observed any difference in the response linked to Julian day. As we relied on the literature and on a prefield session in 2005 to determine the ideal survey period, our field season might have been too short to perceive a decrease in response before and after the period of high activity. Unlike other bird species that are more active during morning (Drapeau et al. 1999), timing of calls (between sunrise and noon) did not seem to have an effect on the response of spruce grouse.

**Fig. 2.** Percentage of available habitats (open bars) and used habitats (shaded bars) for 18 adult male spruce grouse (*Falcipennis canadensis*) followed by radiotelemetry, Abitibi, Quebec, Canada, May–July 2006. Error bars refer to standard deviations. There is a significant difference between selected habitats (A) and avoided habitats (B).




This had already been observed by Lemay and Ferron (1987) as well as Schroeder and Boag (1989) but had never been quantified formally.

Timber harvesting during CT generally opens stands due to three factors: first, the creation of harvesting trails every 30 m, second, the partial harvesting per se between trails, and finally, the gathering of trees with machinery, which prunes lateral branches of residual trees. These activities reduce lateral and vertical cover in the stand. Indeed, the four different strata of lateral cover (i.e., 0–50, 51–100, 101–150, and 151–200 cm) were more open in CT (–21% on average). Thus, cover for grouse may be reduced against ground predators that prey mostly on eggs (Boag and Schroeder 1992). Low vertical cover was also lesser in CT as compared with controls, even if some stands were treated from up to 15 years before grouse censuses were conducted, allowing an increase in basal area to a mean that was only –4% as compared with untreated stands. The decrease of lateral cover, combined with the decrease of vertical cover, could increase grouse vulnerability to avian predators. This type of predation can be important for this species; it has been shown to account for 83% of mortality in a stable population of spruce grouse in Ontario (Szuba 1989).

## Radiotelemetry

Mean home range size in our study (22.7 ha) was similar to those generally reported in the literature (<24 ha; Boag and Schroeder 1992) and, more specifically, in research conducted in Quebec (between 13 and 33 ha; Turcotte et al. 2000). A difference in home range size between adults and yearlings was also observed in a previous study (Ellison 1971).

Similar to results shown during spring using site-occupancy analyses, CT sites were also avoided by males during the summer. Although more than one fifth of the area studied with radiotelemetry was treated with CT, spruce grouse rarely used it. Regardless of presence of mature trees in CT, this treatment was comparable, in terms of grouse selection, with areas without mature trees such as clearcuts or wetlands. Like these two environments, CT had low lateral vegetation cover, which might not be appropriate for males during molting when they need dense protection cover to hide from predators (Szuba and Bendell 1982; Lemay et al. 1998). In Quebec, it has been documented that grouse avoid recently clearcut areas and move to nearby residual stands (Turcotte et al. 1994), despite having a high degree of fidelity to their initial territory (Ellison 1975; Turcotte et al. 2000). Our summer results indicated that both CT and clearcuts are equally avoided by male grouse and that they find refuge in surrounding forests >30 years old and in regenerating forests.

A similar scenario might occur during other periods of the year when this species needs denser vegetation cover. Schroeder and Boag (1991) demonstrated that the density of grouse populations proportionally decreases with cover density. Whether it be for nest concealment (Turcotte et al. 1993), for winter confinement (Allan 1985), for molting (Lemay et al. 1998), or during the shift in diet during the fall (Allan 1985; Turcotte et al. 1993), dense habitat is one of the main characteristics selected by spruce grouse. The only documented periods when spruce grouse used more open habitats are during the mating season and raising of the young during which they select areas with speckled alder (*Alnus incana* subsp. *rugosa* (Du Roi) Clausen) and young balsam fir (Turcotte et al. 1993). Because these tree species are not common in stands eligible for CT in Quebec, CTs are less likely to be used during the raising period.

## Conclusions

Because spruce grouse need dense cover during most parts of the year, CT may not be an adequate habitat for this species. As shown in this study, a lower proportion of sites are used in spring and males clearly deserted it in summer, when they needed more cover. In residual forests following clearcuts, CT or similar practices that consist of harvesting one third of the trees are becoming increasingly frequent in Quebec. However, these residual forests, which can be upland forest strips, riparian buffers, or residual forest blocks, are used as refuges by spruce grouse after clearcuts (Turcotte et al. 1994, 2000). Potvin and Courtois (2006) found that these residual forests can maintain spruce grouse populations if they are left untouched until the clearcut area has grown again into suitable habitat. If they are treated as a CT, our results suggest that these residual stands will not be usable by grouse, leaving no habitat refuge to maintain populations after treatment.

Furthermore, our results suggest that CT will also increase the time before a managed stand becomes suitable again for spruce grouse. Indeed, by doing a regular clearcut, it can take as long as 10 (our study) to 30 years until the habitat can be used again by spruce grouse (Potvin and Courtois 2006). With CT (which is usually followed by a clearcut 15 years later), the period without proper habitat for grouse is lengthened by 15 years for a total of 25–45 years. Even if CT may be perceived beneficial for wildlife as compared with clearcuts, our results have shown that it does not fulfill the needs of spruce grouse, especially males. A similar response to CT can be plausible for other species associated with dense habitats, such as shown by Bois (2009) in the same study area for snowshoe hare (*Lepus americanus* Erxleben, 1777). Therefore, we suggest that it should not be employed on a large scale or in residual stands left after clearcut logging in managed areas. From a wildlife perspective, treating premature forest stands with CT and leaving some residual blocks (>20 ha; Potvin and Courtois 2006) with dense habitat for wildlife might be a positive alternative in comparison with large-scale clearcut logging or extensive CT. Partial cutting has been proposed as a promising means to maintain structural attributes of older forests and hence the biodiversity that depends on such attributes (Drapeau et al. 2003; Bergeron et al. 2007). As our results show, to be functional from a biodiversity standpoint, forestry practices such as partial cutting must be adapted to retain more understory protective cover to maintain game species such as spruce grouse.

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## References

Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology, **74**(5): 1313–1325. doi:10.2307/1940062.

Allan, T.A. 1985. Seasonal changes in habitat use by Maine spruce grouse. Can. J. Zool. **63**(12): 2738–2742. doi:10.1139/z85-408.

Alldredge, J.R., and Ratti, J.T. 1992. Further comparison of some statistical techniques for analysis of resource selection. J. Wildl. Manag. **56**(1): 1–9. doi:10.2307/3808785.

Bergeron, Y., Drapeau, P., Gauthier, S., and Lecomte, N. 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For. Chron. **83**(3): 326–337.

Bertrand, N., and Potvin, F. 2003. Caractérisation des habitats fauniques: méthodologie et résultats observés en forêt boréale. Ressources naturelles, faune et parcs, Québec.

Bingham, R.L., Brennan, L.A., and Ballard, B.M. 2007. Misclassified resource selection: compositional analysis and unused habitat. J. Wildl. Manag. **71**(4): 1369–1374. doi:10.2193/2006-072.

Boag, D.A., and Schroeder, M.A. 1992. Spruce grouse. *In* The birds of North America. *Edited by* A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences, Philadelphia, Pa., and The American Ornithologists' Union, Washington, D.C.

Bois, G. 2009. Impacts à moyen et long terme des éclaircies commerciales sur le Lièvre d'Amérique en forêt boréale. M.Sc. thesis, Université du Québec en Abitibi–Témiscamingue.

Burnham, K., and Anderson, D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Drapeau, P., Leduc, A., and McNeil, R. 1999. Refining the use of point counts at the scale of individual points in studies of bird–habitat relationships. J. Avian Biol. **30**(4): 367–382. doi:10.2307/3677009.

Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S., and Savard, J.-P. 2003. Les communautés d'oiseaux des vieilles forêts de la pessière à mousses de la ceinture d'argile: problèmes et solutions face à l'aménagement forestier. For. Chron. **79**(3): 531–540.

Dussault, C., Courtois, R., and Ferron, J. 1998. Impact à court terme d'une coupe avec protection de la régénération sur la gélinotte huppée (*Bonasa umbellus*) en forêt boréale. Can. J. For. Res. **28**(3): 468–477. doi:10.1139/cjfr-28-3-468.

Dussault, C., Courtois, R., Huot, J., and Ouellet, J.-P. 2001. The use of forest maps for the description of wildlife habitats: limits and recommendations. Can. J. For. Res. **31**(7): 1227–1234. doi:10.1139/cjfr-31-7-1227.

Dussault, C., Ouellet, J.-P., and Courtois, R. 2005. A comparison of distance-based and classification-based analyses of habitat use: comment. Ecology, **86**(11): 3119–3125. doi:10.1890/05-0203.

Ellison, L.N. 1971. Territoriality in Alaskan spruce grouse. Auk, **88**(3): 652–664.

Ellison, L.N. 1975. Density of Alaskan spruce grouse before and after a fire. J. Wildl. Manag. **39**(3): 468–471. doi:10.2307/3800385.

Environmental Systems Research Institute. 2005. ArcGIS 9.1. Environmental Systems Research Institute, Redlands, Calif.

Ferron, J., Potvin, F., and Dussault, C. 1998. Short-term effects of logging on snowshoe hares in the boreal forest. Can. J. For. Res. **28**(9): 1335–1343. doi:10.1139/cjfr-28-9-1335.

Huggard, D.J. 2003. Use of habitat features, edges and harvest treatments by spruce grouse in subalpine forest. For. Ecol. Manag. **175**(1–3): 531–544. doi:10.1016/S0378-1127(02)00212-8.

Kenward, R.E. 2001. A manual for wildlife radio tagging. Academic Press, London, U.K.

Lemay, Y., and Ferron, J. 1987. Évaluation d'une technique de recensement pour le Tétras des savanes (*Dendragapus canadensis*) et proposition d'une méthode de mesure de l'expansion de la population introduite sur l'île d'Anticosti. Ministère du loisir, de la chasse et de la pêche, Québec.

Lemay, Y., Ferron, J., Ouellet, J.-P., and Couture, R. 1998. Habitat selection and nesting success of a spruce grouse population (*Falcipennis canadensis*) introduced on Anticosti Island (Quebec). Can. Field-Nat. **112**(2): 267–275.

Létourneau, J.P. 1999. Norme de cartographie écoforestière —

Confection et mise à jour — Troisième programme de la connaissance de la ressource forestière. Direction des inventaires forestiers, Forêt Québec, Ministère des Ressources naturelles, Québec.

MacKenzie, D.I., and Bailey, L.L. 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. **9**(3): 300–318. doi:10.1198/108571104X3361.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., and Franklin, A.B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology, **84**(8): 2200–2207. doi:10.1890/02-3090.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2006. Occupancy estimation and modeling — inferring patterns and dynamics of species occurrence. Academic Press, New York.

Ministère des Ressources naturelles et de la Faune. 2005. Ressources et industries forestières: portrait statistique. Direction du développement de l'industrie des produits forestiers, Québec.

Ministère des Ressources naturelles, de la Faune et des Parcs. 2003. Manuel d'aménagement forestier. Ministère des Ressources naturelles, de la Faune et des Parcs, Québec.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. **5**(3): 113–117.

Potvin, F., and Courtois, R. 2006. Incidence of spruce grouse in residual forest strips within large clearcut boreal forest landscapes. Northeast. Nat. **13**(4): 507–520. doi:10.1656/1092-6194(2006)13[507:IOSGIR]2.0.CO;2.

Potvin, F., Bélanger, L., and Lowell, K. 1999. The validity of forest maps for the description of wildlife habitats on the local level — a case study in the Abitibi–Temiscamingue region. For. Chron. **75**(5): 851–859.

Schroeder, M.A., and Boag, D.A. 1989. Evaluation of a density index for territorial male spruce grouse. J. Wildl. Manag. **53**(2): 475–478. doi:10.2307/3801152.

Schroeder, M.A., and Boag, D.A. 1991. Spruce grouse populations in successional lodgepole pine. Ornis Scand. **22**(3): 186–191. doi:10.2307/3676588.

Szuba, K.J. 1989. Comparative population dynamics of Hudsonian spruce grouse in Ontario. Ph.D. thesis, University of Toronto, Toronto, Ont.

Szuba, K.J., and Bendell, J.F. 1982. Population densities and habitats of spruce grouse in Ontario. *In* Resources and dynamics of the boreal forest. *Edited by* R.W. Wein, R.R. Riewe, and I.R. Methuen. Association of Canadian Universities for Northern Studies, Ottawa, Ont. pp. 199–213.

Szuba, K.J., Bendell, J.F., and Naylor, B.J. 1987. Age determination of Hudsonian spruce grouse using primary feathers. Wildl. Soc. Bull. **15**(4): 539–543.

Thibault, M., and Hotte, D. 1985. Les régions écologiques du Québec méridional. Ministère de l'Énergie et des Ressources du Québec, Direction de la recherche et du développement, Québec.

Thomas, D.L., and Taylor, E.J. 2006. Study designs and tests for comparing resource use and availability II. J. Wildl. Manag. **70**(2): 324–336. doi:10.2193/0022-541X(2006)70[324:SDATFC]2.0.CO;2.

Turcotte, F., Couture, R., Ferron, J., and Courtois, R. 1993. Caractérisation des habitats essentiels du Tétras du Canada (*Dendragapus canadensis*) dans la région de l'Abitibi–Témiscamingue. Ministère de l'Environnement et de la Faune, Direction de la faune et des habitats, Service de la faune terrestre, Québec.

Turcotte, F., Couture, R., Courtois, R., and Ferron, J. 1994. Réactions du Tétras du Canada (*Dendragapus canadensis*) face à l'exploitation forestière en forêt boréale. Ministère de l'Environnement et de la Faune, Direction de la faune et des habitats, Service de la faune terrestre, Québec.

Turcotte, F., Courtois, R., Couture, R., and Ferron, J. 2000. Impact à court terme de l'exploitation forestière sur le Tétras du Canada (*Falcipennis canadensis*). Can. J. For. Res. **30**(2): 202–210. doi:10.1139/cjfr-30-2-202.

Vanderwel, M.C., Mills, S.C., and Malcolm, J.R. 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. For. Chron. **85**(1): 91–104.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press, New York.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

Zwickel, F.C., and Bendell, J.F. 1967. A snare for capturing blue grouse. J. Wildl. Manag. **31**(1): 202–204. doi:10.2307/3798382.