Habitat selection of American marten in a logged landscape at the southern fringe of the boreal forest[1]

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Abstract: American marten (*Martes americana*), a species sensitive to intensive logging, is often associated with old-growth coniferous forest. Recent results, however, question the specificity of this association. We studied habitat selection of marten at the southern fringe of the boreal forest, in mixed forest types. The presence of a white-tailed deer (*Odocoileus virginianus*) wintering area protected part of the study area from large-scale intensive logging [clear-cuts with protection of regeneration and soils (CPRS) and precommercial thinning (PCT)] but not from partial logging of mature coniferous stands. We radio-tracked 15 marten over 2 y and analyzed habitat selection at 2 scales: landscape and home range. Marten selected mature (> 60 y) coniferous forests at both scales, while they neither selected nor avoided Mature mixed forests. PCT forests (0–15 y old) were strongly avoided at the landscape scale ($P < 0.001$), as were Young forests (21–60 y old; $P = 0.005$). At the home range scale, marten avoided CPRS (0–20 y old; $P < 0.001$). Partial logging had no effect on selection at either scale. Female home ranges were smaller in the partially logged sector of the study area (2.6 ± 0.6 *versus* 7.4 ± 0.2 km^2), while male home range averaged 5.5 ± 1.0 km^2, resulting in a significant interaction between location of home ranges in the white-tailed deer wintering area and sex of individuals ($F_{1, 11} = 5.618$, $P = 0.037$). Also, home ranges tended to be larger as the road density and proportion of light outbreak cover type increased. Our results showed that partial logging, CPRS, and PCT have different impacts on marten habitat selection and use of space. We conclude that partial logging rather than clear-cuts and precommercial thinning should be favored for conservation of American marten.

Keywords: American marten, clear-cuts, habitat selection, partial logging, precommercial thinning, Quebec.

Résumé : La martre d'Amérique (*Martes americana*), une espèce considérée comme sensible à l'exploitation forestière, est généralement associée aux forêts matures conifériennes de la forêt boréale. Par contre, des résultats récents ont remis en cause la spécificité de cette association. Ainsi, nous avons étudié la sélection de l'habitat chez la martre dans la frange sud-est de la forêt boréale, où le couvert forestier mixte est très présent. La présence d'une aire d'hivernage de cerfs de Virginie (*Odocoileus virginianus*) protégeait une partie de l'aire d'étude d'une exploitation forestière intensive [coupes avec protection de la régénération et des sols (CPRS) et éclaircies précommerciales (PCT)] en faveur de coupes partielles dans des forêts de conifères matures. Nous avons suivi 15 individus pendant 2 ans et analysé leur sélection d'habitats à 2 échelles : le paysage et le domaine vital. Les forêts matures (> 60 ans) de conifères étaient sélectionnées aux 2 échelles alors que les forêts mixtes ou décidues étaient ni évitées, ni sélectionnées. Les PCT étaient fortement évitées (0–15 ans; $P < 0,001$) à l'échelle du paysage, tout comme les jeunes forêts (21–60 ans; $P = 0,005$). Les martres évitaient les CPRS à l'intérieur du domaine vital (0–20 ans; $P < 0,001$). Les coupes partielles n'ont eu aucun effet sur la sélection. Les domaines vitaux des femelles étaient plus petits dans le secteur de l'aire d'étude où la coupe partielle est pratiquée ($2,6 \pm 0,6$ *versus* $7,4 \pm 0,2$ km^2) alors que les domaines vitaux des males étaient stables à $5,5 \pm 1,0$ km^2 ce qui créait une interaction entre le sexe des individus et la localisation des domaines vitaux dans l'aire d'hivernage de cerfs de Virginie ($F_{1, 11} = 5,618$, $P = 0,037$). La taille des domaines vitaux avait par contre tendance à augmenter avec la proportion de l'habitat ayant subi une épidémie légère et la densité des routes. Nos résultats démontrent que les coupes partielles, les CPRS et les PCT ont des impacts différents et que pour conserver la martre d'Amérique, les coupes partielles devraient être favorisées par rapport aux CPRS et aux éclaircies précommerciales.

Mots-clés : coupes partielles, coupes totales, éclaircies précommerciales, martre d'Amérique, Québec, sélection de l'habitat.

Nomenclature: Godfrey, 1986; Flora of North America Editorial Committee, 1993; Wilson & Reeder, 1993.

Introduction

Forests in eastern North America underwent major changes in the 20th century due to human population growth, urbanization, and industrialization. Intensive logging during this period resulted in an extensive decrease in coniferous cover, which was replaced by mixed or deciduous forests (Fuller *et al.,* 1998; Boucher, Arseneault & Sirois, 2006). Furthermore, a recent parliamentary commission in Quebec concluded that large parts of the province's forests have been over-harvested, which has led to an increase in early and mid-successional forests (Coulombe *et al.,* 2004). Intensive logging may thus be detrimental to species that are closely associated with mature forests.

Studies on American marten (*Martes americana*) have reported a preference for mature coniferous forests over young or regenerating forests (Thompson, 1988; Thompson

& Harestad, 1994; Sturtevant, Bissonette & Long, 1996). This relationship led to the suggestion that marten be used as a key species in boreal forest management of eastern Canada (Thompson, 1991), and marten presence is now considered an indicator of forest health in many jurisdictions (Bull, Holthausen & Bright, 1992; Buskirk, 1992; Watt *et al.*, 1996). Current management plans for marten involve maintaining large tracts of mature coniferous forest (Bissonette, Fredrickson & Tucker, 1989; Thompson & Harestad, 1994; Watt *et al.*, 1996). Studies conducted in Maine (Chapin, Harrison & Phillips, 1997; Payer & Harrison, 2003) and western Quebec (Potvin, Bélanger & Lowell, 2000), however, question the view of an apparently tight relationship between marten and mature coniferous forest. These doubts are also supported by the long-term observation of a marten population at constant densities and small home ranges in a mostly deciduous forest in British Columbia (Poole *et al.*, 2004; Porter, St. Clair & De Vries, 2005).

Studies on the effects of forest harvesting on populations of American marten have mostly focused on clear-cut logged areas. Marten were found to avoid clear-cut forests (Thompson & Colgan, 1987; Thompson, 1994; Potvin, Bélanger & Lowell, 2000) possibly because clear-cuts reduce habitat connectivity, canopy cover, and coarse woody debris (CWD; Potvin, 1998) and can affect small mammal species populations (Payer & Harrison, 2000; Payer & Harrison, 2003; Etcheverry, Ouellet & Crête, 2005). In Ontario, population densities were shown to remain low even 40 y after clear-cutting (Thompson, 1988), although second-growth forests supported marten populations (Bowman & Robitaille, 1997). In 1996, the province of Quebec abandoned traditional clear-cutting in favour of timber harvesting with protection of advanced regeneration and soils (CPRS clear-cuts). While this method maintains regenerative growth, it opens up the canopy and increases light levels in the ground and shrub layers (Etcheverry, Ouellet & Crête, 2005), which may limit marten populations (Thompson & Harestad, 1994; Potvin, Bélanger & Lowell, 2000). Although we currently have a good understanding of the impact of traditional clear-cutting on marten, that is not the case for other forestry practices such as partial logging and precommercial thinning (PCT). Partial logging is generally defined as a reduction in residual basal area over small areas through some form of selective logging (Fuller & Harrison, 2005). Few studies have considered the impact on marten, despite a considerable increase in partial logging throughout various jurisdictions of northeastern North America (Canadian Council of Forest Ministers, 2002; Simard & Fryxell, 2003; Fuller, Harrison & Lachowski, 2004). Despite small sample sizes (≤ 4 marten), 3 early studies suggested that partial logging has little effect on marten habitat use (Major, 1979; Soutière, 1979; Steventon & Major, 1982). Recently, however, it was suggested that the reduction in canopy cover leads marten to avoid partially logged sites in winter (Fuller & Harrison, 2005). PCT is a forestry technique whereby the density of stands of young saplings and small pole-sized timber is reduced to encourage growth of desired tree species and shorten the rotation length for commercial timber production (Smith *et al.*, 1997). No studies have examined the effect of PCT on marten to date. Impacts on small mammals, the prey basis for

marten (Strickland & Douglas, 1999), have recently been described. Generally, the effect of this technique is unclear, since increases (red-backed voles, *Cletherionomys gapperi*: Homyack, Harrison & Krohn, 2005; Sullivan *et al.*, 2005; masked shrew, *Sorex cinereus*: Homyack, Harrison & Krohn, 2005), decreases (Sullivan, Sullivan & Lindgren, 2001; deer mouse, *Peromyscus maniculatus*: Sullivan *et al.*, 2005), and no changes in numbers (deer mouse: Homyack, Harrison & Krohn, 2005; red-backed voles: Sullivan *et al.*, 2002; 2005) have all been observed. In our study area, PCT has a species-specific impact, although the practice generally decreases species richness and overall density of small mammals (Etcheverry, Ouellet & Crête, 2005).

The study of habitat selection leads researchers to examine habitat quality. The home range size of mammals is affected by many factors, including climate (McLoughlin & Ferguson, 2000), prey abundance (Thompson & Colgan, 1987), habitat quality (Thompson & Colgan, 1987; Buskirk & McDonald, 1989; Sturtevant *et al.*, 1997), and body size (Buskirk & McDonald, 1989). Within a marten population, habitat quality and prey availability are the primary factors affecting home range size (Thompson & Colgan, 1987; Buskirk & McDonald, 1989; Smith & Schaefer, 2002). Increase of home range size may therefore serve as an indicator of decreased habitat quality (Buskirk & McDonald, 1989; Poole *et al.*, 2004; Fuller & Harrison, 2005). Furthermore, a reduction of habitat quality has been linked to reduced densities in marten (Latour, Maclean & Poole, 1994; Poole *et al.*, 2004).

We examined habitat selection and space use of American marten in a logged landscape where CPRS clear-cuts, partial logging, and PCT occurred in the transition zone between boreal and mixed forest in eastern Canada. The presence of a wintering area for white-tailed deer (*Odocoileus virginianus*) partially protected the northern part of the study area from CPRS clear-cuts and PCT. Partial logging has been conducted in the study area for more than 20 y, with extensive PCT appearing in the last 15 y. We thus took advantage of the opportunity to study the simultaneous impact of these 3 forestry practices on marten.

We hypothesized that the structure and maturity of forests would influence marten habitat selection and space use. Considering that marten have been observed to thrive in mature deciduous forest (Poole *et al.*, 2004) and that coniferous forests are not selected at similar latitudes in Quebec (Potvin, Bélanger & Lowell, 2000), we predicted that mature forests would be selected, regardless of species composition. Because CPRS and PCT open canopy cover, fragment mature forest habitat, and reduce small mammal richness (Etcheverry, Ouellet & Crête, 2005), we expected plots subjected to these practices to be avoided by marten. Since partial logging can maintain prey densities while reducing cover (Fuller, Harrison & Lachowski, 2004; Fuller & Harrison, 2005), we expected this practice to have less impact on habitat selection than either PCT (Etcheverry, Ouellet & Crête, 2005) or CPRS clear-cutting (Potvin, 1998). Finally, we expected marten to compensate for less suitable habitat by increasing home range size (Buskirk & McDonald, 1989; Poole *et al.*, 2004; Fuller & Harrison, 2005).

Methods

STUDY AREA

We conducted the study in the eastern part of the Duchénier Wildlife Reserve (128.7 km², 48° 11' N, 68° 33' W; Figure 1), located approximately 30 km south of Rimouski, Quebec. The Quebec government suspended fur trapping in the wildlife reserve in 1977 and maintained the moratorium throughout the study area although trapping was allowed in the adjoining western part of the reserve

starting in 2002. The study area has a yearly mean temperature of 3.9 °C, with summer maxima of 22 °C and winter minima around −16 °C (Environnement Canada, 2002). Total yearly precipitation is 915 mm, of which 642 mm is rain. Ground snow generally persists from mid-December until the end of April. Rolling hills along the southern shore of the St. Lawrence River characterize the area. Elevations vary from approximately 200 m to 625 m above sea level.

Mixed forest is typical of the transition zone from coniferous boreal forest to deciduous forest (Marie-Victorin,
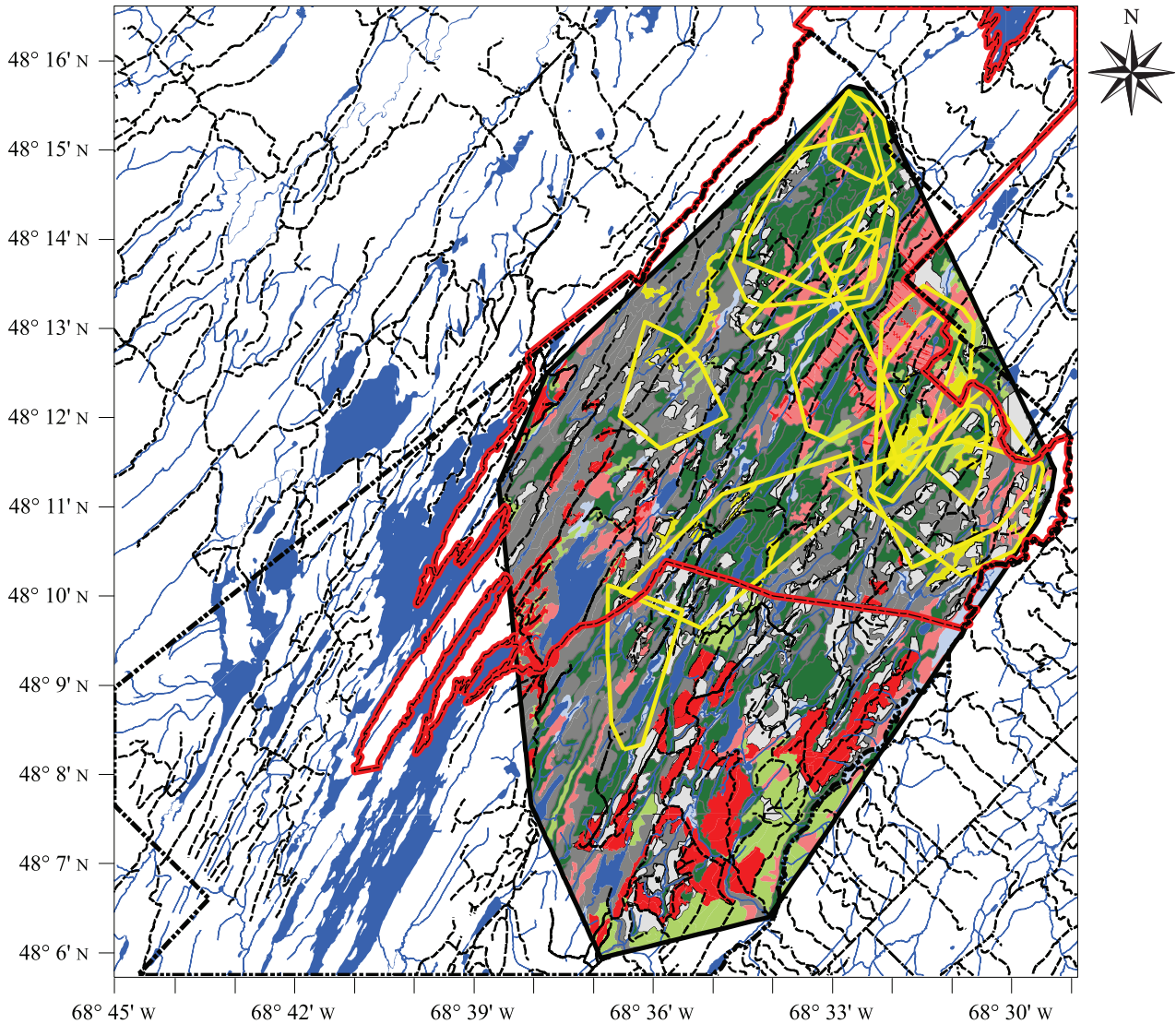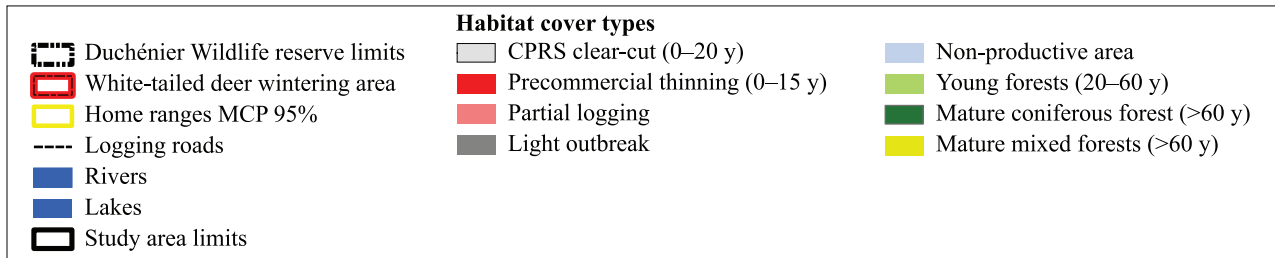

FIGURE 1. Map of study area showing marten (*Martes americana*) home ranges and habitat cover types in the northeastern part of the Duchénier Wildlife Reserve, eastern Quebec, between 2002 and 2004.

1995). Balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), red maple (*Acer rubrum*), and sugar maple (*A. saccharum*) dominate tree cover. Logging companies have harvested timber in a discontinuous manner. In the southwestern part of the study area, logging practices were dominated by CPRS clear-cuts and PCT. In contrast, the northeastern part of the study area (77.3 km^2) was partially protected for white-tailed deer in winter, which forced logging companies to limit activities to partial cuts and smaller-sized CPRS clear-cuts and PCTs.

FIELD PROCEDURES

We captured martens using a variety of Tomahawk traps (#107, #108.5, #109 and #207, Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) over 3 capture sessions: July–November 2002, January–March 2003, and November 2003 – March 2004. We placed traps under forest canopy and protected them from the elements with a cover of litter or snow or by placing them in wooden boxes fixed to trees. Traps were baited with meat, blood, star anise oil, or skunk oil. Once captured, martens were anesthetized with a mixture of ketamine and xylazine and then sexed, weighed, measured, and marked with an individual numbered metallic ear tag. A MI2 Holohil VHF radio-collar was attached, and animals were subsequently located by ground triangulation and direct observation. We attempted to locate each animal every 2 d over summer (mid-June to mid-September) and winter (December to March) during 2002–2003 and 2003–2004. For triangulation, we used a minimum of 3 bearings measured with a magnetic compass and a global positioning system. The Animal Care Committee of the Université du Québec à Rimouski approved handling procedures (CPA14-02-4).

HABITAT SELECTION

To determine the positions of radio-collared martens, we used maximum likelihood ratios estimated with LOAS v2.8 (Ecological Software Solutions, 2003). After projecting locations using ArcView 9.1 and the HRT extension, we modelled individual home ranges using 95% minimum convex polygons (MCPs) and estimated seasonal (summer and winter) and annual (June–March) home range sizes. Because there was little variation in location (> 75% overlap) and size of home ranges between years (overlap: $t_5 = -0.373$, $P = 0.362$; size: $t_5 = -2.135$, $P = 0.086$) and seasons (overlap: $t_{11} = -1.684$, $P = 0.06$; size: $t_{11} = 0.153$, $P = 0.811$), data were pooled to estimate multi-annual home range sizes (Figure 1).

To characterize habitat selected by marten, home ranges were overlaid on forestry maps of the Ministère des Ressources naturelles et de la Faune du Québec that had been drawn in 2000. Maps were updated by adding all logging activities performed from 2000 to 2004. From these updated maps, we described 8 forest cover types (Figure 1), taking into account the forestry map limitations (Potvin, Bélanger & Lowell, 1999; Dussault *et al.,* 2001) and the proportion of cover types actually available in the study area. The final forest cover types were 1) Partial log-

ging, including stands heavily affected by spruce budworm (*Choristoneura fumiferana*) epidemics that were partially harvested; 2) CPRS clear-cuts (≤ 20 y old); 3) PCTs (pre-commercial thinning ≤ 15 y old); 4) Light outbreaks, *i.e.,* unlogged sites lightly affected by spruce budworm epidemics; 5) Young forests (21–60 y old); 6) Mature mixed forests (> 60 y old), including deciduous forests; 7) Mature coniferous forests (> 60 y old), including mixed forests dominated by coniferous cover; and 8) Non-productive areas (water, wetlands, bare areas, etc.).

FOREST COVER CHARACTERIZATION

In the summer of 2003, we characterized the vegetative structure of the various stand types available to marten in the study area and randomly sampled 94 sites. At each sample plot, we first established a 15-m transect originating from the plot centre to estimate canopy closure (%) for both deciduous and coniferous trees (> 4 m). We recorded the presence of foliage at 10 intervals of 1.5 m along the transect and then estimated density of lateral cover (%) at 5 m and 15 m from the plot center in three height strata: 0–49 cm, 50–99 cm, and 100–149 cm. To do so, we used a checkered banner marked off in thirty 10- × 10-cm black and white squares. We also estimated density and basal area of both deciduous and coniferous trees using a plotless method and a factor-2 prism at both ends of the transect (Grosenbaugh, 1952), and we counted the number of items of CWD that intercepted the 15-m transect. To be counted, a fallen log had to be physically sound, > 9 cm in diameter, and in the 2 m directly above the transect.

STATISTICAL ANALYSIS

Radio-tracking data were analyzed for 26 marten. For all individuals, locations were separated by at least 12 h to avoid pseudo-replication (Fedriani, Palomares & Delibes, 1999). Since home range size is generally related to number of locations when using MCPs, we performed a re-sampling of our data using a bootstrapping technique (Animal Movement SA v2.04 beta; Hooge & Eichenlaub, 1997). We found that a plateau was reached after 12 locations for all individuals, so we limited our analyses to individuals that had > 12 locations, yielding home ranges for 15 individuals.

We used multivariate analysis of variance (MANOVA) to examine habitat preference of marten by testing the null hypothesis that there was no difference between the average proportion of habitat type used and the average proportion available (GLM procedure; SAS Institute, 1992; Mosnier *et al.,* 2003). This analysis used a Hotelling's T^2 test, similar to that used by Aebischer, Robertson, and Kenward (1993), but without calculating a ratio, which is controversial in literature (Tangri & Wright, 1993; McClean *et al.,* 1998). Data fulfilled the assumptions of multivariate normality of residuals (Mardia, 1975). We analyzed marten habitat selection at 2 hierarchical levels, using individual marten as the sampling unit to avoid pseudo-replication. First, we compared composition of home ranges to availability of forest cover types in the study area (landscape scale), and then we contrasted forest cover types found at marten locations to home range composition (home range scale).

In an attempt to explain selection patterns, we compared habitat characteristics among forest cover types using ANOVAs and also compared home range size in relation to whether or not the home range was located within the white-tailed deer wintering area, where partial logging was common. Vegetation variables were transformed (using logarithmic, square root, or arcsine transformations) where appropriate. In a few cases where we could not normalize the residuals, we used a non-parametric Kruskal–Wallis test. In all cases, the non-parametric and parametric tests yielded similar results, and we therefore present results of parametric tests. To identify specific differences among forest cover types, *a posteriori* Fisher's LSD tests were performed.

Using recapture data from trapping and resighting data from telemetry, we estimated abundance of marten located within the outer boundaries of the combined annual ranges (Latour, Maclean & Poole, 1994) and trapping area for the 2002–2003 and 2003–2004 sampling session. Jolly–Seber analysis was performed with the MARK 4.3 software using the POPAN formulation, which allows for emigration and immigration of individuals. We converted the abundances into densities by dividing the estimated total abundance by the sampled area. The sampled area was defined by the outermost boundaries of traps and marten locations.

To explore the impact of habitat selection on home range size, we performed linear regressions using the proportion of forest cover types as independent variables. Road density within the home range and weight of individuals were also included. To obtain normality of residuals, data were transformed using appropriate transformations. Since many models were tested using pooled data per individual, we calculated the Bayesian Information Criteria (BIC), as it is less sensitive to small sample sizes ($n = 15$) than other information criteria (Quinn & Keough, 2002). We tested 112 models and selected the model with the smallest BIC. Whenever appropriate, we present means $\pm$ 1 SE.

Results

FOREST COVER CHARACTERIZATION

The 8 forest cover types considered in this study differed in terms of vegetative characteristics (Table I). Canopy closure was generally open ($< 50\%$) in areas affected by logging and in Non-productive areas. Apart from totally open Non-productive areas, CPRS clear-cut was the most open forest type, with 14.6% canopy closure, mostly deciduous. PCTs provided some coniferous cover, but were generally open (26% closure). Of the 3 logging practices, Partial logging had the highest canopy closure (40%), which was mostly provided by coniferous trees. All other forest cover types had high levels of canopy closure ($> 55\%$).

CPRS clear-cuts and PCTs resulted in a reduction in tree basal area from 15 to 25 m²·ha⁻¹ in Mature forests to approximately 5 m²·ha⁻¹ (Table I). This was due to a 33–73% reduction in tree density (CPRS: ~120 stems·ha⁻¹; PCT: ~300 stems·ha⁻¹) from Mature forests (~450–650 stems·ha⁻¹). In contrast, mean basal area after partial logging (13.4 m²·ha⁻¹) was not significantly different from that of mature forests. Although partially logged sites showed overall tree density (~300 stems·ha⁻¹) similar to that

of PCT areas, tree density was not significantly less than in mature forests due to increased variance. The reduction in basal area in PCTs was more noticeable in the coniferous than the deciduous layer. Young forests initially showed strong regeneration in deciduous cover, because the basal area of deciduous trees was twice that of coniferous trees and deciduous tree density was 5 times as high as coniferous density. Subsequently, an examination of Mature mixed forests revealed that although this habitat included a great diversity of tree species (*e.g.,* sugar maple and other deciduous species), a considerable proportion of both total basal area and tree density was composed of coniferous trees.

CPRS clear-cuts and Mature mixed forests had similar levels of lateral cover at both 5 m (~60 *versus* ~50%) and 15 m (~85 *versus* ~80%, respectively; Table I), but CPRS clear-cuts had higher cover than Mature coniferous forest (25 and 35%, respectively). Partial logging provided lateral cover similar to that of Mature coniferous habitat, being ~15% at close range and only ~45% at 15 m. PCTs provided intermediate cover (~40% at 5 m) when compared to mature forests and the other logging practices. Overall, CPRS clear-cuts, PCTs, and mature mixed habitat provided the highest levels of lateral cover, while Partial logging, Non-productive areas, and Mature coniferous habitat provided the least.

More CWD was found in CPRS clear-cuts and Light outbreaks than in Partially logged sites, Non-productive areas, or Young forests (Table I). Mature forests and PCTs, on the other hand, showed intermediate abundance of CWD.

HABITAT SELECTION AT THE LANDSCAPE SCALE

Habitat use differed significantly from availability at the landscape scale (MANOVA: $F_{7, 8} = 96.06$, $P < 0.001$; Table II), but there was no difference between sexes (MANOVA: $F_{7, 7} = 2.08$, $P = 0.1768$). We therefore pooled data for further analyses, and *post hoc* tests indicated that Mature coniferous forests represented twice the percentage within home ranges as in the study area (49 *versus* 29%). In contrast, the amounts of PCTs (1 *versus* 9%), Non-productive areas (4 *versus* 8%), Young forests (3 *versus* 6%), and Light outbreaks (15 *versus* 24%) found in marten home ranges were significantly lower than in the study area. The other forest cover types (*i.e.,* CPRS clear-cuts, Partially logged sites, and Mature mixed forests) were neither selected nor avoided by marten at this scale.

All home ranges were either enclosed within or overlapping the limits of the white-tailed deer wintering area in the northeast. This led us to compare forest characteristics inside and outside the wintering area. Several significant differences were observed. Mean area of PCTs was 10 times larger outside than inside the wintering area (20.9 $\pm$ 6.3 *versus* 2.1 $\pm$ 0.4 ha, respectively; $F_{1, 178} = 91.866$, $P < 0.001$). Young forests were also 5 times smaller within the wintering area (4.2 $\pm$ 1.0 *versus* 19.9 $\pm$ 6.5 ha outside; $F_{1, 69} = 7.236$, $P = 0.009$). CPRS clear-cuts outside the wintering area varied greatly in size and tended to be larger than inside (13.3 $\pm$ 3.0 *versus* 6.4 $\pm$ 0.3 ha, respectively), but the difference was not significant ($F_{1, 204} = 1.286$, $P = 0.256$). Other forest cover types did not show any significant differences in mean size; however, we noted that the intensive logging operations (*i.e.,* CPRS and PCTs) and Young forests

TABLE I. Vegetative characteristics (mean ± SE) of 8 forest cover types sampled in the summer of 2003 in the Duchénier Wildlife Reserve, eastern Quebec. Forest cover types were clear-cuts with protection of regeneration and soils (CPRS), precommercial thinning (PCT), partial logging (PL), light outbreak (LO), non-productive area (NPA), young forest (YF), mature coniferous forest (CON), and mature mixed forest (MIX). Values followed by different letters refer to forest cover types that were significantly different ($P < 0.05$) for that variable according to ANOVA and Fisher's LSD tests.

Vegetative Variable	Forest cover types								Statistic	P
	Logging practice									
	CPRS (13)[1]	PCT (29)[1]	PL (8)[1]	LO (13)[1]	NPA (5)[1]	YF (4)[1]	CON (14)[1]	MIX (8)[1]		
TREE LAYER										
CANOPY CLOSURE (%)										
Coniferous trees (> 4m)	1.5 ± 1.0 a	13.9 ± 4.9 ab	27.5 ± 11.5 ab	40.8 ± 10.3 b	0.0 ± 0.0 a	7.5 ± 7.5 a	51.4 ± 9.7 c	27.5 ± 10.0 bc	$F_{7, 85} = 5.84$	< 0.001
Deciduous trees (> 4m)	13.1 ± 5.6 a	12.1 ± 4.0 a	12.5 ± 10.0 a	13.9 ± 6.7 a	0.0 ± 0.0 a	65.0 ± 22.6 b	5.7 ± 3.3 a	37.5 ± 13.2 b	$F_{7, 85} = 4.03$	0.001
BASAL AREA ($m^2 \cdot ha^{-1}$)										
Total	3.5 ± 1.3 a	5.8 ± 1.0 ab	13.4 ± 3.7 bc	16.3 ± 3.3 bc	7.4 ± 3.3 ab	10.5 ± 4.3 abc	24.3 ± 4.0 c	15.3 ± 2.2 bc	$F_{7, 83} = 4.05$	0.001
Coniferous	2.2 ± 1.2 bc	3.7 ± 0.9 bc	11.8 ± 3.9 ab	13.2 ± 2.8 ab	7.4 ± 3.3 abc	3.3 ± 1.8 bc	20.9 ± 4.0 a	8.6 ± 2.1 ab	$F_{7, 83} = 5.35$	< 0.001
Deciduous	1.4 ± 0.4 a	2.1 ± 0.6 a	1.6 ± 1.1 a	3.2 ± 1.5 ab	0.0 ± 0.0 a	7.3 ± 3.4 b	3.4 ± 1.7 a	6.6 ± 2.6 b	$F_{7, 83} = 2.45$	0.025
DENSITY ($stems \cdot ha^{-1}$)										
Total	120.6 ± 49.4 a	301.5 ± 47.9 b	291.9 ± 101.6 abc	379.4 ± 76.4 bc	367.5 ± 198.9 abc	363.9 ± 119.9 abc	653.6 ± 116.8 c	445.8 ± 59.0 bc	$F_{7, 83} = 2.77$	0.012
Coniferous	66.5 ± 40.1 a	204.8 ± 40.7 b	267.6 ± 106.1 bc	301.2 ± 62.8 bc	367.5 ± 198.9 abc	57.1 ± 35.7 ab	579.1 ± 113.5 c	259.5 ± 55.3 bc	$F_{7, 83} = 3.63$	0.002
Deciduous	54.1 ± 18.8 ab	96.7 ± 37.2 ab	24.3 ± 15.9 ab	78.3 ± 37.3 ab	0.0 ± 0.0 a	306.8 ± 97.9 c	74.5 ± 38.4 ab	186.3 ± 83.0 bc	$F_{7, 83} = 2.61$	0.017
SHRUB LAYER										
LATERAL COVER IN THE 50- TO 99-CM STRATUM (%)										
At 5 m	61.2 ± 10.0 c	39.6 ± 4.9 b	13.8 ± 10.3 a	57.3 ± 9.9 bc	38.0 ± 23.3 abc	15.0 ± 9.6 ab	23.6 ± 8.0 ab	51.3 ± 10.9 bc	$F_{7, 85} = 3.70$	0.002
At 15 m	86.2 ± 4.4 c	75.5 ± 5.4 c	45.0 ± 13.1 ab	56.5 ± 10.4 bc	40.0 ± 24.5 ab	75.0 ± 21.7 bc	34.3 ± 10.7 a	80.6 ± 12.3 c	$F_{7, 85} = 3.93$	0.001
GROUND LAYER										
Coarse woody debris ($n \cdot 15\ m^{-1}$)	5.5 ± 1.5 b	3.3 ± 0.5 ab	2.0 ± 1.1 a	4.2 ± 0.8 b	1.2 ± 0.7 a	1.0 ± 0.4 a	3.6 ± 0.8 ab	3.3 ± 1.3 ab	$F_{7, 84} = 2.24$	0.038

[1] Sample size.

comprised 11, 4 and 2%, respectively, of the wintering area. These values increased to 19, 16 and 12%, respectively, outside the wintering area. In contrast, the proportion of partial logging was almost twice as high inside the wintering area as outside (11 *versus* 6%).

HABITAT SELECTION AT THE HOME RANGE SCALE

At the home range scale, marten habitat use did not differ significantly between seasons (MANOVA: $F_{7, 21} = 0.98$, $P = 0.470$) and sexes (MANOVA: $F_{7, 7} = 1.11$, $P = 0.445$), so we pooled the data for subsequent analyses. Habitat use differed from availability for 3 forest cover types (MANOVA: $F_{7, 8} = 4.57$, $P = 0.024$; Table III). Marten locations were observed more frequently in Mature coniferous forest than expected based on availability within home ranges (57 *versus* 49%). The proportion of locations in CPRS clear-cuts (4%) was significantly lower than expected based on availability (11%). PCT proportions did not differ significantly, but this forest cover type was rare within home ranges (1%), and significant detection would have been difficult given the sample size. Use of other forest cover types did not differ significantly from availability.

DENSITY AND HOME RANGE SIZE

Population density estimates were 0.145 ± 0.002 individuals·km^{-2} in 2002–2003 and 0.294 ± 0.001 individuals·km^{-2} in 2003–2004.

Mean home range size of marten was 4.4 ± 0.7 km^2 ($n = 15$). Overall, male home ranges (5.5 ± 1.0 km^2, $n = 6$) were not larger than female home ranges (3.4 ± 0.9 km^2, $n = 9$; $F_{1, 13} = 1.920$, $P = 0.189$), possibly due to 2 females that had very large home ranges (11.5 and 15.4 km^2). The other 7 females had home ranges (2.6 ± 0.6 km^2) that were 50% smaller than male home ranges ($F_{1, 11} = 6.496$, $P = 0.027$). Furthermore, there was an interaction between sex and location in relation to the wintering area to explain home range size variation ($F_{1, 11} = 5.618$, $P = 0.037$). Female home ranges enclosed in the white-tailed deer wintering area were roughly one-third the size of those overlapping the outer limits of the wintering area (2.6 ± 0.6 *versus* 7.4 ± 0.2 km^2, respectively), while male home range size did not vary (5.1 ± 1.0 *versus* 8.4 ± 2.9 km^2).

We examined the relationships between home range sizes, body mass, road density, and proportion of forest cover types. We tested 111 models using linear regressions.

Most models included some form of disturbance, human or natural, to explain increase in home range size. The road density (ROADDENS; $\rho = 0.374$, $P = 0.191$; Figure 2a) and the proportion of Light outbreaks (PLO; $\rho = 0.416$, $P = 0.123$; Figure 2a) best explained the distribution of home range sizes (BIC = 57.378; Equation [1]). The relationship ($F_{2, 14} = 3.13$, $P = 0.081$), although non-significant, explained 34% of the variation in home range size.

$$\text{Home range size}^{0.5} = 6.780 + 0.455 \cdot \text{ROADDENS} + 14.336 \cdot \text{PLO}^{0.5} \qquad [1]$$

Road density was strongly correlated with the proportion of human disturbances (sum of PCT, CPRS, and Partial logging; $\rho = 0.793$, $P < 0.001$; Figure 2b). On the other hand, PLO was strongly correlated with the proportion of CPRS ($\rho = 0.739$, $P = 0.002$; Figure 2b) and negatively correlated with the proportion of Mature coniferous cover ($\rho = -0.817$, $P < 0.001$; Figure 2b).

Discussion

In accordance with recent results (Smith & Schaefer, 2002; Poole *et al.,* 2004; Gosse, Cox & Avery, 2005), we

TABLE II. Landscape-scale proportional habitat availability and use (mean ± SE) of 8 forest cover types by 15 marten in the Duchénier Wildlife Reserve, eastern Quebec, between 2002 and 2004.

Forest cover type	Use	Availability	t	P
CPRS clear-cut (0–20 y)	0.110 ± 0.076	0.141	–1.59	0.133
PCT (0–15 y)	0.010 ± 0.021	0.086	–14.31	< 0.001
Partial logging	0.132 ± 0.113	0.087	1.54	0.145
Light outbreak	0.148 ± 0.164	0.244	–2.26	0.040
Non-productive area	0.043 ± 0.037	0.075	–3.40	0.004
Young forest (21–60 y)	0.028 ± 0.037	0.061	–3.49	0.004
Mature coniferous forest (> 60 y)	0.487 ± 0.227	0.285	3.44	0.004
Mature mixed forest (> 60 y)	0.044 ± 0.056	0.021	1.53	0.147

TABLE III. Home range–scale proportional habitat availability and use (mean ± SE) of 8 forest cover types by 15 marten in the Duchénier Wildlife Reserve, eastern Quebec, between 2002 and 2004.

| Forest cover type	Use	Availability	t	P
CPRS clear-cut (0–20 y)	0.037 ± 0.039	0.110 ± 0.076	–4.46	< 0.001
PCT (0–15 y)	0.009 ± 0.020	0.010 ± 0.021	–0.82	0.429
Partial logging	0.121 ± 0.113	0.132 ± 0.113	–0.40	0.694
Light outbreak	0.166 ± 0.175	0.148 ± 0.164	0.66	0.521
Non-productive area	0.026 ± 0.040	0.043 ± 0.037	–1.59	0.134
Young forest (21–60 y)	0.041 ± 0.086	0.028 ± 0.037	0.64	0.531
Mature coniferous forest (> 60 y)	0.573 ± 0.237	0.487 ± 0.227	2.34	0.034
Mature mixed forest (> 60 y)	0.028 ± 0.052	0.044 ± 0.056	–1.71	0.110
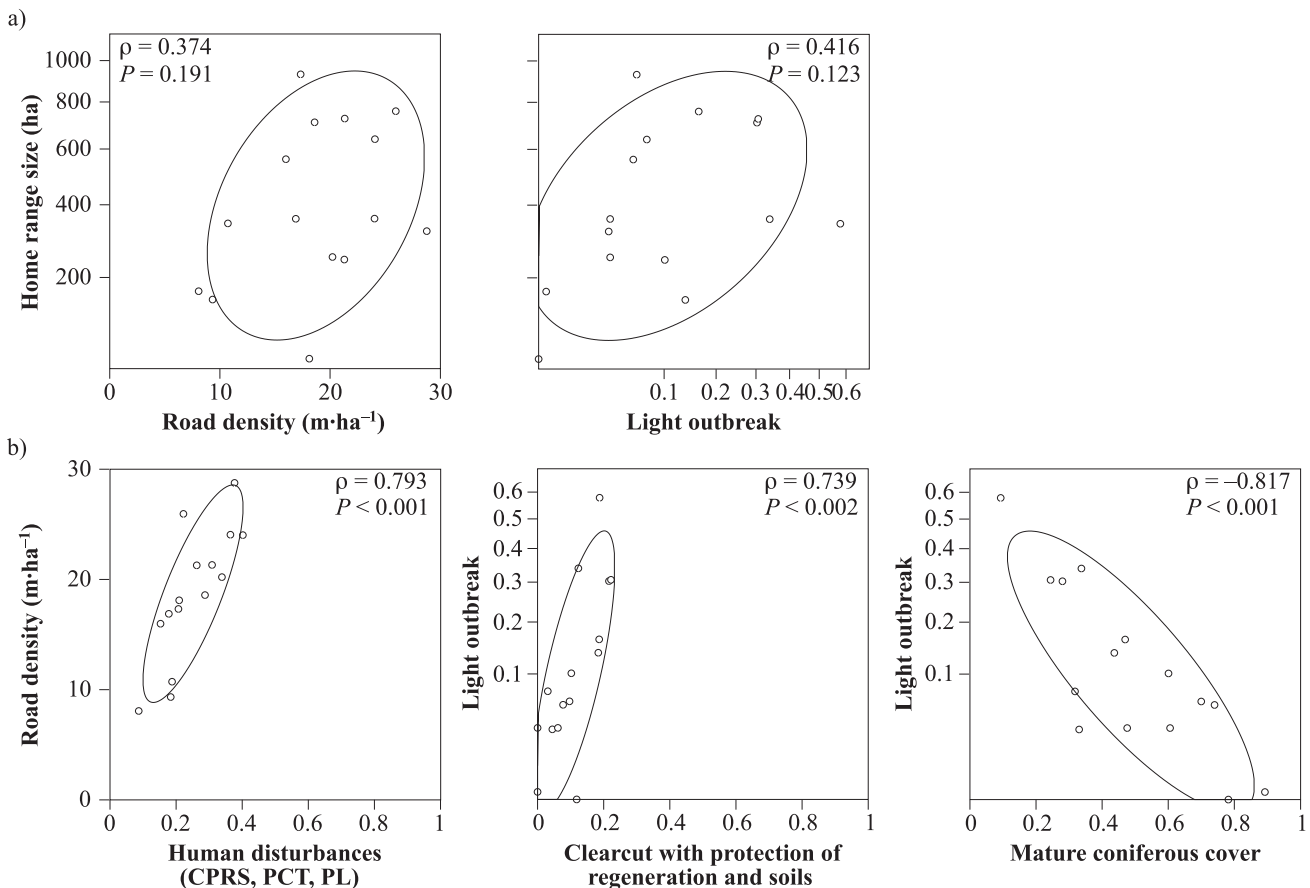
FIGURE 2. Scatterplots of a) home range size of marten in relation with road density and proportion of light outbreak cover and b) collinear variables (proportion of human disturbances, clearcut with protection of regeneration and soils, coniferous cover aged more than 60 y) in the Duchénier Wildlife reserve, eastern Quebec, between 2002 and 2004.

hypothesized that forest maturity and structure rather than forest cover type would influence marten habitat use and selection, since coniferous forests are not preferred at similar latitudes (Potvin, Bélanger & Lowell, 2000). We also predicted that selection for CPRS clear-cuts, PCTs, and partial logging would differ since the 3 logging practices do not affect forest structure in the same manner (Potvin, 1998; Payer & Harrison, 2003; Fuller & Harrison, 2005). Finally, we predicted that marten would compensate for the presence of logging by increasing home range sizes. Contrary to our first prediction, composition of tree cover did have an impact on habitat selection because marten established home ranges in areas dominated by old coniferous cover. As for effects of logging, proportions of regenerating forests (PCTs, Light outbreaks, and Young forests) and Non-productive areas in home ranges were significantly lower than at the landscape scale, which may indicate avoidance. Furthermore, we observed that home ranges were concentrated inside or adjacent to a white-tailed deer wintering area where logging interventions, particularly PCTs and Young forests, were less extensive. CPRS clear-cuts represented a relatively small proportion of the wintering area since partial logging was favoured there. As a result, PCTs were almost totally absent within individual home ranges. In contrast, CPRS clear-cut proportions were significantly lower than expected at the home range scale. Meanwhile, Partial logging had no effect on selection, a result that concurred with our second hypothesis. Home ranges that were located within the white-tailed deer wintering area (*i.e.,* where partial logging was the main harvesting technique) were smaller than those that extended beyond its limits. In addition, home range size tended to increase directly with road density and proportion of Light outbreak cover. These were in turn strongly correlated with the proportions of human disturbances. Both of these results supported the third prediction, which stated that an increase in low-quality habitat would force marten to increase home range size.

COVER TYPE SELECTION

Marten exhibited a habitat selection pattern in the study area that supported previous findings on habitat requirements for this species (*e.g.,* Thompson, 1994; Gosse, Cox & Avery, 2005). However, contrary to results from Maine (Chapin, Harrison & Phillips, 1997; Payer & Harrison, 2003) and western Quebec (Potvin, Bélanger & Lowell, 2000), marten actively selected Mature coniferous forests. Reasons that could explain selection for this forest type vary. The high amount of canopy closure may provide protection from avian predation (Hargis & McCullough, 1984; Thompson, 1994), which was suspected in at least one observed mortality over the course of the study. Increased tree density may provide arboreal escape from terrestrial predators (Storch, Lindstrom & Dejounge, 1990; Strickland & Douglas, 1999). Also, as coniferous forests age, they accumulate CWD (Sturtevant *et al.,* 1997), a structural element that appears to influence habitat quality for marten. CWD is used for resting and hunting (Steventon & Major, 1982), provides subnivean access for thermoregulation during winter (Buskirk *et al.,* 1989; Wilbert, Buskirk & Gerow, 2000), and is associated with high prey abundance

(Sherburne & Bissonette, 1994; Gosse, Cox & Avery, 2005). However, these 3 landscape elements can also be found in other cover types, as was observed in mixed forests of Maine (Payer & Harrison, 2003) and western Quebec (Potvin, Bélanger & Lowell, 2000) and regenerating deciduous forests of British Columbia (Poole *et al.,* 2004). Vertical and horizontal structure may thus be more important than overstory species composition for habitat selection in marten (*e.g.,* Smith & Schaefer, 2002; Poole *et al.,* 2004).

In our case, Mature coniferous and Mixed forests, although similar in some aspects, showed subtle but important differences. Mean canopy cover of coniferous forests was well above the 30% threshold reported in the literature for marten (Bowman & Robitaille, 1997; Potvin, Bélanger & Lowell, 2000; Smith & Schaefer, 2002). Although this variable was not significantly different in mixed forests, the cover was mostly composed of deciduous trees that shed their leaves in winter, opening up the canopy. Mean basal area in coniferous stands was also greater than the required threshold reported for marten (24 m^2·ha^{-1} > 18 m^2·ha^{-1}; Payer & Harrison, 2003). Basal area was lower in mixed compared to coniferous forests. Mean tree density in Mature coniferous stands was also the highest of those forest covers considered in this study, while tree density in Mature mixed stands was average. Canopy closure, basal area and tree density in the coniferous stands appeared to provide marten with the vertical structure necessary for predator protection (Strickland & Douglas, 1999), but they probably did not in mixed stands. In Mature coniferous forest, the amount of CWD was among the highest of all forest cover types, and CWD is positively associated with abundance of certain prey (Etcheverry, Ouellet & Crête, 2005). Mature coniferous forests had intermediate levels of lateral cover, which could provide further protection to marten from avian predators (Potvin, Bélanger & Lowell, 2000). However, dense lateral cover also provides effective escape cover for snowshoe hares (Beaudoin *et al.,* 2004), an important prey item for marten (Bateman, 1986; Strickland & Douglas, 1999), and such may have been the case in Mature mixed forests, where lateral cover tended to be high. Further studies are needed to determine whether marten seek a balance between prey availability and protection from predators.

IMPACT OF LOGGING PRACTICES

We expected CPRS logging and PCTs to have a negative impact on marten habitat selection. The proportion of CPRS clear-cuts was significantly lower at the home range scale, as was PCT cover at the landscape scale. At the home range level, marten appeared to avoid CPRS clear-cuts because of reduced vertical escape habitat (Snyder & Bissonette, 1987; Thompson, 1988; Payer & Harrison, 2000) and increased mortality by predation (Thompson, 1994). Clear-cuts also reduce prey availability through a reduction in CWD (small mammals; Soutière, 1979; Steventon & Major, 1982) or canopy closure and lateral cover (snowshoe hare; Potvin, Courtois & Bélanger, 1999; Beaudoin *et al.,* 2004). In the Duchénier Wildlife Reserve, tree density, basal area, canopy closure, and lateral cover were lower in CPRS clear-cuts compared to Mature coniferous forests, which may have increased mortality risk and

decreased availability of snowshoe hares. While the amount of CWD remained similar in CPRS clear-cuts and Mature coniferous forests, other studies in the same area have shown that overall prey density and richness decreases with clear-cut logging (Etcheverry, Ouellet & Crête, 2005).

PCTs reduced forest complexity by reopening the canopy and reducing lateral cover, tree density, and CWD, while decreasing forest maturity time (Homyack, Harrison & Krohn, 2004). This has led to the suggestion that PCT may favour animal species associated with simple forest systems, which is not the case for marten. Furthermore, although the effects of PCTs on marten prey are somewhat unclear (Sullivan, Sullivan & Lindgren, 2001; Homyack, Harrison & Krohn, 2005; Sullivan *et al.,* 2005), PCTs can decrease prey richness and overall density, especially that of red-backed voles (*Clethrionomys gapperi*) and northern short-tailed shrews (*Blarina brevicauda*; Etcheverry, Ouellet & Crête, 2005). It is difficult to summarize the impact of PCTs on marten habitat selection since the extensive use of PCTs is recent and many authors did not identify this forest cover type in their studies. Our results tend to support the view that PCT does not create favourable habitat for marten because we observed strong avoidance at the landscape level and less than 1% of marten home ranges were composed of PCTs.

Despite small sample sizes, early studies in Maine indicated that marten did not reduce forest use after partial logging (Soutière, 1979; Steventon & Major, 1982). An avoidance in winter was recently observed, apparently due to reduced hare density, basal area, and canopy closure (Fuller & Harrison, 2005). At Duchénier, average basal area and canopy closure following Partial logging were close to the thresholds given above and may therefore have provided sufficient cover for predator evasion. CWD abundance was similar in mature coniferous and partially logged sites, suggesting that prey abundance may also have been maintained with this logging practice. The fact that marten used this type of habitat in proportion to availability also suggests that partial logging had less impact on the marten population than either CPRS clear-cutting or PCT.

Regenerating forests tend to be used by marten if a dense substratum of coniferous regeneration is present to provide protective cover (Potvin, Bélanger & Lowell, 2000). In our study, Young forests showed low to intermediate amounts of lateral cover in the shrub layer (Table I) and the extent of shrub canopy did not differ between forest covers (G. Godbout & J.-P. Ouellet, unpubl. data). Shrubs provided only partial protective cover, which could explain the reduction of Young forest proportion in home ranges, as in the greater study area.

Additional explanation of marten habitat selection may lie in landscape configuration. In agreement with our study, Chapin, Harrison, and Katnik (1998) suggested that 60% of mature forest was required in the landscape for marten to establish and maintain a home range. Large areas of Young forests, PCTs, and CPRS clear-cuts were located outside the white-tailed deer wintering area and together comprised 47% of the southwestern sector. In contrast, Partial logging and small-scale CPRS clear-cuts and PCTs inside the wintering area reduced the amount of Young forests and maintained mature forests. Logged and Young forests together thus comprised less than 20% of the wintering area.

Mean home range sizes in our study area were at the mid to high end of the range reported elsewhere for marten (Buskirk & McDonald, 1989; Poole *et al.,* 2004). Harvested landscapes are known to increase home range sizes (Potvin & Breton, 1997), while logging appears to reduce habitat quality. We located 2 females with extremely large home ranges in a sector that was extensively logged using CPRS and PCT, which supports this hypothesis.

Our results support the view that intensive logging practices have an adverse effect on the marten populations in eastern Quebec, causing increased home ranges and reduction in use of logged habitat. In addition, although the study area has been under a trapping moratorium since 1977, marten density was low (0.24 and 0.43 individuals·km^{-2} in 2002–2003 and 2003–2004, respectively), approximating one tenth of densities reported in Ontario (Thompson & Colgan, 1987) and Maine (Soutière, 1979). However, our densities were similar to those reported in British Columbia (Poole *et al.,* 2004) and the Northwest Territories (Latour, Maclean & Poole, 1994), where marten occur in sub-optimal habitat. Low densities of marten confined to residual mature coniferous forests surrounded by young, clear-cut, or thinned forest suggest that our population followed a typical pattern of habitat selection: large tracts (> 15 ha) of Mature coniferous forests with basal area > 18 m^2·ha^{-1} and < 30% open canopy. Since home ranges established in sectors with a high density of roads, correlated with human disturbance cover types, tended to be larger, we believe that these ranges were located within low-quality habitats. Because partial logging proportions did not differ significantly at either scale, whereas PCTs and CPRS clear-cuts did, partial logging should be favoured over other practices when attempting to preserve marten habitat in harvested landscapes. Furthermore, since PCT reopens the canopy and decreases CWD, the use of PCT should be limited. Factors that were not detectable at such a large scale may also influence selection patterns of marten, *e.g.,* localized amount of CWD, availability of cover, visual obstruction, etc. Although we measured these variables at the home range scale, we did not record them at the site scale. Further analysis is warranted to obtain a clear understanding of habitat selection for American marten.

Acknowledgements

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