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# Paradigm Shifts in Habitat Ecology of Threatened Newfoundland Martens

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**ABSTRACT** We evaluated multiscale habitat selection by threatened Newfoundland (Canada) martens (*Martes americana atrata*) across landscapes composed of a range of habitat types to test the hypothesis that martens preferred mature (61–80-yr-old) and overmature (>80 yr) conifer stands. At both the landscape and stand scales, adult ( $\geq 1$  yr) resident martens ( $n = 58$ , 92 yr-specific home ranges) selected for, or used in proportion to availability, a broad range of habitat types, including recent cuts  $\leq 5$  yr old, regenerating forest  $< 6.5$  m, precommercially thinned stands, and mature and overmature forest. Marten home ranges were not dominated by mature and overmature forest; median availability of mature and overmature forest within individual home ranges was only 30% (range = 11–76%). Age distributions were not different among martens with high, intermediate, and low quantity of mature and overmature forest in their home range; our data do not indicate that martens inhabiting ranges with little mature and overmature forest were compromising fitness. Habitat selection by martens in Newfoundland was more generalized than has traditionally been inferred, and we suggest that inherent landscape fragmentation, in combination with absence of many predators and competitors (i.e., ecological release), caused the Newfoundland marten to evolve to use a more generalized habitat niche than many mainland populations of American martens. We recommend that landscapes suitable for marten not exceed  $> 29\%$  younger aged forest. Maintaining resident martens in landscapes where forest harvesting is occurring requires prescriptions that recognize the highly fragmented nature of the natural landscape, the prevalence of mature and overmature forest, younger forests, avoided land-cover types, and human access.

**KEY WORDS** habitat, marten, *Martes americana*, Newfoundland, preference, scale, selection.

Newfoundland martens (*Martes americana atrata*), a genetically distinct and threatened population of American martens endemic to the island of Newfoundland, Canada, experience ecological conditions different than those for other marten populations throughout North America (Kyle and Strobeck 2003, Hearn et al. 2006). Newfoundland, like most islands, has fewer native species compared with continental areas of similar size and latitude (MacArthur and Wilson 1967). Moreover, the composition of the terrestrial mammalian community is highly skewed, with a disproportionate number of predators and few prey species (Dodds 1983, Hearn et al. 2006). The island of Newfoundland has only one native microtine, the meadow vole (*Microtus pennsylvanicus*), previously thought to be the primary small mammal prey for Newfoundland martens (Bateman 1986, Thompson and Curran 1995, Sturtevant and Bissonette 1997). It is hypothesized that the depauperate prey base in Newfoundland has restricted martens to older forests where low-density meadow vole populations are more abundant than in younger ( $< 80$  yr) forests, and that Newfoundland martens require mature and overmature conifer because of limited prey availability (Thompson and Curran 1995, Sturtevant et al. 1996, Bissonette et al. 1997, Sturtevant and Bissonette 1997). Recent studies, however, suggest a more generalized diet of Newfoundland martens and extensive use of snowshoe hare (*Lepus americanus*)

during winter (Gosse and Hearn 2005). Given that hares typically occur at higher densities in regenerating forests than in mature conifer stands and that meadow voles occur at low density in forests, we predicted that marten may be more generalized in habitat selection than has previously been inferred (Parker 1986, Thompson and Curran 1995, Fuller and Harrison 2005, Fuller et al. 2007; but see Gosse et al. 2005).

American martens have often been described as a habitat specialist for late-successional, conifer-dominated forests (Koehler and Hornocker 1977, Hargis and McCullough 1984, Buskirk and Powell 1994). Hypotheses to explain the forest-dependent associations of martens (Thompson and Harestad 1994) include 1) martens require overhead canopy for security or avoidance of terrestrial and avian predation (Hargis and McCullough 1984); 2) martens require structurally complex forests with abundant coarse woody debris and large-diameter trees to provide suitable winter resting sites, maternal dens, and subnivean access to small mammal prey in winter (Bergerud 1969, Steventon and Major 1982, Wynne and Sherburne 1984, Corn and Raphael 1992, Sherburne and Bissonette 1994); and 3) martens are more successful in accessing prey in older, structurally complex forests and not necessarily where prey are most abundant (Thompson and Colgan 1987).

More recent evidence from across the geographic range of the marten suggests that habitat associations may be broader than previously understood (Bowman and Robitaille 1997, Potvin et al. 2000, Payer and Harrison 2003, Poole et al. 2004, Mowat 2006). In the transitional Acadian forests of northeastern North America, martens utilize a wide range of

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**Table 1.** Description of land-cover classes, percent of landscape composed of each class, and mean patch size (ha) within our 1,900-km<sup>2</sup> marten study area, southwestern Newfoundland, Canada, 1995–2000. Land-cover classes were derived from the provincial forest inventory (Anonymous 1991).

Land-cover class	Code	Description	%	Mean patch size
Bog-barren	BB	Open, generally treeless bogs; rock and soil barrens	22	14.7
Recent cuts	RC	Recent ( $\leq 5$ yr) cuts; residual patches of conifer and mixed wood	4	25.6
Scrub	SC	Unmerchantable conifer $\leq 6.5$ m in ht; generally low-productivity sites	9.5	6.8
Regenerating forest	RF	Conifer regeneration $\leq 6.5$ m in ht, $\geq 75\%$ canopy closure	3.6	8.2
Precommercially thinned	PCT	20–30-yr-old conifer stands, 7–17 yr postthinning, $>50\%$ canopy closure, typical density of 1,500 stems/ha	3.4	29.7
Medium-ht open-canopy conifer	MOC	Conifer stands, 6.6–12.5 m in ht, $\leq 50\%$ canopy closure	13.3	7.6
Medium-ht closed-canopy conifer	MCC	Conifer stands, 6.6–12.5 m in ht, $>50\%$ canopy closure	4.3	7.3
Tall open-canopy conifer	TOC	Mature and overmature conifer stands $\geq 12.6$ m in ht, $\leq 50\%$ canopy closure	6.4	6.9
Tall closed-canopy conifer	TCC	Mature and overmature conifer stands $\geq 12.6$ m in ht, $>50\%$ canopy closure	10.9	11.0
Insect-killed stands	IK	Insect-killed conifer stands, primarily $\geq 12.6$ m in ht, $<25\%$ canopy closure, understory typically dense advanced conifer ( <i>Abies balsamea</i> ) regeneration	2.4	6.2
Other <sup>a</sup>		Rare forest types, including hardwood, mixed wood, stand remnants, cleared land, transmission lines, roads, gravel pits, and disturbed areas	6.1	27.2
Water <sup>a</sup>		All ponds, lakes, streams, and rivers	14.1	21.8

<sup>a</sup> We did not evaluate selection of these classes.

forest types, including mixed coniferous–deciduous and deciduous-dominated stands (Katnik 1992, Chapin et al. 1997, Payer 1999, Fuller and Harrison 2005), as well as open-canopy stands regenerating following insect defoliation (Chapin et al. 1997; Payer and Harrison 2000, 2003). Similarly, martens inhabiting second-growth boreal forests in western Quebec, Canada, preferred deciduous and mixed deciduous forests  $>30$  years old and showed no selection for coniferous forests (Potvin et al. 2000). Forest structure may be a more important determinant of marten habitat than forest species composition or forest age (Chapin et al. 1997, Porter et al. 2005). Within home ranges, martens are better defined as structural obligates, requiring complex horizontal and vertical structure (Chapin et al. 1997; Payer and Harrison 2000, 2003); these structural requirements are likely provided by a variety of forest types throughout the range of the species.

We examined habitat ecology of Newfoundland martens in southwestern Newfoundland, the region of the island thought to contain the largest remaining population (Thompson 1991, Forsey et al. 1995). Our objectives were to 1) evaluate multiscale habitat selection by martens across landscapes composed of a range of habitat types, including mature and overmature coniferous forests, extensive areas of conifer scrub on poorer quality sites, regenerating clear-cuts, areas of insect-killed overmature coniferous forest, and precommercially thinned conifer stands; 2) test the hypothesis that mature and overmature conifer stands were preferred by martens over other forest types; and 3) compare the age structure of resident martens with differing amounts of mature and overmature forests in their home ranges.

## STUDY AREA

We defined the boundary of the 1,900-km<sup>2</sup> study area in southwestern Newfoundland, Canada (48°30'N, 57°30'W) as the effective trapping area, determined by creating a 6.26-km buffer (diam of the mean 95% min. convex polygon home

range; Hearn 2007) around all trap locations. The area was composed of extensive areas without a history of forest harvesting where natural disturbance occurred with few anthropogenic influences, as well as substantial areas with past (prior to 1960) and recent ( $\leq 10$  yr) forest harvesting activities. Forests were composed primarily of balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) mixed with white pine (*Pinus strobus*), larch (*Larix laricina*), white birch (*Betula papyrifera*), and white spruce (*Picea glauca*). Hemlock looper (*Lambdina fuscicollis*) and spruce budworm (*Choristoneura fumiferana*) infestations resulted in stands dominated by standing and downed conifer trees; those insect-killed (IK) softwood stands ranged in size from 0.60 ha to 200 ha (median patch size = 2.85 ha). Insect-killed stands typically had little to no crown closure, an abundance of snags in various stages of decay, and substantial coarse woody debris. Most were 10–20 years postinfestation and typically had a dense ground cover of balsam fir regeneration (Table 1).

Clear-cutting began in the late 1970s and 6,840 ha of the landscape was in regenerating forest (RF,  $>5$  yr since harvest), 6,400 ha recent cuts (RC,  $\leq 5$  yr), and an additional 5,760 ha was composed of 20–30-year-old clear-cuts that were subsequently precommercially thinned (PCT) to reduce stem densities (Table 1). Other land-cover classes represented 9.5–17.6% of the landscape and included unmerchantable softwood scrub forest (SC) that had no previous harvest history; tall ( $\geq 12.6$  m), mature, and overmature open-canopy (TOC) and closed-canopy (TCC) conifer forest; medium-height (6.6–12.5 m) closed-canopy conifer (MCC); medium-height open-canopy conifer forest composed of mature trees occurring on poorer quality sites (MOC); bogs and barrens (BB); and water (ponds, lakes, streams and rivers; Table 1).

## METHODS

We trapped martens in collapsible live-traps (18 × 18 × 48 cm) for a 2–4-week period throughout the year (typically

Jun–Aug, late Sep–Oct, and Mar–Apr), 1995–2000. We located traps every 1–2 km along roads, snowmobile trails, or shorelines to maximize likelihood that all potential marten territories would include  $\geq 1$  trap. We sexed, weighed, and fitted martens with a 34–36-g very high frequency radiocollar (Lotek Wireless Inc., Newmarket, ON, Canada; Holohyl Systems, Inc., ON, Canada) that incorporated a 12-hour delay mortality switch and had an expected operational life of  $\geq 13$  months. We removed a first premolar ( $PM_1$ ) from each marten for cementum aging (Matson's Laboratory, Milltown, MT); whenever possible we extracted a fourth premolar ( $PM_4$ ) tooth from animals that died during the study.

We located radiocollared martens every 7–10 days, primarily using fixed-wing aircraft (58.1% of locations) or helicopter (26.9%). We used similar telemetry methods and equipment as Gosse et al. (2005) who reported a mean relocation error of 105 m (error ellipse of 3.5 ha) for locations from fixed-wing aircraft in eastern Newfoundland. We estimated helicopter relocation error as the mean distance between aerial and ground locations when retrieving marten mortalities.

We estimated 95% minimum convex polygon home ranges for all resident adult ( $\geq 1$  yr) martens with  $\geq 19$  locations (i.e., area-observation curve asymptote) during the biological year using the Animal Movement Extension (Hooge et al. 1999) for ArcView® 3.2 (Hearn 2007). We classified a marten as resident (Phillips et al. 1998) if it was  $\geq 12$  months old; was monitored for  $\geq 10$  temporally independent ( $\geq 24$  hr apart) locations  $>90$  days; and was nontransient based on having a mean minimum distance moved between consecutive independent locations (MIND-IST) that was not farther than the mean distance + 3 standard deviations for all consensual martens (Harrison and Gilbert 1985, Phillips et al. 1998). We defined the biological year as 1 May–30 April and pooled data to produce individual marten- and year-specific databases. We tested for seasonal shifts in home-range area and did not calculate annual home ranges for animals with discrete seasonal ranges.

We created a habitat map of the study area using the Provincial Forest Inventory (PFI), which was interpreted from 1:12,500-scale stereoscopic, black and white aerial photography taken in 1986 with a minimum mapping unit of approximately 0.30 ha. To account for changes in stand height between 1986 and the beginning of our study in 1995, we increased stand height by one height class (2.9 m) for all stands with a site-quality index of medium or better based on local growth and yield equations (Anonymous 1991). We incorporated annual updates to the PFI (i.e., forest harvesting, road construction, silvicultural activities, and insect disturbance) to produce year-specific land-cover maps for each year of the study.

We created 12 land-cover classes (Table 1) based on forest composition and structural characteristics (i.e., stand ht, crown closure). Tall open-canopy conifer, TCC, and IK classes represented mature (61–80-yr-old) and overmature ( $>80$ -yr-old) coniferous forests. We combined all rare or

structurally uncharacterized land-cover types into an “other” class (6.1% of study area) and excluded it from further habitat selection analyses.

We evaluated landscape- and stand-scale habitat selection by calculating selection indices (SI) for each land-cover class as follows:  $SI = \ln(\text{use/availability})$ . We used a Design III approach (Thomas and Taylor 1990, Manly et al. 2002), where we estimated use and availability of resource units (i.e., habitat classes) separately for each animal and, thus, the individual radiomarked animal was the experimental unit. We used natural logs to rescale the SI and to center the index on zero;  $SI > 0$  indicated preference,  $SI < 0$  indicated avoidance, and  $SI = 0$  indicated use of a habitat type proportional to its availability. We used a Kruskal–Wallis test (Conover 1999) to evaluate our hypothesis that martens used habitats in proportion to availability and inferred differences in habitat selection across land-cover types based on rankings of median SI across habitat categories. Many home ranges had little or no availability for  $\geq 1$  of our land-cover classes; therefore, our approach eliminated the statistical issues associated with the use of substitution values for land-cover types that were unavailable, as is required in other common resource selection analyses (e.g., Aebischer et al. 1993, Bingham et al. 2007).

Martens are intrasexually territorial and display home-range fidelity (Katnik et al. 1994, Phillips et al. 1998, Payer et al. 2004). Additionally, socially dominant animals presumably occupy higher quality habitats or home ranges, thereby increasing their fitness in accordance with the ideal-despotic hypothesis (Fretwell 1972, Pulliam and Danielson 1991). Thus, annual home ranges occupied consecutively by the same individual are likely of higher quality, so we considered the individual year-specific home range as the unit of replication for habitat selection analyses. This approach avoided the underrepresentation of high-quality portions of the study area that received repeated use by resident individuals whose survival spanned  $>1$  annual monitoring period after being radiocollared.

We explored whether seasonal variation in habitat use was a factor in our habitat selection results (Buskirk and Powell 1994). We used chi-square analysis to test whether habitat use was independent of season (summer = 1 May–30 Nov; winter = 1 Dec–30 Apr). We also conducted a multivariate analysis of variance on ranked habitat SI to test effects of gender on habitat selection.

For landscape-scale habitat selection (second-order selection; Johnson 1980), we calculated a SI for each land-cover class by comparing the percent of each class within the home range (use) to the percent of the class available on the landscape (availability) for individual martens, on a year-specific basis. We defined habitat availability using the year-specific study area (excluding water) excluding all areas within the home ranges of consensuals, to account for intrasexual territoriality. We calculated simulated home ranges for individuals with too few locations ( $n = 10$ – $18$ ) to calculate asymptotic home ranges. Based on data from 30 individual martens (41 marten-yr) with  $\geq 30$  radiolocations/animal, we developed a regression equation to predict home

range area (i.e., 95% min. convex polygon Area [km<sup>2</sup>] = 0.013 [MINDIST] - 13.785,  $r^2 = 0.79$ ; Harrison and Gilbert 1985, Phillips et al. 1998). We used this regression equation to simulate home ranges for animals with 10–18 locations to estimate the area unavailable to adjacent conspecific territorial martens (Katnik et al. 1994, Fuller 2006). We otherwise excluded simulated home ranges from habitat selection analyses.

We included 6 land-cover classes to test (Kruskal–Wallis  $T$ -statistic) whether martens displayed similar selection for all 6 land-cover classes at the landscape scale, eliminating young RF  $\leq 6.5$  m, RC  $\leq 5$ -years old, IK stands, and PCT stands. By restricting our landscape-scale analyses, we eliminated the need for nonzero substitution values for habitat use when no use was recorded (Aebischer et al. 1993). Additionally, we separately analyzed habitat use for the 4 land-cover types eliminated from our global analyses; those types represented all 60 cases (17.8%) where we substituted a value of 0.01 for nonuse, using a sign test (Conover 1999) to evaluate whether individual land-cover classes were selected (SI  $\neq 0$ ).

We evaluated stand-scale habitat selection (within home range; third-order selection; Johnson 1980) by determining the proportion of locations in each of the 10 habitat classes (use) and availability as the proportion of each class within the individual marten- and year-specific home range (excluding water). We used a Kruskal–Wallis test (Conover 1999) to evaluate our hypothesis that martens selected habitats types in proportion to availability. To avoid computing spurious measures of habitat selection for rare habitat classes or those receiving sporadic use, we applied 2 criteria when calculating a stand-scale SI. First, we did not calculate a SI if the expected number of locations occurring in a land-cover class was  $< 2$  ( $\leq 10.5\%$  of the home range). Secondly, if a land-cover class had an expected value  $> 2$ , but was unused, we arbitrarily substituted a 0.001 value for use. Selection index values calculated using substitution values (6.3%) appropriately resulted in negative SI at a similar range of values ( $< 0$ ,  $> -3$ ) as observed for SI calculated without substitutions.

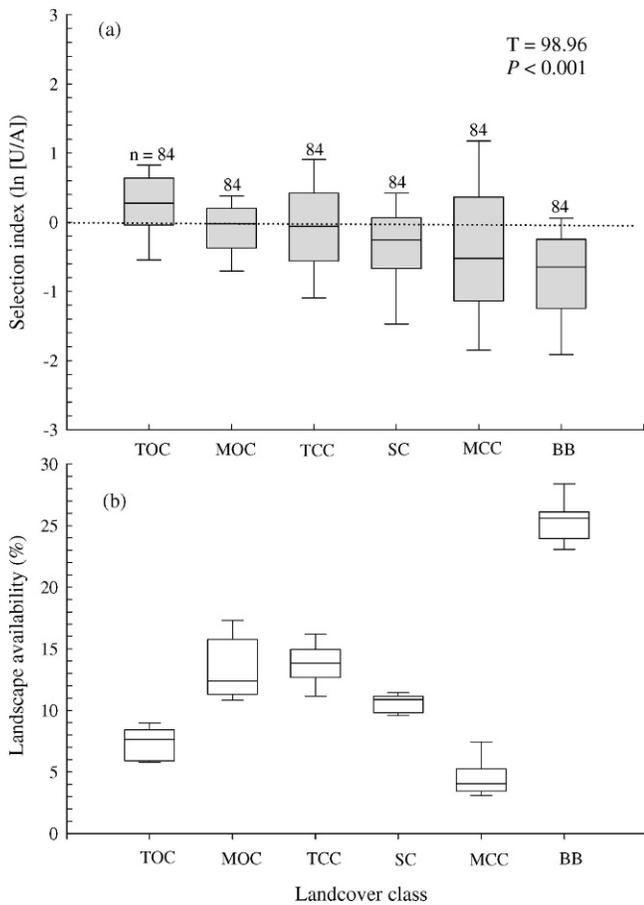
We evaluated 3 a priori questions regarding habitat selection by martens using pairwise comparisons of SI between habitat classes. Our first question evaluated whether martens in Newfoundland select TCC forests over medium-height forests or those with more open canopy. Specifically, we tested whether TCC stands had higher SI than MCC stands, which would suggest that height of conifer stands was an important determinant of habitat choice. We also tested whether TCC stands had greater SI compared with TOC stands, which would suggest that martens prefer tall conifer-dominated stands only if they have a closed canopy. Last, we tested whether TOC stands had greater SI than MOC stands, which would suggest that conifer stands with canopy closure  $< 50\%$  are used only when tree heights exceed 12.5 m. Our second question considered whether IK stands were selected comparably to mature conifer stands regardless of overstory canopy closure. Specifically, we evaluated whether TCC stands and TOC

stands had SI equal to IK stands. Our third question evaluated whether closed-canopy, conifer-dominated stands received equal preference by Newfoundland martens as younger forests regenerating after timber harvesting by testing whether TCC stands had SI equal to regenerating conifer forests at both landscape and stand scales. When comparing SI between common habitat classes, we used Fisher's Least Significant Difference tests (Conover 1999) where  $n$  was total number of SI across both habitat classes. We considered a pairwise test significant if  $P < 0.10$ . We did not adjust the alpha level to control experiment-wise error rate, judging that the latter procedure would have substantially decreased our ability to discern habitat types of significantly different value to martens in Newfoundland (i.e., inflated Type II error rates), which potentially have greater conservation implications for a species at risk than Type I errors (Taylor and Gerrodette 1993).

Territorial mustelids have delayed age at sexual maturity and greater longevity (body mass adjusted) relative to other carnivores (Ferguson and Larivière 2004); therefore, population age structure is associated with both survival and lifetime reproductive potential. Accordingly, we indexed population performance of martens in relation to their home-range availability for mature and overmature conifer forest (TCC + TOC + IK) by comparing year-class age distributions (i.e., 5 age [yr] classes: 1, 2, 3, 4,  $> 5$ ) of animals with low (10–27%), medium (28–34%), or high (34–74%) prevalence of these land-cover classes within the home ranges; we based class boundaries on the 33rd and 66th percentiles for the distributional range of availability of mature and overmature forest within the home ranges. Subsequently, we used a chi-square test to compare age distributions among the 3 classes.

## RESULTS

We captured 159 individual martens during June 1995–August 2000, including 93 adults ( $\geq 1$  yr) and 54 juveniles ( $< 1$  yr); we did not obtain ages for 12 animals. We equipped 155 animals with radiocollars and collected 5,086 locations. Of the 93 confirmed adults, we monitored 58 individuals for a sufficient period to meet residency and asymptotic home-range criteria (Hearn 2007), from which we produced 92 year-specific home ranges (43 M, 49 F). Each year-specific database was a product of all aerial-telemetry (88%), ground-telemetry (5%), and trapping (7%) locations ( $n = 2,861$ ) that were temporally independent (i.e.,  $> 24$  hr apart; Katnik et al. 1994). Data met our minimum criteria to calculate a year-specific home range for 32 of the 58 individual martens; however, 20 martens provided annual home ranges across 2 years, 5 across 3 years, and 1 marten provided estimates across 5 years. Mean number of relocations per annual home range was 31 (range = 19–54). Mean distance between aerial and ground locations ( $n = 24$ ) obtained by helicopter for radiocollars retrieved from marten mortalities was 40 m (SE = 9.0) yielding an error ellipse of 0.50 ha. Overall, the ratio of estimated circular errors around telemetry locations relative to mean size of patches of each of our 10 habitat classes



**Figure 1.** Landscape-scale habitat selection indices (a) and habitat availability (b) for 84 annual home ranges of 54 adult ( $\geq 1$  yr) resident martens, southwestern Newfoundland, Canada, 1995–1997; U = land-cover class use, A = land-cover class availability. Land-cover class descriptions are as follows: TOC = tall open-canopy conifer, MOC = medium-height open-canopy conifer, TCC = tall closed-canopy conifer, SC = conifer scrub, MCC = medium-height closed-canopy conifer, BB = bog and barren. Land-cover classes are displayed in rank order of relative preference from highest (TOC) to lowest (BB).  $T$  is the Kruskal–Wallis test statistic. Selection indices  $> 0$  indicate preference and values  $< 0$  indicate avoidance; lower box boundary is the 25th percentile, line within the box marks the 50th percentile (median), and the upper box boundary is the 75th percentile. Whiskers below and above the box indicate the 10th and 90th percentiles, respectively.

(Table 1) ranged from 0.06:1 to 0.18:1 for fixed-wing telemetry and 0.02:1 to 0.08:1 for helicopter telemetry, which were substantially less than the upper limit of 1.5:1 suggested by Nams (1989).

### Habitat Selection

Land-cover accuracy of the aerial photography derived PFI based on permanent forest inventory sample plots (ground) on the study area was 84% (J. Luther, Natural Resources Canada-Canadian Forest Service, unpublished data). Further, height was a reliable surrogate of forest age; 84% of marten locations ( $n = 769$ ) in the TCC, TOC, and IK classes ( $> 12.6$  m) were in forest stands documented as  $\geq 81$  years old in the PFI (Anonymous 1991). Additionally, 76% of stands classified as MCC (6.6–12.5 m) were  $< 80$  years old. Stand age was not available for  $> 75\%$  of MOC in the PFI, because these stands were classified as

**Table 2.** Landscape-scale selection analyses (nonparametric sign tests) for 4 land-cover classes excluded from the global test for landscape-scale habitat selection. We based analyses on data for 54 individual (29 M, 25 F) adult ( $\geq 1$  yr) resident martens representing 84 marten-years (40 M, 44 F), southwestern Newfoundland, Canada, 1995–1997.

Selection index	Land-cover class <sup>a</sup>			
	RF	RC	IK	PCT
Positive	55	19	40	35
Negative	29	16	31	48
Total <sup>b</sup>	84	35	71	83
$P$ -value	0.006	0.735	0.342	0.188

<sup>a</sup> Land-cover class descriptions are provided in Table 1; RF = young regenerating forest, IK = overmature insect-killed stands, RC = recent cuts  $\leq 5$  yr old, and PCT = precommercially thinned stands.

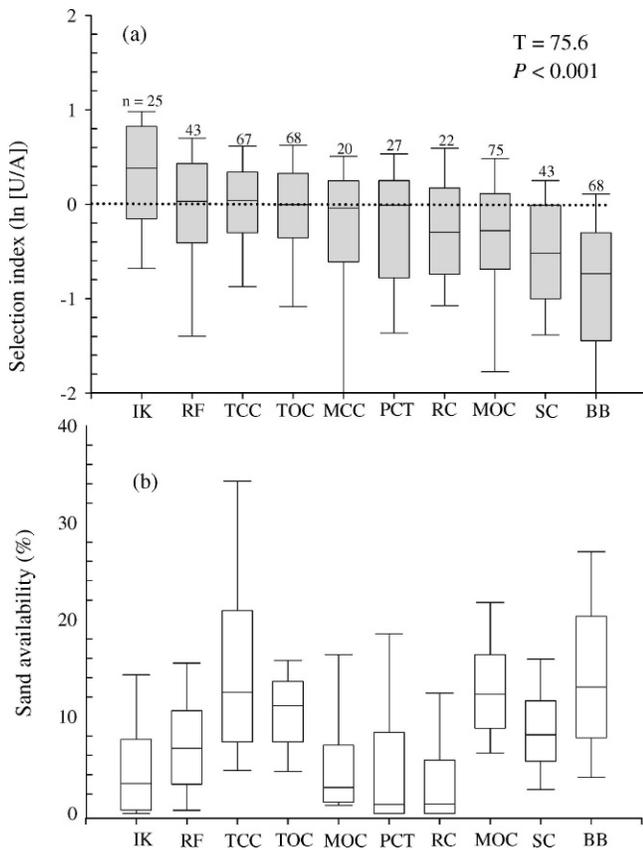
<sup>b</sup> Total no. of landscape-scale selection indices calculated for each land-cover class.

unmerchantable. Seasonal distribution of locations ( $n = 2,271$ ) did not differ across the 10 habitat types ( $\chi^2_9 = 11.53$ ,  $P = 0.24$ ); therefore, we pooled habitat selection data across seasons for subsequent analyses.

Landscape-scale SI did not differ between sexes ( $F_{1,5} = 1.11$ ,  $P = 0.35$ ); therefore, we combined data across sexes. We based landscape-scale habitat selection analyses on 54 martens (29 M, 25 F) representing 84 marten-years (40 M, 44 F), 1995–1997. Martens did not use habitat classes in proportion to their availability at the landscape scale (Fig. 1). Across all martens, TOC had the highest SI and the distribution of SI indicated that use of this class was 1.3 times availability at the landscape scale (Fig. 1). Distribution of selection values for MOC and TCC indicated proportional use of those classes by martens. Both SC and BB classes had lower selection values relative to mature and overmature coniferous forest (Fig. 1) and generally were avoided (i.e., use was only 0.77 and 0.52 times availability for SC and BB, respectively).

Landscape-scale SI for the 4 habitat types not included in the global analysis strongly suggested that young RF was positively selected nearly twice as frequently as they were avoided (Table 2). We had insufficient evidence to conclude that IK stands, RC, or PCT stands were selected disproportionately to availability on the landscape (Table 2).

Across all comparisons, there was little evidence that TCC stands were selected positively (Fig. 1) or that these stands had higher relative preference by martens than did RC (Fig. 1; Table 2). Further, martens did not occupy home ranges dominated by tall mature and overmature forest. Median occurrence of mature and overmature forests (TCC + TOC + IK) within home ranges occupied by resident, adult ( $\geq 1$  yr) martens was only 30.0% (range = 10.7–75.6%). Seventy-five percent of martens had  $< 36\%$  tall mature and overmature types within their home ranges and 90% had  $\leq 45\%$ . Tall closed-canopy conifer stands did not receive the highest selection at the landscape scale, and comprised only 12.5% of resident martens' home ranges; 75% of home ranges were composed of  $< 20\%$  TCC stands and 90% had  $< 34\%$ . Medium-height closed-canopy conifer stands received landscape-scale use by all individuals but had the greatest variation in SI. Although MCC stands ranked



**Figure 2.** Stand-scale habitat selection indices (a), and habitat availability (b), for 92 annual home ranges of 58 adult ( $\geq 1$  yr) resident martens, southwestern Newfoundland, Canada, 1995–2000; U = land-cover class use, A = land-cover class availability. Land-cover class descriptions are as follows: IK = insect-killed, RF = regenerating forest, TCC = tall closed-canopy conifer, TOC = tall open-canopy conifer, MCC = medium-height closed-canopy conifer, PCT = precommercially thinned, RC = recent cuts, MOC = medium-height open-canopy conifer, SC = conifer scrub, BB = bog and barren. Land-cover classes are displayed in rank order of selection from highest (IK) to lowest (BB).  $T$  is the Kruskal–Wallis test statistic. Selection indices  $>0$  indicate preference and values  $<0$  indicate avoidance; lower box boundary is the 25th percentile, line within the box marks the 50th percentile (median), and the upper box boundary is the 75th percentile. Whiskers below and above the box indicate the 10th and 90th percentiles, respectively.

second lowest in relative preference among all classes and below the SI for SC, the wide range of SI (Fig. 1) suggested that this class (MCC) was either used proportionally or avoided at the landscape scale.

Stand-scale use of habitat classes did not differ between sexes ( $F_{1,8} = 1.16, P = 0.32$ ); therefore, we dropped sex as a covariate. After screening for low ( $<2$ ) expected values and missing habitat classes, we calculated 458 SI of a possible 920 (10 types  $\times$  92 home ranges); no animals provided SI for all 10 possible habitat classes. At the stand scale, martens did not use habitat classes in proportion to their availability (Fig. 2). Martens displayed positive selection for IK stands (use 1.47 times availability) and avoidance of MOC, coniferous SC, and BB land-cover types. In fact, use was 0.75 times, 0.59 times, and 0.48 times that of availability for the latter 3 classes, respectively. The 6 remaining habitat classes (RF, TCC, TOC, MCC, PCT, and RC) were used

in proportion to availability within home ranges of martens (Fig. 2). Importantly, our RF land-cover class included 2 height categories (ht class 1 = 0–3.5 m, ht class 2 = 3.6–6.5 m), and 99.2% ( $n = 242$ ) of marten locations observed in the RF class were in stands  $>3.5$  m. Thus, our results indicating high relative preference for regenerating stands are applicable only to stands  $>3.5$  m in height.

Median percent of mature and overmature forests in marten home ranges ( $n = 86$ ) that were characterized as having low, medium, and high availability of these paradigm habitats was 21.2% (range = 10.7–27.6%), 30.2% (range = 28.1–33.8%), and 40.4% (range = 33.9–74.6%), respectively. Year-class age distributions did not differ ( $\chi^2_8 = 4.49, P = 0.81$ ) among martens with different amounts of mature and overmature forests in their home range.

In general, comparisons of relative preference between pairs of habitat classes indicated similar patterns of habitat selection by martens across spatial scales (Table 3). Tall mature and overmature stands were selected similarly by martens at landscape and stand scales, regardless of whether they had closed or open canopies (Table 3). Tall mature and overmature closed-canopy conifer stands were ranked higher in selection over MCC stands at the landscape scale, but selection of those types by martens did not differ at the stand scale (Table 3; use:availability ratios of 1.04 and 0.96, respectively). Notably, MCC stands had a wide SI range for landscape-scale selection; thus, our SI result for that class was somewhat equivocal (Fig. 1). Unequivocally, however, TOC stands were selected over shorter MOC stands at both the landscape and stand scales (Table 3), suggesting that height, which was also positively associated with site quality, may be an important correlate of habitat preference by Newfoundland martens when comparing stands that have advanced beyond the pole stage.

Insect-killed and TCC stands were both used in proportion to availability at the landscape scale, but IK stands were preferred over TCC stands at the stand scale, had a median selection index 1.5 times availability, and ranked highest in relative preference (Fig. 2). Similarly, IK stands were preferred over TOC at the stand scale (Table 3), but at the landscape scale, TOC received positive selection (use was 1.32 times availability; Fig. 1), whereas IK stands were used in proportion to availability (Table 2). Despite their low canopy cover and general absence of live overstory, IK stands had the highest relative preference of all habitat classes at the stand scale (Fig. 2). Thus, insect-defoliated stands dominated by dead or downed trees were preferred similarly to living mature and overmature coniferous stands by Newfoundland martens.

Finally, the paradigm that mature and overmature coniferous forests are preferred by martens over young RF was not supported by our results. Regenerating forest was selected at the landscape scale (use was 1.57 times availability), whereas TCC stands were used in proportion to availability (Table 3). At the stand scale, martens exhibited similar selection for RF and TCC stands (Table 3).

**Table 3.** Seven predictions we tested to evaluate 3 a priori questions related to habitat selection by 58 individual (31 M, 27 F) adult ( $\geq 1$  yr) resident Newfoundland martens at the stand and landscape scales, southwestern Newfoundland, Canada, 1995–2000. Land-cover class codes and descriptions are provided in Table 1.

Habitat question	Hypotheses tested	Landscape			Stand		
		Outcome	<i>n</i>	<i>P</i> -value	Outcome	<i>n</i>	<i>P</i> -value
1. Do martens select tall closed-canopy conifer forests > intermediate-old forests that are shorter or have more open canopy?	TCC has higher SI <sup>a</sup> than TOC	TCC = TOC	168	0.999	TCC = TOC	135	0.386
	TCC has higher SI than MCC	TCC > MCC	168	0.004	TCC = MCC	87 <sup>b</sup>	0.125
	TOC has higher SI than MOC	TOC > MOC	168	$\leq 0.001$	TOC > MOC	142	0.004
2. Are insect-killed stands selected comparably to mature conifer stands regardless of overstory canopy closure?	SI for TCC and IK are equal	TCC = IK <sup>c</sup>			IK > TCC		
	SI for TOC and IK are equal	TOC > IK <sup>d</sup>			IK > TOC		
3. Do closed-canopy, conifer-dominated stands receive equal preference by Newfoundland martens as forests regenerating after timber harvesting?	SI for TCC and RF are equal	RF > TCC <sup>e</sup>			RF = TCC	110	0.939

<sup>a</sup> SI (selection index) =  $\ln(U/A)$  where  $U$  = land-cover class use,  $A$  = land-cover class availability.

<sup>b</sup> We pooled no. of selection indices among habitat classes.

<sup>c</sup> IK and TCC both used proportionally at landscape scale.

<sup>d</sup> TOC is selected for at landscape level ( $n = 84$ ,  $P \leq 0.001$ ); IK used proportionately ( $n = 71$ ,  $P = 0.342$ ).

<sup>e</sup> RF is selected for at landscape scale ( $n = 84$ ,  $P = 0.006$ ); TCC used proportionally ( $n = 84$ ,  $P = 0.585$ ).

## DISCUSSION

Martens used a wider range of forest-stand conditions than traditionally reported in Newfoundland (Snyder and Bissonette 1987, Thompson and Curran 1995, Sturtevant et al. 1996, Bissonette et al. 1997; but see Gosse et al. 2005), suggesting that habitat quality for martens does not necessarily equate with the extent and degree of maturity of conifer-dominated stands. We had little evidence to support the paradigm that Newfoundland martens prefer overmature conifer forest relative to all other forest types, including mid-successional and young regenerating conifer forests. Mature and overmature forest were previously hypothesized to be required by Newfoundland martens; however, these types typically represented about 25% of the forested habitats available for marten occupancy and only about one-third of home ranges for adult resident martens. Thus, our results generally agree with more recent habitat selection studies elsewhere indicating that forests do not need to be overmature to provide suitable habitat for American martens (Bowman and Robitaille 1997, Potvin et al. 2000, Poole et al. 2004, Fuller and Harrison 2005, Mowat 2006). In fact, martens selected for or proportionally used all forest classes including tall mature and overmature forest, RF >3.5 m, PCT RF, and recent ( $\leq 5$  yr) cuts at both the landscape and stand scales. Martens exhibited avoidance of only SC forest <6.6 m (both scales), BB (both scales), closed-canopy mid-height forest (landscape scale), and MOC stands (stand scale); however, these classes still comprised about one-quarter of home ranges. Further, our results and those of Gosse et al. (2005) in central Newfoundland both reported that martens did not select against IK stands with canopy closure <25%. Finally, similar selection for regenerating forest (RF and RC) relative to TCC stands at both scales suggests that a variety of forest age, stocking, and successional classes are suitable

for home range occupancy by Newfoundland martens and that these types, in aggregate, determine probability of home-range occupancy (Fuller 2006).

Overall, our findings suggest that martens did not avoid forest stands recently (<20 yr) altered by logging and that martens did not avoid regenerating stands that had been treated with PCT, with the caveat that we obtained only 2 locations of martens in cuts with vegetation <3.5 m in height. Snyder and Bissonette (1987:169) concluded that “martens seldom use clear-cuttings” in western Newfoundland based on live-captures. However, only 6.5% of their trapping effort focused within clear-cut stands occurred in cuts with regenerating vegetation >2 m and >15 years after harvest. Thus, conclusions of Snyder and Bissonette (1987) may not apply to regenerating stands where woody vegetation exceeds 3.5 m in height. In Maine, USA, martens did not select against RF 6–9 m in height, but strongly selected against recent clear-cuts <6 m in height (Katnik 1992, Payer 1999, Fuller and Harrison 2005). Thus, we assert that forest structure, rather than forest age per se, determines stand-scale habitat suitability for martens, but that in Newfoundland, cuts may be unsuitable for only the first 1–2 decades after harvest and before regenerating woody vegetation reaches 3.5 m in height (Chapin et al. 1997, Payer and Harrison 2003).

Based on survival modeling (Hearn 2007) and age-structure information from our resident individuals, martens on our study site that inhabited home ranges composed of little mature and overmature forest did not compromise their fitness and there was no evidence that those martens occupied sink habitats (Pulliam and Danielson 1991). Age distributions were not different among martens with high, intermediate, and low amounts of mature and overmature forest in their home range. Further, a companion study suggested that quantity of mature and overmature forests in

home ranges was not a dominant variable explaining survival of resident adult martens (Hearn 2007). In fact, Hearn (2007) reported a positive association between survival of residents and the percent of home range composed of RC. However, it would be a misinterpretation of that result to conclude that extensive logging increases survival because the median amount of RC observed within marten home ranges was only 9.6% (90th percentile = 12.3%).

Our conclusions differed from previous studies regarding the habitat requirements of Newfoundland martens (but see Gosse et al. 2005); those disparities are likely explained by the history of the range contraction of this island population. By the mid-1950s, distribution and habitat occupancy of martens in Newfoundland was restricted to inaccessible areas of mature and overmature timber remaining on the island where forest harvesting was absent, human access was limited due to the lack of roads, and over-exploitation by trappers was precluded by poor access (Bergerud 1969). Thus, the co-occurrence of martens with areas of mature and overmature forest types, by default, likely defined the scope of observed habitat use in previous studies (Snyder and Bissonette 1987, Bissonette et al. 1997, Sturtevant and Bissonette 1997).

Habitat productivity or variation in food availability is likely the most important factor affecting territoriality and home-range size in carnivores (Lindstedt et al. 1986, Thompson and Colgan 1987, McLoughlin and Ferguson 2000, Powell 2000). The meadow vole was the primary prey for Newfoundland martens, and previous researchers subsequently hypothesized an obligate association of martens with overmature conifer forest because of its inferred quality for meadow voles (Bateman 1986, Thompson and Curran 1995, Sturtevant et al. 1996, Sturtevant and Bissonette 1997). Recent data, however, indicate that Newfoundland martens utilize meadow voles extensively during summer (80% frequency of occurrence in scats) but that occurrence declines during winter (47%) when prevalence of snowshoe hares in diets increases 10-fold (Gosse and Hearn 2005). Further, 31% frequency of occurrence of larger prey, principally hares, represented 95% of caloric intake by martens (Cumberland et al. 2001). Thus, hares may be a critical component of marten diets in Newfoundland, where both hare densities and overall prey biomass were 7–23 times higher in 40-year-old semi-mature stands than in mature and overmature stands (Thompson and Curran 1995, Gosse and Hearn 2005). Additionally, harvests of American martens across Canada are historically synchronized with snowshoe hare numbers and at the stand scale, snowshoe hare densities are typically greatest in regenerating conifer stands (Parker 1986, Thompson 1988, Fryxell et al. 1999, Fuller and Harrison 2005). Thus, the higher prey biomass and caloric value of hares in regenerating stands may explain the selection we observed by martens for RF. Low vole densities in western Newfoundland across all forest types (i.e., only 0.01–0.54 snap-trap captures/100 trap-nights; Thompson and Curran 1995) likely increase profitability and importance of hares to Newfoundland martens during the critical limiting winter season, when

martens may not be able to survive energetically if eating exclusively small mammals (Buskirk and Harlow 1989, Thompson and Colgan 1991). If, as suggested, habitat preferences of mustelids parallel those of their prey species and if martens forage to maximize captures of large prey, then it is unlikely that mature and overmature coniferous forests can be considered a strict habitat requirement for Newfoundland martens (Zielinski et al. 1983; Buskirk and MacDonald 1989; Thompson and Colgan 1990, 1991; Buskirk and Powell 1994).

Avoidance of avian and mammalian predators has been proposed as a significant selective pressure to explain why American martens are sometimes associated with mature closed-canopy forests, avoid areas without overhead cover, and are restricted to stands with many large trees where martens can use their arboreal ability for escape (Spencer et al. 1983, Hargis and McCullough 1984, Hodgman et al. 1997, Buskirk and Powell 1994, Payer and Harrison 2003). Although predation risk may be a dominant habitat selection pressure elsewhere, Newfoundland martens contend with few potential predators. We suspect that the substantial use of younger aged forests exhibited by martens in our study is partially related to reduced necessity to seek escape cover from larger mammalian predators (i.e., fisher [*Martes pennanti*], coyotes [*Canis latrans*]) in the depauperate faunal landscape of Newfoundland (Dodds 1983, Hearn et al. 2006). Thus, martens in Newfoundland may have experienced ecological release from this selective pressure, allowing them to expand their habitat use into areas with greater prey densities, but less secure cover, relative to mainland populations of American martens (Whittaker 1998).

Fishers, an important natural predator of martens, are absent in Newfoundland (Dodds 1983, Hodgman et al. 1997, Krohn et al. 1995, Payer 1999). Further, we did not observe lynx (*Lynx canadensis*) or their tracks on the study area during 5 years of extensive aerial and ground fieldwork and we did not suspect them in any mortality observed during our study. Similarly, we observed coyotes or their tracks on only 4 occasions. Likewise, avian predators capable of killing martens are generally uncommon in southwestern Newfoundland compared with mainland North America and were not implicated in the deaths ( $n = 52$ ) of any radiomarked individuals (Gosse and Montevicchi 2001, Hearn 2007). Red foxes (*Vulpes vulpes*) were common on the study area and were the dominant natural predator of martens during our study (Hearn 2007). We conclude that the depauperate prey base and specialized habitat requirements of available prey combined with the limited number of potential predators on the island, has broadened, rather than constrained, the habitat choices made by Newfoundland martens.

## MANAGEMENT IMPLICATIONS

Newfoundland martens used a wide variety of forest conditions at both stand and landscape scales, suggesting that previous habitat interpretations have been overly conservative. We recommend that areas managed for marten occupancy at the landscape scale should include >24%

mature and overmature (TCC + TOC + IK) forest (25th percentile for resident ad). We caution, however, that our results should not be inferred to suggest that landscapes dominated by RF, PCT forest, and RC are sufficient to provide for occupancy by resident martens; median representation of those types within home ranges of adults was only <1%, 7%, and <1%, respectively. Collectively, we recommend that home-range size landscapes suitable for marten not exceed >29% younger aged forest (75th percentile for resident ad). Maintaining resident martens in landscapes where forest harvesting is dominant will require prescriptions that recognize constraints imposed by the highly fragmented nature of the natural landscape (also see Fuller 2006), while also considering prevalence of mature and overmature forest, younger forests, avoided land-cover types, and human access.

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