

# Suitability of a young deciduous-dominated forest for American marten and the effects of forest removal

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**Abstract:** American marten (*Martes americana* (Turton, 1806)) are generally considered to be reliant upon and most successful in continuous late-successional coniferous forests. By contrast, young seral forests and deciduous-dominated forests are assumed to provide low-quality marten habitat, primarily as a result of insufficient structure, overhead cover, and prey. This study examined a moderate-density population of marten in northeastern British Columbia in what appeared to be comparatively low-quality, deciduous-dominated habitat, overgrown agricultural land primarily consisting of 30- to 40-year-old stands of regenerating trembling aspen (*Populus tremuloides* Michx.). Over 4 years, we monitored 52 radio-collared marten. The population appeared to be stable, as indicated by large numbers of adults, relatively constant densities, long-term residency of many individuals, low mortality rates, and older age structure. Relatively small home ranges (males, 3.3 km<sup>2</sup>; females, 2.0 km<sup>2</sup>) implied good habitat quality and prey availability. Shearing (removal of immature forest cover) of 17% of the study area resulted in home range shifts at the individual level but no detectable impact at the population level. Categorically, marten avoided nonforested cover types and preferred mature coniferous (>25% conifer) stands (7% of the study area) but otherwise appeared to use all forested stands relative to their availability, including extensive use of deciduous-dominated stands and deciduous stands <40 years of age. Thus, these young deciduous forests appeared to have sufficient structure, overhead cover, and prey to maintain moderate densities of resident marten on a long-term basis.

**Résumé :** On considère généralement que la martre d'Amérique (*Martes americana* (Turton, 1806)) a besoin de forêts de conifères continues et en fin de succession et que c'est là qu'elle se développe le mieux. Au contraire, les forêts jeunes en mi-succession et les forêts dominées par les arbres décidus sont des habitats de faible qualité pour les martres, principalement à cause d'un manque de structure, de couverture forestière et de proies. Notre étude examine une population de densité moyenne de martres du nord-est de la Colombie-Britannique dans un milieu dominée par les arbres décidus qui semble être un habitat de qualité comparativement basse; c'est une ancienne région agricole recouverte principalement par des boisés de peupliers faux-trembles (*Populus tremuloides* Michx.) en régénération et âgés de 30–40 ans. Nous avons suivi au cours de quatre années 52 martres munies d'un collier émetteur radio. Le grand nombre d'adultes, les densités relativement constantes, la durée de séjour prolongée de nombreux individus, les faibles taux de mortalité et la structure en âge dominée par les individus âgés indiquent que la population est stable. Les domaines vitaux relativement restreints (3,3 km<sup>2</sup> chez les mâles et 2,0 km<sup>2</sup> chez les femelles) laissent croire que l'habitat est de bonne qualité et la disponibilité des proies adéquate. La coupe, par retrait de la couverture forestière immature, de 17 % de la zone d'étude a entraîné des changements dans les domaines vitaux au niveau individuel, mais elle est restée sans effet décelable au niveau de la population. De façon stricte, les martres évitent les couverts végétaux non forestiers et préfèrent les surfaces couvertes de conifères (>25 % de conifères), soit 7 % de la zone d'étude; pour ce qui est du reste, elles utilisent toutes les surfaces forestières en proportion de leur disponibilité, y compris les zones dominées par les feuillus et les forêts décidues de <40 ans dont elles font grand usage. Ces jeunes forêts décidues semblent donc posséder une structure, une couverture forestière et une densité de proies suffisantes pour le maintien à long terme de densités moyennes de martres résidentes.

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## Introduction

American marten (*Martes americana* (Turton, 1806)) in western North America and boreal regions are generally considered to be reliant upon and most successful in continuous, late-successional coniferous forests characterized by large trees, large amounts of standing and downed woody material (e.g., coarse woody debris (CWD)), and adequate overhead cover (Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Lyon et al. 1994; Thompson and Colgan 1994; Thompson and Harestad 1994). Complex physical structure, especially near the ground, is thought to provide habitat for prey species, easier access to prey during winter, and protective thermal microenvironments, while the overhead cover is required to reduce predation risk (Hargis and McCullough 1984; Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Raphael and Jones 1997). Young seral forests are generally considered to be low-quality marten habitat (Buskirk and Ruggerio 1994), although limited research has been conducted in these stands (Snyder and Bissonette 1987; Baker 1992; Lofroth 1993; Johnson et al. 1995). Existing research does suggest, however, that viable marten populations can be maintained at reduced densities in early seral and second-growth forests where sufficient physical structure is present (Baker 1992; Johnson et al. 1995; Bowman and Robitaille 1997; Payer and Harrison 2003), when prey populations are high (Snyder and Bissonette 1987; Baker 1992; Lofroth 1993; Paragi et al. 1996; Potvin et al. 2000), or if sufficiently large residual forest patches are maintained (Chapin et al. 1998). Marten seldom use recent clearcuts (<10 years) exclusively, although recent clearcuts within the landscape may be used to some degree and may support reduced densities of marten in a broader landscape (Soutiere 1979; Steventon and Major 1982; Snyder and Bissonette 1987; Baker 1992; Thompson 1994; Potvin et al. 2000).

In their review of the characteristics of marten habitat, Buskirk and Ruggerio (1994) emphasized that marten prefer conifer-dominated stands to deciduous stands, even though stable, high densities of marten have been recorded in deciduous-dominated and mixed stands, primarily in eastern North America (Francis and Stephenson 1972; Soutiere 1979; Wynne and Sherburne 1984; Chapin et al. 1997). Recent work suggests that one of the conditions under which marten may prefer deciduous or mixed stands is when a dense coniferous shrub layer is present (Potvin et al. 2000). However, Buskirk and Ruggerio (1994) emphasized that juveniles are less habitat selective, and therefore, the mere presence of marten in deciduous-dominated forests should not be taken as evidence of appropriate habitat. Instead, Buskirk and Ruggerio (1994) asserted that marten population density and age structure should be used as a reflection of habitat quality.

Population density has elsewhere been a useful indicator of habitat suitability for marten. For example, Thompson and Harestad (1994) reviewed the effects of clear-cut logging on marten and concluded that regenerating clearcuts (<45 years after cutting) supported 0%–33% of the marten population levels found in nearby uncut forest. Consistent with this finding, several studies have shown that early seral habitats resulting from timber harvesting are generally avoided by marten (Soutiere 1979; Steventon and Major 1982; Huggard 1999). However, other workers have found

that early seral habitats may be used or even preferred if abundant CWD, visual cover, and prey populations are present (Baker 1992; Potvin et al. 2000).

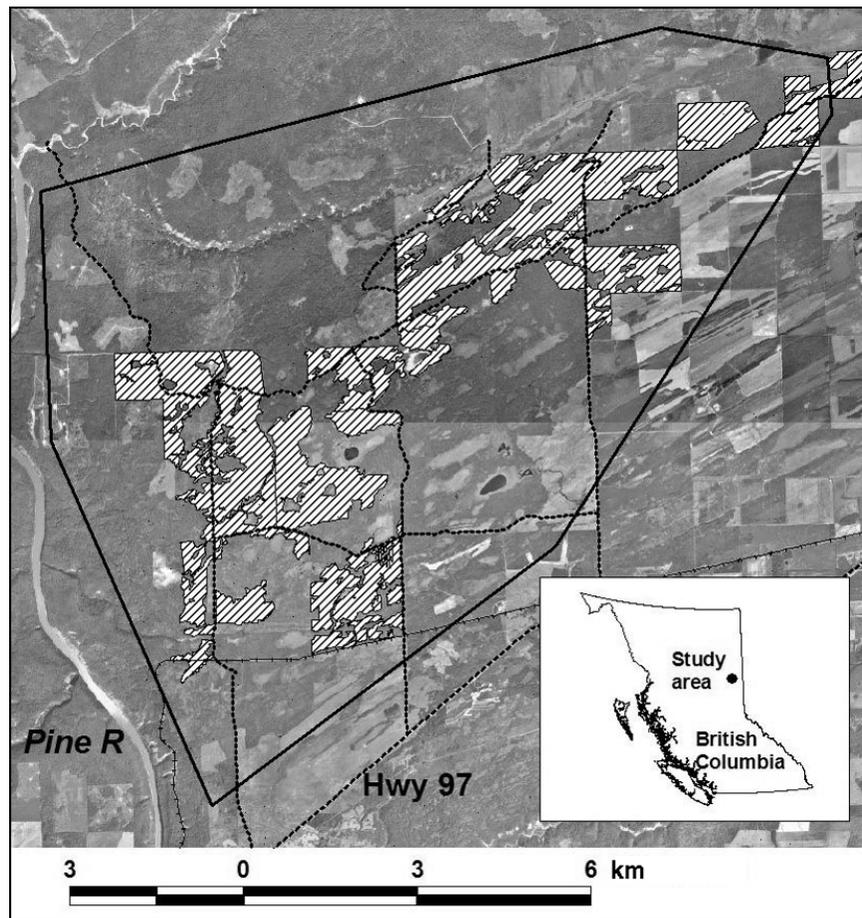
High prey populations may be another key to resolving why marten occur in some seemingly unsuitable habitats but not in others. Because timber harvesting alters overhead and horizontal structure (Thompson 1994), it necessarily affects prey species composition. Although study results are equivocal (reviewed in Klenner 1998), recent (<5 years old) clearcuts in interior western North America generally resulted in decreased red-backed vole (*Clethrionomys gapperi* (Vigors, 1830)) populations but increased numbers of both deer mice (*Peromyscus maniculatus* (Wagner, 1845)) and meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) (Scrivner and Smith 1984; Klenner 1998). Red-backed voles are a staple prey in most areas, being taken in proportion to or more than their availability, while *Microtus* species are taken in excess of their availability and deer mice are generally eaten less than expected based on their abundance and are not a preferred prey (Soutiere 1979; Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Martin 1994; Paragi et al. 1996; Coffin et al. 1997; but see Nagorsen et al. 1989). Snowshoe hares (*Lepus americanus* Erxleben, 1777) contribute significantly to marten diet in some populations (Thompson and Colgan 1990; Poole and Graf 1996; Cumberland et al. 2001). Although generally absent from recently cut areas (Potvin et al. 1999), hares prefer successional habitats 15–30 years of age (Monthey 1986; Thompson et al. 1989). Fruits such as raspberry (*Rubus* spp.), which are seasonally important to marten in some areas (Martin 1994), may increase in abundance as a result of clear-cutting (Soutiere 1979; Steventon and Major 1982). Thus, in the short term, timber harvesting affects both habitat structure and prey composition.

Here, we examined a moderate-density population of marten in what appeared to be comparatively low-quality, deciduous-dominated habitat, overgrown agricultural land primarily consisting of 30- to 40-year-old stands of regenerating trembling aspen (*Populus tremuloides* Michx.). To our knowledge, little research has been conducted on marten in this type of habitat, but conventional assessments of preferred marten habitat (Buskirk and Ruggerio 1994) would suggest that it is generally unsuitable. Analyses conducted early in the study showed that marten use of the area did not conform to a habitat suitability index model developed for the boreal coniferous forests of western United States (Grindal et al. 1999). Our objectives were to examine marten population attributes (home range size, density, age structure) and assess stand-scale habitat selection in a deciduous-dominated forest over a 4-year period during which a program of afforestation by shearing (removal by bulldozers with sharpened blades) of the immature aspen forest to plant coniferous trees affected roughly 17% of the study area. We also indexed prey abundance in an effort to determine why marten were using this habitat.

## Study area

Research focussed on Canadian Forest Products Ltd.'s (Canfor) 5880-ha Rice Property (55°42'N, 121°48'W) composed of rolling upland located 40 km east of Chetwynd in

**Fig. 1.** Study area (heavy polygon) in northeastern British Columbia, Canada. The background image was derived from orthophotos taken in 1996 (preshearing). Dashed lines are roads. Areas sheared in 1999–2002 are indicated by hatching.



northeastern British Columbia, Canada (Fig. 1). Elevations on the study area range from 725 to 820 m, and 90% of the area has slope  $\leq 14\%$ . Marten use of the area surrounding the property resulted in a 9060-ha study area. The study area was within the Boreal White and Black Spruce biogeoclimatic zone, moist warm variant (BWBSmw1), characterized by long, very cold winters and short growing seasons (DeLong et al. 1990). July and January mean temperatures for Fort St. John, 50 km northeast of the study area, are 15.8 and  $-15.0$  °C, respectively, and the area receives an average of 468 mm of precipitation annually, including 198 cm of snowfall (Environment Canada, 30-year climatic norms). The area is within the Boreal Plains Upland natural disturbance unit characterized by historic stand-replacing fire-return intervals of 100 years (DeLong 2002). These typically large-scale forest fires ( $>1000$  ha) generally left small amounts (3%–15%) of unburned mature forest remnants within their boundaries (Eberhart and Woodward 1987).

The study area was dominated by aspen stands of various ages, including younger stands regenerating from agricultural clearing that occurred during the 1960's, which left windrows of debris within the forest matrix. Small portions of the area were composed of remnant stands of mixed wood (primarily aspen, white spruce (*Picea glauca* Moench (Voss)), and lodgepole pine (*Pinus contorta* Dougl. ex Loud.)), black spruce (*Picea mariana* (Mill.) BSP) bogs, wetlands, and overgrown pastures. During March 1999 and

each January–March through to 2001, Canfor progressively sheared a total of 1520 ha of the immature and sapling-sized deciduous stands (26% of the property, 17% of the study area). An additional 520 ha (6% of the study area) was sheared in February 2002 but had little bearing on the study, since monitoring of marten ended in early March 2002. Planting with spruce and (or) pine generally took place within 1 year of shearing. Woody debris piles (windrows and piled slash) were retained to varying degrees, and riparian buffers were maintained in widths varying from 5 to 100 m. Sheared areas are similar to conventional timber harvested areas in many respects (e.g., retention of riparian zones, wildlife tree patches, and shrub response after harvest) but differ in that they generally lack large woody debris because of the small diameter of the trees sheared, the efficiency of piling by large bulldozers, and the general retention of patches of larger diameter trees. Shearing activities also generally lack the flexibility to retain single or small clumps of standing live trees. Conventional forest harvesting techniques can leave varying amounts of woody debris and standing tree retention within cutovers.

## Methods

### Habitat base and stratification

We derived habitat information from geographic information system (GIS) databases that are widely available in Brit-

**Table 1.** Cover types based on age class and dominant species composition in the American marten (*Martes americana*) study area in northeastern British Columbia (adapted from Grindal et al. 1999).

Cover type	Age (years)	Description	Percent of study area	
			1998	2002
Sheared	<3	Forests that have been sheared, piled into windrows, and burned, 1999–2001	0	17 <sup>a</sup>
Shrub/disturbed	na	Shrub or herb areas with no overstory trees species in the database; also disturbed habitats (road edges, landings, gravel pit)	18	17
Sapling deciduous	1–39	Primarily aspen (>75%) saplings with height from 6 to 13 m, 2600–3500 stems/ha; some spruce, cottonwood, and pine	42	33
Immature deciduous	40–80	Primarily aspen (>75%) with height from 13 to 24 m, ~1300 stems/ha; some spruce, cottonwood, and pine	8	7
Mature deciduous	81–150	Primarily aspen (>75%) with height >24 m, ~850 stems/ha; some spruce, cottonwood, and pine	21	16
Sapling coniferous	1–39	Conifer (>25%) and aspen (<75%) saplings with height from 6 to 13 m, 2600–3500 stems/ha	2	2
Immature coniferous	40–80	Conifers (>25%) and aspen (<75%) with height from 13 to 24 m, ~1300 stems/ha; some cottonwood	3	2
Mature coniferous	81–150	Conifers (>25%) and aspen (<75%) with height >24 m, ~850 stems/ha; some cottonwood	7	7

**Note:** na, not applicable.

<sup>a</sup>An additional 6% of the study area was sheared in February 2002 but had little bearing on the study and was not included in this summary table, since monitoring ended in early March 2002.

ish Columbia. We used digital 1 : 20 000 scale Vegetation Resource Inventory (VRI) mapping (Resources Inventory Committee 2001) for the Rice Property alone, and Forest Cover forest inventory planning files (Resources Inventory Branch 1995) for adjacent areas not covered by VRI. Forest Cover maps forest structure based on overstory species; data are derived from interpretation of 1 : 15 000 scale black and white aerial photographs and ground plots. Most of the Forest Cover mapping adjacent to the property was completed in 1987 (83%), with the bulk of the remainder completed in 1992–1993. VRI maps forest structure from interpretation of 1 : 10 000 to 1 : 20 000 scale aerial photographs and more detailed ground surveys than Forest Cover. Compared with Forest Cover, VRI typically provides more detail on understory vegetation and nonvegetated areas and is considered more current and more accurate where both inventory systems are available. The mean (SE) size of Forest Cover polygons was 22.6 ha ( $\pm 2.4$ ) and that of VRI polygons was 6.6 ha ( $\pm 0.7$ ). We corrected stand age in both habitat inventories to 1998–2002, as appropriate, and updated coverage of sheared areas to 1 April each year. We stratified cover type based on age class and dominant species composition (Table 1). Deciduous-leading stands (>75% of stands) dominated the study area (56%–71% of all available cover types and 85%–87% of all forested stands). We defined coniferous stands as those with >25% coniferous component because study area sample sizes for mixed (25%–75% coniferous) and pure coniferous (>75%) stands were too low for meaningful analysis (<3.5% each). We grouped sapling coniferous and immature coniferous stands for analysis because of the low availability of each.

#### Marten capture and telemetry

Marten were originally identified as being present in the study area in moderate numbers by means of snow track counts made in December 1997 to March 1998 (Grindal and Setterington 1998). We conducted trapping sessions for

marten during November–December 1998–2001 and during June 2001 and 2002. We distributed our marten capture effort throughout the study area, often moving traps to concentrate in specific areas to target individual marten for recapture or to increase sampling effort where there were not yet any collared animals. Marten were captured in Havahart traps (Ketchum Manufacturing Inc., Ottawa, Ont.) placed inside waxed cardboard boxes and baited with meat, sardines, and (or) raspberry jam. We applied commercial marten lure and rancid fish oil to nearby trees. For all initial captures during each trapping session, we restrained marten in a handling cone and immobilized them using a 1:1 mixture of tiletamine–zolazepam (Telazol<sup>®</sup>) administered intramuscularly at ~3–5 mg/kg body mass. We cared for animals by following the principles and guidelines of the Canadian Council on Animal Care (1993) under provincially approved handling and immobilization procedures. Sex was determined based on external genital characteristics, and age (juvenile versus adult) was subjectively determined based on the presence of a sagittal crest and tooth wear (Poole et al. 1994). We applied a numbered metal ear tag to one or both ears and measured animal mass. We fitted marten with 28- to 50-g VHF radio collars (Holohil Systems Ltd., Carp, Ont.; Lotek Engineering, Newmarket, Ont.; Telonics, Mesa, Ariz.). We placed lighter collars on lighter individuals and replaced collars on all marten captured for the first time in each session. Marten were released after complete recovery in the live traps. Animals caught more than once during any capture session were identified and immediately released. We removed collars during the last trapping session of the study. The ages of six marten that died during the study were determined by cementum analysis of each animal's fourth premolar (Poole et al. 1994) (Matson's Laboratory, Milltown, Mont.).

We located radio-collared marten using standard ground telemetry procedures (White and Garrott 1990). Three to six bearings were taken from permanent ground stations along

roads and seismic lines or within cutblocks. The coordinates of each ground station were obtained using a differentially corrected global positioning system (Trimble TSC1 Pro XR™). Most locations were taken during daylight hours (~0900–1700); however, we occasionally conducted evening (1700–2300) monitoring. Animals were systematically monitored so that sampling effort was roughly equal among animals. We used LOCATE II software (Nams 1990) to calculate the position of animals and provide confidence error ellipses based on the maximum-likelihood estimator (Lenth 1981). Data were scrutinized for possible errors in locations of animals and spurious locations were deleted. To calculate telemetry error, we placed test collars at roughly 500 m distance and determined estimated collar locations using bearings from three stations. True test collar locations were determined using the differentially corrected global positioning system.

We summarized the fate of all marten trapped on the study area. Animals were censured if contact was lost and they were not recaptured. Flights were conducted in February and March 2001 up to 20 km from the study area to search for radio-collared marten that had apparently disappeared from the study area.

### Small-mammal monitoring

We determined the abundance of small mammals in the study area following methodology modified from Sullivan (1997). Small-mammal trapping occurred in early June and mid-October 2001. Bolton live traps (B.N. Bolton, Vernon, B.C.) were placed along snow track transects that were already established in cover types of four age classes in the study area (sheared, sapling deciduous, immature deciduous, and mature deciduous). To provide some replication within cover types, we sampled two transect lines of 10 stations within each cover type, selected randomly from east and west sides of the study area. Points of commencement of transects were located a minimum of 50 m from stand edges. Trap stations were 15 m apart, and two traps were placed within 2 m of each station. Trap stations were prebaited with peanut butter and rolled oats and then set for three consecutive nights. Captures were identified to species and sex and weighed. We compared our capture rates and species composition with captures conducted at the element and patch scales in 1999 and 2000 by Porter (2002), who used a different study design and different traps (five multiple-capture live traps (Tincat™ and (or) Longworth™) at each site prebaited and then set for two consecutive nights, with design layout based on marten use).

### Track transects

We followed standard snow-tracking methodology to obtain an index of the relative abundance of marten, snowshoe hare, and red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)) among cover types (Thompson et al. 1989; Bull et al. 1992; Poole 1994; Thompson and Colgan 1994). Four transects were established in each of four cover types (shearing, sapling deciduous, immature deciduous, and mature deciduous) following previous stratification and transects (Grindal and Setterington 1998; Grindal et al. 1999) whenever possible to maintain consistency among years. Track counts were conducted on foot 24–96 h after snowfall. Each

transect was 1 km in length and was located >100 m from adjacent cover types. Track counts were conducted between dawn (~0900) and dusk (~1800) during two track counting sessions in February 2001 and between late January and early March 2002. All tracks intercepting or within 1 m of either side of transects were recorded and summarized over 1-km intervals. Where trails were present and the number of individual tracks could not be accurately ascertained, we assigned a value of five tracks; field workers can usually distinguish up to three or four individual tracks in a given crossing. For analysis, all track counts were divided by days since last snowfall (to the nearest 12 h) to correct for track accumulation with time, yielding a measurement unit of tracks per kilometre per day. To avoid temporal pseudo-replication, counts from individual transects were averaged for each season for analysis (Thompson et al. 1989). To examine differences in use of cover types, we pooled data from 2001 and 2002 to increase the power of analysis.

### Home range

We calculated home range using the Animal Movement extension (Hooze and Eichenlaub 1997) and the Home Range extension (Rodgers and Carr 1998) for ArcView™ (Environmental Systems Research Institute, Redlands, Calif.). We used the 90th percentile of marten location error ellipses (75 ha, mean ellipse 9.8 ha ( $\pm 0.42$ )) as the upper limit to the error that we would accept in calculations of home range and deleted all locations with larger error. We used this limit to avoid significantly decreasing sample size and because our calculated home range areas are likely conservative estimates of actual home ranges because of our lower sampling effort for nocturnal activities, the relatively low sample sizes, and limitations on the detectability of radio-collared marten in poorly accessible areas. Home range size was estimated for the entire year (1 April to 31 March) using both the 100% and 95% minimum convex polygon (MCP) methods (Mohr 1947). We used the area-added method (White and Garrott 1990; Rodgers and Carr 1998) to generate 95% MCPs. We used the MCP method because low sample sizes were not appropriate for kernel-based estimators (Seaman et al. 1999). We used marten locations separated by  $\geq 12$  h (generally  $\geq 1$  day apart) for home range and habitat selection analysis to maximize spatial independence of observations (Katnik et al. 1994; Phillips et al. 1998). We plotted cumulative home range sizes against the number of locations for a sample of three male and two female marten and found that we could detect only a minimal increase in home range size (three additional locations produced an increase in home range area of <10%; Phillips et al. 1998) for home ranges with more than 18–24 locations. Thus, for reporting of annual home range size, we used marten with a minimum of 18 locations (mean =  $27.5 \pm 1.22$  locations per marten per year).

We estimated minimum marten density from the number of radio-collared marten within the outer bounds of the combined annual ranges (Latour et al. 1994). We are confident that we captured the majority of residents that regularly encountered our grid in each trapping session. For example, in November 2001, we missed capturing only 1 of 16 animals known or suspected to be resident within the study area prior to the trapping session from radiotelemetry evidence.

### Habitat selection

We conducted habitat selection analysis at the within home range (stand) scale (third order; Johnson 1980) using Manly et al.'s (2002) design III approach, which compares the use of individual animals with areas that were individually available to them. Attribute availability was determined by placing random points within the home range of each marten, equal to 10 times the number of locations for each animal. We pooled locations for all marten for each year because we had relatively small numbers of locations for a relatively large number of animals (52 annual home ranges; White and Garrott 1990). We compared habitat availability inside the annual home range (95% MCP for marten with  $\geq 18$  locations,  $n = 31$ ; 100% MCP for those with 9–17 locations,  $n = 21$ ) with sites used by animals (telemetry locations) to identify habitat selection at the stand scale. We did not include animals with less than nine radiolocations for habitat analysis. We combined analysis over all 4 years of the study and used locations with error ellipses of  $< 40$  ha (mean error ellipse 6.8 ha ( $\pm 0.27$ )) to increase the power of detecting habitat selection. To account for changes in habitat availability over the study (primarily resulting from cutting of existing forest via shearing), we summed habitat availability across years. Use of cover types did not differ between summer and winter (likelihood ratio,  $\chi^2 = 8.94$ ,  $df = 6$ ,  $P = 0.18$ ); therefore, we combined seasons in our analysis.

To test if marten react to specific attributes of their habitat, rather than broad cover types, we examined a suite of continuously distributed habitat variables from VRI and Forest Cover that we believed might influence marten use of a stand. These included stand age, proportion of conifers in the stand (conifer cover), crown closure, shrub cover, density of snags per hectare, density of live stems per hectare, and stand height.

### Statistical analysis

We used Kruskal–Wallis ( $H$ ) tests and Dunn's multiple comparison procedure and Mann–Whitney ( $U$ ) tests (Zar 1984) to examine differences in small-mammal captures and track counts among cover types and years (Thompson et al. 1989). We tested differences in our success in livetrapping marten among years using a  $\chi^2$  analysis of total captures for age and sex classes. One-way analysis of variance and Duncan's multiple range tests were used to test for differences in body masses and home range size among years. We used Student's  $t$  tests (Zar 1984) to determine if there was a difference in home range size between sexes.

We tested for relative preference among categorical cover types using the selection index  $w$  (Manly et al. 2002). This index was calculated as the proportion of all locations in cover type  $i$  divided by the proportion of type  $i$  available (Manly et al. 2002). Selection indices  $> 1$  indicate preference and values  $< 1$  indicate avoidance. Binomial confidence intervals calculated using the programs that accompany Krebs (1999) were used to assess differences among cover types. To reduce the risk of a Type I error when making multiple comparisons,  $\alpha$  was reduced using the Bonferroni correction procedure (Manly et al. 2002). We performed data summarization and analyses using SAS software (SAS Institute Inc. 1997). Except when using Bonferroni corrections, statistical

tests were considered significant at  $P < 0.05$ . We present means with associated standard errors.

To complement this categorical analysis of habitat selection, we used logistic regression of telemetry locations compared with random points to test for selection of biologically plausible continuous habitat attributes (Hosmer and Lemeshow 1989; Manly et al. 2002). We included stand age, stand height, crown closure, and percent conifer as candidates for inclusion in a multivariate model because these variables were available for the entire study area. We conducted separate univariate assessments of shrub cover, live stems per hectare, and snags per hectare because this information was limited to the VRI database, which covered only the Rice Property portion of our study site. For both the univariate and multivariate analyses, variables were considered to be significant if the likelihood ratio test ( $G$  test) produced a  $P$  value of  $< 0.05$  and the Wald statistic was  $> 1$ . We used the Hosmer and Lemeshow (1989) goodness-of-fit statistic ( $C$ ) to provide an estimate of the ability of the model to predict the observed outcome. To check for nonlinear relationships, we divided each variable into quartiles and, for each group, plotted the logit of the average value of the dependent variable versus the group midpoint (Hosmer and Lemeshow 1989). For the multivariate model, we subjected the variables to correlation analysis to detect collinearity. If two variables were correlated at Spearman's  $\rho > 0.5$ , we removed the variable that appeared to have the least biological relevance. The model was fit using the remaining variables; we eliminated those with  $P > 0.05$  from a  $G$  test. We tested for nonlinear effects for those variables that were identified during our initial data investigation. Finally, we tested all possible two-way interactions.

## Results

### Marten captures and telemetry

We captured and handled 54 marten 286 times during the study (Table 2): 18 adult ( $> 1$  year old) males, 10 males initially captured as juveniles, 21 adult females, 4 juvenile females, and 1 female for which estimated age was not recorded. Half of the juveniles were recaptured and monitored as adults. Although the number of individuals captured per 100 trap-nights during early-winter trapping sessions remained relatively constant (4.1–5.7 per 100 trap-nights;  $\chi^2 = 1.11$ ,  $df = 3$ ,  $P > 0.5$ ), juvenile captures declined to 0%–6% of total captures during the last 2 years of the study ( $\chi^2 = 11.2$ ,  $df = 3$ ,  $P < 0.01$ ) (Table 2). Mean mass of adult marten was lower during November–December 2000 compared with other early-winter capture sessions (males,  $F_{[3,29]} = 4.86$ ,  $P = 0.007$ ; females,  $F_{[3,20]} = 2.76$ ,  $P = 0.069$ ) (Table 2). During June trapping, one of seven adult females was lactating in 2001, and two of three were lactating in 2002. Density of marten remained relatively constant during the last 3 years of the study at values slightly higher than those observed in the first winter of research (Table 2).

Considering that nine marten were monitored for more than 2 years and marten were followed for 50 marten-years, observed mortality rates were generally low (Table 3). Seven natural mortalities were recorded, all of which occurred between December and May during the final 2 years of the study. Raptors were implicated (based on tracks and han-

**Table 2.** American marten capture data from northeastern British Columbia, 1998–2002.

Capture session	Trap-nights	No. of marten	No. of marten collared	Individuals per 100 trap-nights	Percent juvenile	Percent male	Density (no./km <sup>2</sup> ) <sup>a</sup>	Mean adult mass (g) ( <i>n</i> )	
								Males	Females
3–17 Dec. 1998 <sup>b</sup>	338	16	13	4.7	31	69	0.24	1126 (7)	738 (4)
4 Nov. – 4 Dec. 1999 <sup>c</sup>	561	29	18	5.2	41	72	0.34	1172 (8)	750 (5)
5–20 Dec. 2000	419	17	12	4.1	6	59	0.37	1006 (10)	678 (6)
5–12 June 2001	234	16	15	6.8	—	56	—	1122 (9)	815 (7)
5–14 Nov. 2001	296	17	17	5.7	0	47	0.31	1148 (8)	756 (9)
10–18 June 2002	281	11	0	3.9	—	73	—	1123 (8)	760 (3)

<sup>a</sup>Density provided for early winter for comparison among years.

<sup>b</sup>Data from Grindal et al. (1999; personal communication).

<sup>c</sup>Data from Porter (2002). Twenty-two marten were immobilized and handled, and an estimated seven males were released without immobilization; thus, data presented here are based on sample sizes of 29 (columns 3–5) or 22 (columns 6–10), as appropriate.

**Table 3.** Fate of American marten (number (percentage in parentheses) of total known to be alive at the end of the capture session) until the subsequent capture session, northeastern British Columbia, December 1998 – June 2002.

Capture session	Total no. of marten <sup>a</sup>	No. alive	No. censured <sup>b</sup>	Fur trapped and capture-related mortality	Natural mortality
3–17 Dec. 1998	13	9 (69)	4 (31)	0	0
4 Nov. – 4 Dec. 1999	22	12 (55)	9 (41)	1 (4)	0
5–20 Dec. 2000	20	11 (55)	3 (15)	3 (15) <sup>c</sup>	3 (15)
5–12 June 2001	19	17 (89)	2 (11)	—	0
5–14 Nov. 2001	19	8 (42)	4 (21)	3 (16)	4 (21)

<sup>a</sup>Includes the total number of marten known to be alive at the end of the capture session that were collared.

<sup>b</sup>Censured marten include those with which contact was lost (and that were not recaptured) and those that dropped collars.

<sup>c</sup>Includes two capture-related mortalities.

dling of the carcass) in all three deaths where predation was suspected, and four deaths were from unknown natural causes. Five marten died from fur harvesting (all December–January) and two from capture-related mortalities. Through cooperation with the local trappers, fur harvesting was restricted to the northern edge of the study area and primarily occurred during the later half of the study.

We aged six marten (five study animals and one incidental pickup) by cementum analysis. One marten was aged at 6 years, one at 5 years, one at 3 years, and the remaining three at 2 years. Telemetry of collared marten was conducted from January 1999 to March 2002, with the exception of August–November 2000. We obtained 1351 locations, of which 1227 were considered for home range analysis and 1150 were used in habitat analysis. We obtained 81 locations (7%) by backtracking radio-collared animals during the first year of study (Grindal et al. 1999). Using test collars, average error of location was 144 m ( $\pm 23.0$ ) ( $n = 15$ ).

**Home range**

We obtained 31 annual home ranges (29 for adults and 2 for juveniles) from 21 marten for use in home range size calculations. Annual 95% MCP home range size among years did not differ for adult males ( $F_{[3,18]} = 0.03$ ,  $P = 0.99$ ) (Table 4). Comparison among years was not valid for females because of low sample size for the first 3 years. Summing adult home ranges over all years, males had about 50% larger 95% MCP annual home ranges than females (2.3 versus 1.5 km<sup>2</sup>;  $t = 1.75$ ,  $df = 27$ ,  $P = 0.098$ ) and 70% larger 100% MCP annual home ranges than females (3.3 versus 2.0 km<sup>2</sup>;  $t = 2.35$ ,  $df = 27$ ,  $P = 0.03$ ).

**Table 4.** Home range size (km<sup>2</sup> (SE)) among years for adult American marten in the study area in northeastern British Columbia, 1998–2002.

Year	Males		Females	
	<i>n</i>	95% MCP	<i>n</i>	95% MCP
1998–1999	3	2.1 (1.13)	1	2.3
1999–2000	8	2.3 (0.67)	2	0.7 (0.11)
2000–2001	4	2.4 (0.77)	0	—
2001–2002	7	2.2 (0.15)	4	1.7 (0.38)
All years 95% MCP	22	2.3 (0.30)	7	1.5 (0.31)
All years 100% MCP	22	3.3 (0.42)	7	2.0 (0.40)

**Note:** All home ranges were 95% minimum convex polygons (MCP) except for the bottom row, where 100% MCP home ranges were provided for comparative purposes.

**Small-mammal monitoring**

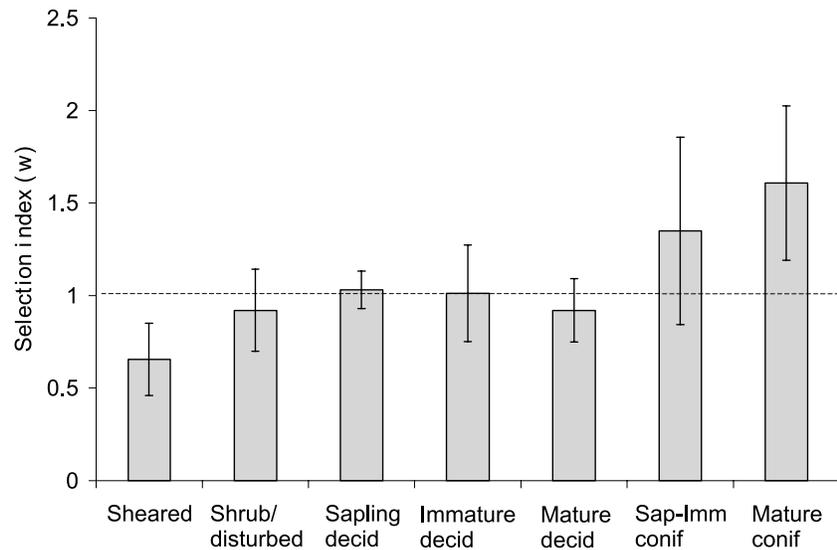
Small-mammal abundance varied during the study (Table 5). We captured between 12.4 and 58.9 small mammals per 100 trap-nights per session. Red-backed voles and deer mice comprised 92% of the 1655 captures. Although differences in trap type, trap location, study design, and season require caution in comparing small-mammal trapping success among years, it appeared that overall small-mammal numbers, especially red-backed voles, were comparatively low at some point between late 2000 and mid-2001. Overall capture success of small mammals did not differ among cover types in 2001 (June,  $H = 0.3$ ,  $df = 3$ ,  $P = 0.95$ ; October,  $H = 6.0$ ,  $df = 3$ ,  $P = 0.11$ ).

**Table 5.** Small-mammal capture success (captures per 100 trap-nights), northeastern British Columbia, 1999–2001.

Period	Trap-nights	DM	RBV	MV	JM	SH	Total
Aug.–Sept. 1999 <sup>a</sup>	1800	10.6	34.6	11.8	0.1	1.8	58.9
Aug. 2000 <sup>a</sup>	360	61.1	13.3	0.8	0.6	6.4	82.2
June 2001	452	8.6	1.8	0.9	1.1	0	12.4
Oct. 2001	475	20.2	28.0	2.3	0	0.6	51.2

**Note:** DM, deer mice; RBV, red-backed vole; MV, meadow vole; JM, western jumping mice (*Zapus princeps* J.A. Allen, 1893); SH, unidentified shrew (Soricidae).

<sup>a</sup>From Porter (2002).

**Fig. 2.** American marten (*Martes americana*) stand preference (with 95% binomial confidence intervals) at the home range (stand) scale, northeastern British Columbia, 1998–2002. Selection indices >1 indicate preference and values <1 indicate avoidance.

### Habitat selection

Marten use of cover types was not random at the stand scale ( $\chi^2 = 41.1$ ,  $df = 6$ ,  $P < 0.0001$ ) (Fig. 2). Sheared areas were avoided and mature coniferous stands were preferred. Across all years, 68% of marten locations were in deciduous-dominated stands (56%–71% of the study area). Track transects suggested that marten avoided sheared areas because no tracks were found in this cover type (Table 6). When sheared areas were removed from the comparison, marten used all forested cover types equally ( $H = 0.58$ ,  $df = 2$ ,  $P = 0.75$ ). Snowshoe hares strongly favoured sapling stands, and red squirrels used immature stands and avoided sheared and sapling cover types.

The logistic regression tests of continuous variables supported the categorical preferences of marten. The largest effect size, and hence strongest selection, was associated with percent conifer cover for which marten used sites with an average of 37% more conifer cover than was available at random (Table 7). Stand height was not considered for inclusion in the multiple regression modeling because it was highly correlated with stand age. No multivariate combination provided a significantly better fit than did percent conifer cover tested alone. There were no significant interactions or nonlinear effects.

Martens also selected increased shrub cover and increased stand age when these variables were tested as univariates; used sites had 17% higher shrub cover and 8% older stands

**Table 6.** Mean counts of tracks (tracks per kilometre per day) among sheared and forested cover types, northeastern British Columbia study area, January to March 2001–2002.

Cover type	Marten	Hare	Squirrel
Sheared	0	0	0
Sapling deciduous	1.34	22.62	0
Immature deciduous	0.62	2.02	1.87
Mature deciduous	0.93	0.41	0.07
<i>P</i>	0.02	0.001	0.001
<i>n</i> tracks	109	821	91

(Table 7). Although these variables were highly significant (log-likelihood test,  $P \leq 0.02$ ) and appeared to fit adequately ( $P > 0.05$ , except for stand age), they explained almost none of the overall deviation in the data ( $R_L^2 = 0.002$ ).

### Reaction to shearing

We observed 13 instances where a significant portion of a marten's home range was sheared and we were able to monitor the animals' response. All 13 martens responded negatively to shearing. Six martens either disappeared (five) or died (one) when an average of 37% ( $\pm 9\%$ ) of their home range was sheared. The seven other martens, whose home ranges were sheared by an average of 36% ( $\pm 8\%$ ), shifted

**Table 7.** Model mean values, coefficients, and diagnostics of habitat variables assessed with logistic regression to examine habitat selection by marten in a young deciduous forest in northeastern British Columbia, 1998–2002.

Variable	Mean (SE)		Coefficient	Wald	Deviance	$P^a$	$C$	$P^b$	$R^2_L$
	Available	Used							
Stand age (years)	42.3 (0.38)	45.3 (1.15)	0.002	2	5.85	0.016	26.9	<0.001	<0.001
Conifer cover (%)	7.4 (0.21)	10.2 (0.74)	0.005	5	14.71	<0.001	0.81	0.39	0.002
Crown closure (%)	40.6 (0.30)	40.5 (0.87)	−0.000	−0.09	0.01	0.92	42.9	<0.001	<0.001
Shrub cover (%)	12.6 (0.18)	14.7 (0.60)	0.007	3.5	12.58	<0.001	6.0	0.20	0.002
Snags (no./ha)	3.9 (0.22)	4.5 (0.70)	0.001	0.5	0.68	0.41	—	—	<0.001
Live stems (no./ha)	3580 (38)	3560 (114)	−0.000	−0.2	0.04	0.84	23.9	0.002	<0.001

<sup>a</sup>Significance of the log-likelihood value.

<sup>b</sup>Significance of the Hosmer and Lemeshow (1989) goodness-of-fit statistic ( $C$ ). For this test, models are considered to be adequate when  $P > 0.05$ .

their ranges in the subsequent year so that 19% ( $\pm 7\%$ ) of their range contained sheared areas. Although home range size declined in five of seven cases where we were able to monitor marten following shearing events, the mean difference was not significant (before shearing,  $2.6 \pm 0.53 \text{ km}^2$ ; after shearing,  $2.0 \pm 0.42 \text{ km}^2$ ; Mann–Whitney  $U = 60.0$ ,  $P = 0.37$ ,  $n = 7$ ).

## Discussion

### Marten in deciduous-dominated forest

The study area appeared to maintain a moderate density of marten over 4 years, suggesting that this predominately deciduous and early seral dominated forest offered suitable habitat for marten. The population appeared to be stable, as indicated by the presence of large numbers of adults, relatively constant densities, long-term residency of many individuals, low mortality rates, and older age structure (from cementum ages and numerous observations of moderately to severely worn canines). Reproduction occurred in the study area, as evidenced by lactating females. Annual home range sizes of marten were stable and on the low end of those reported for marten elsewhere in North America (Buskirk and McDonald 1989; 100% MCP home ranges averaging 8.1 and 2.3  $\text{km}^2$  for males and females, respectively, Powell 1994). Together, these factors suggest that these marten were primarily resident adults, not the transient juveniles or adults that might be expected in suboptimal habitats (Buskirk and Ruggerio 1994; Thompson 1994; Paragi et al. 1996), and that they were living in habitat of sufficient quality (i.e., for prey, security from predators, denning habitat, etc.) to maintain a viable population. Indeed, because home range size and habitat quality (especially prey availability) are strongly correlated (Thompson and Colgan 1987, 1994; Buskirk and McDonald 1989), the small home ranges in the study area provide ample evidence that this species does not require mature, conifer-dominated cover.

The prevailing paradigm for marten habitat use in western North America and boreal regions, which includes reliance on continuous late-successional coniferous forests with large trees, complex physical structure, and adequate overhead cover (Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Lyon et al. 1994; Thompson and Colgan 1994; Thompson and Harestad 1994), may place too much emphasis on stand type and not enough on stand structure (Buskirk and Powell 1994; Chapin et al. 1997; Payer and Harrison 2003). Our analysis of the telemetry data, supported by track

count data, suggested avoidance of sheared and open stands and preference for mature coniferous stands. However, mature coniferous stands accounted for only 7% of the study area, and marten made extensive use of deciduous-dominated areas and deciduous stands <40 years of age. This estimate is likely to be conservative because marten locations were primarily obtained during daylight hours, and marten may make greater use of more open stands at night when risk of predation is reduced. Habitat selection may also vary with marten activity, although possibly at a scale finer than we were able to detect (Lofroth 1993; Porter 2002).

Despite its rarity, the analysis of continuously distributed habitat attributes further supports the preference for coniferous cover when it is available. Marten selected habitat with increased coniferous coverage, higher shrub cover, and older stands. Yet these habitat attributes, although significant, accounted for very little of the variability in the data, again suggesting that marten actually used a wide range of habitats. Furthermore, on average, the stands in which marten occurred were not mature (mean = 45 years) and provided comparatively low coniferous forest (10%) and shrub (15%) cover.

Thus, while preference for mature coniferous stands was evident, marten demonstrated limited selection of forest types or attributes. From this, we can assume that the physical structure and overhead cover needed for prey habitat, access to prey, protective thermal microenvironments, and reduced predation risk (Buskirk and Powell 1994; Buskirk and Ruggerio 1994) were available in sufficient quantities within stands other than mature coniferous stands to provide quality marten habitat. These results are consistent with recent thinking that vertical and horizontal structure may be more important habitat attributes than overstory age or species composition (Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Chapin et al. 1997; Smith and Schaefer 2002; Payer and Harrison 2003).

Because of our reliance on digital data sources, we were unable to examine the abundance of all types of structure within the cover types selected. Other studies suggest that CWD is a limiting feature to marten for hunting (e.g., Steventon and Major 1982; but see Thompson and Colgan 1994) and, in some areas, for sufficient prey abundance (Thompson and Curran 1995). Paragi et al. (1996) further suggested that even in recently burned habitats, prey and CWD might be sufficient to maintain marten populations even though the disturbance (wildfire in this case) produced

low canopy cover. Supporting this finding, marten responded to structural characteristics in second-growth boreal forests of Ontario, including greater amounts of CWD, in a manner similar to that described for uncut forests (Bowman and Robitaille 1997). However, marten avoided second-growth forests in Newfoundland because their main small-mammal prey species was absent, reportedly a result of a lack of structure at ground level (Thompson and Curran 1995). This difference may reveal a reliance on forest structure at smaller scales than those that are typically assessed with GIS, producing some of the apparent contradictions in the existing literature. Indeed, Porter (2002) found that marten select habitat strongly at the scale of individual habitat elements (e.g., a log), especially for denning and foraging sites. Deadwood was important for these activities even though marten did not appear to react to the age or species of the forest overstory (Porter 2002). Given the history of land management within the study area, it is possible that adequate or sufficient levels of ground structure existed in all forested cover types. We observed old windrows and evidence of slash in most young forests within the study area, and older stands generally had large amounts of downed trees and CWD. However, decay of remnant structure over time may affect long-term use of stand types by marten. Thus, given adequate structure and prey availability, the use of young, deciduous-dominated stands reported here suggests that marten may be more flexible in their habitat use patterns than previously thought.

Examination of the prey base provides additional information with which to assess the suitability of our study area for marten. Voles are preferred prey for marten in most areas (Buskirk and Powell 1994; Buskirk and Ruggiero 1994; Martin 1994). Larger prey species, especially snowshoe hare, red squirrel, and grouse, may play an important role in marten diet and caloric intake, especially during winter (Thompson and Colgan 1990; Poole and Graf 1996; Cumberland et al. 2001). Although snowshoe hare levels were highest in sapling stands, fall densities of red-backed voles were similar among different-aged stands, suggesting no differences in the availability of their suspected main prey among stand age classes. Similarly, on the basis of prey abundance in their area, Potvin et al. (2000) suggested that mature or overmature forests cannot be considered a strict requirement for marten.

A number of factors suggest that the marten population experienced a decline in prey numbers (primarily voles) during late 2000 (judging by marten masses) through early 2001, resulting in 10%–12% lower masses in December 2000, poor survival of juveniles born in 2000 (only one juvenile was captured in December 2000), and little or no reproduction or survival of young in 2001 (only one of seven adult females was lactating in June 2001 and no juveniles were captured in November 2001). This prey decline may have been short-lived, as prey numbers and marten masses appeared to have rebounded by fall 2001. Thompson and Colgan (1987) found that during a 3- to 4-year decline in all major prey species, responses of marten included reduced population density, enlarged home ranges, reduced production of young, dispersal of formerly resident adults, and cannibalism. However, these authors also found that male masses did not differ among years, and female masses were

higher in early winter in the year of scarce food compared with years of more abundant food.

### Response of marten to shearing

A final objective of our study was to examine the response of our study population to shearing. Our analysis suggested that marten generally avoided but still made limited use of sheared areas and tolerated some sheared areas within their home ranges. At the population level, we detected no decrease in marten density and no change in male marten home range size as shearing progressed. However, we did detect individual-level reactions to shearing, which generally involved a shift in home range to adjacent areas with less sheared area and more intact forest or abandonment of home ranges altogether. We were unable to determine whether marten were reacting to the temporary noise and disturbance from the shearing or the permanent changes to cover type, but we suspect the latter given that the marten did not “recolonize” sheared areas after shearing was completed. These reactions occurred after an average of 35% of the home range was sheared and resulted in new home ranges for the affected individuals that contained half that amount of shearing. This is comparable to findings by Chapin et al. (1998) that marten tolerated a median of 20% regenerating clearcuts in their home ranges. Together, these results suggest that marten can tolerate small amounts of cleared area within their home ranges but not large percentages. Correspondingly, clear-cut areas have been shown to reduce marten density by 33%–90% relative to uncut areas (Soutiere 1979; Thompson 1994; Potvin and Breton 1997; Huggard 1999). Hargis et al. (1999) found that marten were absent from landscapes with >25% nonforest cover, but these harvested areas were devoid of any remnant structure.

There are two interpretations of the apparent lack of an effect of shearing on marten at the population level in our study area. First, we may not have detected a decrease in marten density in the study area because of the short time period that we were able to monitor after shearing (1–3 years). This interpretation would suggest that a subsequent decline related to the shearing may still occur. Another possibility is that the area affected by shearing (<17% of the study area) was too small to create population-level effects and was accommodated by shifts in home range (above) for most individuals. According to a model proposed by Thompson and Harestad (1994), marten density should decrease rapidly when more than 20%–30% of the landscape is cut, and our study area may have been under this threshold. Yet even in areas with greater amounts of cutting, marten seem to exhibit some capacity to adapt. Potvin and Breton (1997) found that animals frequenting cutovers (~50% of the landscape) had home ranges almost twice as large as those living in areas without cutovers, suggesting that marten may be more tolerant of forest fragmentation than was previously accepted and may adapt to clear-cutting by increasing linear movements within their home ranges (Heinemeyer 2002).

By showing consistent and productive use of young, deciduous forests, our results provide some clarification for the apparent contradiction between prior studies that report marten reliance on old-growth forest (Buskirk and Powell 1994; Buskirk and Ruggiero 1994; Thompson and Colgan 1994; Thompson and Harestad 1994) and those that indicate toler-

ance of a broader range of habitat conditions (e.g., Francis and Stephenson 1972; Chapin et al. 1997; Potvin et al. 2000). The paradox might be resolved by more precisely contrasting the costs and benefits of these alternative forest types. For example, clearcuts might be generally avoided by marten but still used as travel corridors (Heinemeyer 2002), presumably depending on season, clearcut size, and the presence of slash piles or windrowed debris (Soutiere 1979; Snyder and Bissonette 1987; Baker 1992). Marten may actually seek out clearcuts in late summer when berries are present (Steventon and Major 1982). In other seasons, marten may preferentially forage along the high-contrast edges caused by deforestation (Buskirk and Powell 1994; Huggard 1999) or at least show no avoidance of it (Chapin et al. 1998). Subtle differences in the degree to which marten select or avoid these open areas may often be dependent on their own predator guild because these areas correspond to higher mortality risk to marten than forests, especially from raptors (Hargis and McCullough 1984; Baker 1992; Thompson and Colgan 1994; this study).

### Management implications

Researchers appear to differ on landscape-level management recommendations to maintain marten in forested landscapes that also contain human disturbance. Some suggest consolidating clearcuts, keeping large residual patches to retain the largest amount of interior forest, and minimizing distance between large residual forests (Hargis and Bissonette 1997; Chapin et al. 1998; Potvin et al. 1999). In contrast, there is evidence to suggest that in some cases marten are positively affected by landscape heterogeneity at fine scales (Buskirk and Powell 1994; Huggard 1999). Steventon and Major (1982) found heavy use of islands of softwood within and adjacent to clearcuts. Our analysis at a smaller scale shows that marten also used unshaded areas adjacent to and within the sheared matrix.

Over the longer term (more than 30–40 years), the coniferous stands being created in the study area could provide moderate-quality marten habitat, provided that sufficient CWD has been retained and the remaining forest mosaic is untouched (Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Lyon et al. 1994; Thompson and Colgan 1994; Thompson and Harestad 1994; Potvin et al. 1999; Payer and Harrison 2003). Potvin et al. (1999) have suggested that, with these ideal characteristics, marten may tolerate up to 50% cutover forest within the landscape, although typical home ranges had less than 30%–35% clearcuts. Employing a smaller scale, our study provides evidence that changes in home ranges occur when 35% of forested cover is removed but that marten still utilize the area, comparable with Potvin et al.'s (1999) results. Thus, it appears reasonable that, provided there is sufficient conservation of features such as riparian areas and the provision of wildlife tree patches and CWD, marten can tolerate some forest harvesting. Additional work on determining thresholds is required, and results will likely vary by forest type and the spatial and temporal positioning of the cutovers (Potvin et al. 2000). A starting point may be to follow the suggestion of Potvin et al. (2000) that no more than 30% of an area be clear-cut over a 30-year period. As noted, these recommendations emphasize mitigating impacts to marten populations at the

stand scale and do not include spatial configuration attributes of the forest mosaic (Potvin et al. 2000; Payer and Harrison 2003). It should be possible to lessen the negative effects of habitat alteration at larger spatial scales by maintaining attributes at small scales. Management for forestry or management integrating or promoting other species within the landscape will require alterations to the forestry prescriptions that we have suggested (Hunter 1990; Potvin et al. 1999).

Although not specifically addressed in this analysis, investigation of finer scale selection from the study area (Porter 2002) and a sizable body of literature (summarized in Buskirk and Powell 1994; Buskirk and Ruggerio 1994; Coffin et al. 1997; Payer and Harrison 2003) suggested that CWD is likely of paramount importance in maintaining marten populations in areas like our study area. Marten use logging slash for resting and denning (Steventon and Major 1982; Raphael and Jones 1997). In recent clearcuts, the presence of CWD may encourage faster return of marten to these areas (Baker 1992). Red-backed voles, preferred prey for marten in many areas, are strongly associated with high structural complexity (Coffin et al. 1997). Therefore, within sheared areas, forest managers should leave unburned slash piles and windrows and other large-diameter CWD and islands or patches of standing structure where practical. Riparian buffers and other travel corridors should be maintained to encourage marten movement (Grindal et al. 1999). Marten use of regenerating stands may also be enhanced in areas with dense shrub layer and coniferous regeneration (Potvin et al. 1999). If possible, silviculture prescriptions for sheared and regenerating areas should encourage dense shrub regeneration once conifer seedlings have overcome competing species. At the very least, managers should not dismiss nonconiferous stands in assessing and modeling marten habitat quality.

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