

INFLUENCE OF PARTIAL TIMBER HARVESTING ON AMERICAN MARTENS IN NORTH-CENTRAL MAINE

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Abstract: We investigated habitat selection and home-range characteristics of American martens (*Martes americana*) that occupied home ranges with partially harvested stands characterized by basal area of trees <18 m²/ha and canopy closure <30%. During the leaf-on season (1 May–31 Oct), martens selected second-growth (80–140-years-old, >9-m tree height) forest stands (deciduous, coniferous, and mixed coniferous-deciduous) and mixed stands that were partially harvested (\bar{x} = 13 m²/ha residual basal area, >9-m tree height), and they selected against forests regenerating after clearcutting (\leq 6-m tree height, cuts \leq 24-years-old). Marten home ranges included a greater proportion of partially harvested stands during the leaf-on season (maximum = 73%) than during leaf-off (1 Nov–30 Apr; maximum = 34%). Higher use of partially harvested stands during the leaf-on season coincided with greater canopy closure, higher use of small mammals, and greater relative densities of small mammals. During the leaf-off season, martens exhibited reduced relative selection for partially harvested and regenerating stands and increased selection for second-growth forest types. Partially harvested and regenerating clearcut stands had canopy closure <30% and basal area of trees >9-m tall of <13m²/ha; both were below published thresholds required by martens. Coincidentally, home-range areas of martens increased during the leaf-off season to include a greater proportion of second-growth forest and less partially harvested forest. Further, martens with partial harvesting in their home ranges used areas almost twice as large during the leaf-off season as martens with no partial harvesting. Snowshoe hares (*Lepus americanus*) were prevalent prey for martens during the leaf-off season, and partially harvested stands had the lowest density of hares among all forest overstory types. Our findings suggest that the combination of insufficient basal area and overhead canopy closure, subnivian behavior of small mammals, increased reliance on hares, and reduced density of snowshoe hares relative to second-growth forest types reduced habitat quality in partially harvested stands during the leaf-off season. We suggest land managers retain basal areas >18 m²/ha and canopy closure >30% during winter to maximize use by martens in stands where partial harvesting is practiced.

JOURNAL OF WILDLIFE MANAGEMENT 69(2):710–722; 2005

Key words: American marten, habitat, *Lepus americanus*, Maine, *Martes americana*, partial harvesting, prey, selection, snowshoe hare.

Several researchers have reported that American martens require structural complexity in forests (Bowman and Robitaille 1997; Chapin et al. 1997; Potvin et al. 2000; Payer and Harrison 2003, 2004). These requirements include overstory canopy closure >30% during the winter (Spencer et al. 1983, Thompson and Harestad 1994) and a preference for mature forests over young or regenerating forests (Buskirk and Ruggiero 1994, Thompson and Harestad 1994, Sturtevant et al. 1996). Payer and Harrison (2003, 2004) evaluated forest conditions in areas receiving different use intensities by martens and recommended that forest stands retain basal areas of live trees >9-m tall of >18 m²/ha and winter canopy closure >30% to maintain comparable use by martens after harvesting. We evaluated those thresholds by studying habitat selection, seasonal home-range areas, and prey use by martens that inhabited partially harvested stands that were reduced below minimum recommended levels.

Studies of the effects of forest harvesting on populations of American marten have focused primarily on clearcut logging (Snyder and Bissonette 1987, Thompson 1994, Hargis and Bissonette 1997); however, silvicultural practices in parts of eastern North America are shifting from a reliance on clearcutting to an emphasis on partial harvesting. Partial harvesting composed 96% of the total acreage harvested in Maine during 2002, and it was associated with a major decrease in clearcutting (Maine Forest Service 2003). This pattern is also occurring within other areas of the transitional, mixed coniferous-deciduous Acadian forest of eastern North America. For example, partial harvesting composed only 8% of the area harvested in New Brunswick in 1990, but it increased to 37% in 2000 (Canadian Council of Forest Ministers 2002).

Although partial harvesting is a prevalent management practice in many areas of the marten's geographic range, few studies have evaluated use of partially harvested stands by martens (but see: Campbell 1979, Soutiere 1979, Steventon and Major 1982). Despite small (\leq 4 marten) sample

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sizes, these studies reported that martens did not reduce their use of these areas following harvest. Partial cuts of 10–75 ha, with up to 57% overstory removal in Wyoming received comparable use to uncut forests (Campbell 1979), and partially harvested stands in Maine that retained 20–25 m²/ha of basal area provided “adequate” marten habitat (Soutiere 1979). Finally, partially harvested mixed-wood stands in Maine received substantial use by 4 martens during summer and winter (Steventon and Major 1982).

Recent clearcuts were generally avoided by martens (Steventon and Major 1982, Thompson and Harestad 1994, Potvin et al. 2000), and previous studies suggested that martens do not establish home ranges in areas with >25–40% early-successional forest (Hargis and Bissonette 1997, Chapin et al. 1998, Potvin et al. 2000). Clearcutting did not retain sufficient overstory canopy closure or vertical structure for martens immediately after harvesting, but it may become suitable habitat for martens as stands mature (i.e., minimum basal areas of 14–18 m²/ha, tree height ≥9 m; Payer and Harrison 2003). Further, landscape-scale effects of partial overstory removals on adjacent lands could be additive to prior effects of clearcutting.

Martens may switch from small mammals to larger prey items such as snowshoe hares during winter (Raine 1983, Bateman 1986, Thompson and Colgan 1990, Cumberland et al. 2001) because hares have higher digestibility and higher metabolizable energy per unit volume than mice and voles (Zielinski 1986, Cumberland et al. 2001). Several studies have reported a positive association between hare densities and early-successional forests with dense conifer regeneration and little forest overstory canopy closure (Conroy et al. 1979; Keith et al. 1984; Litvaitis et al. 1985*a,b*; O'Donoghue 1983; Pietz and Tester 1983). Despite potentially higher prey availability in young regenerating stands during winter, martens were reported to require overstory canopy closure of mature trees >30% (Spencer et al. 1983, Thompson and Harestad 1994) and to avoid open areas (Koehler and Hornocker 1977). Selection against regenerating clearcuts may also result from low small mammal abundances (Fuller et al. 2004) that are the primary prey of martens during summer (Soutiere 1979, Zielinski et al. 1983, Strickland and Douglas 1987, Thompson and Colgan 1987).

Previous studies of partial harvesting have not considered the ages of animals inhabiting partially harvested stands. Population age structures can change if juveniles are excluded from high-quality

habitat at high population densities (Brown 1969) and are forced to select suboptimal habitats (Hobbs and Hanley 1990). For example, resident martens in harvested forests were younger than martens in unharvested forests in Ontario (Thompson 1994). Younger age structures in marten populations could result if partial harvesting reduces the relative quality of forest stands.

We evaluated published basal area and canopy closure thresholds previously defined as suitable marten habitat (Payer and Harrison 2003, 2004) by evaluating stand-scale habitat selection and home-range characteristics by martens during leaf-on (1 May–31 Oct) and leaf-off (1 Nov–30 Apr) seasons in areas where recent partial harvesting has exceeded those recommended thresholds. Because home-range area may be a surrogate for habitat quality (Sanderson 1966, Buskirk and McDonald 1989, Sandell 1989), we evaluated whether inclusion of partially harvested stands reduced overall habitat quality within an individual home range by comparing home-range areas of marten that used partially harvested stands to marten that did not use partially harvested stands. We also compared age structure between martens with and without partial harvesting in their home ranges. We compared relative densities of snowshoe hares among 5 overstory forest types and compared absolute densities of hares between partially harvested and second-growth mixed stands. Last, we evaluated food habits of martens to enhance our understanding of stand-scale habitat selection.

STUDY AREA

Our study area (138 km²) was located in 2 townships in north-central Maine, USA (T4 R11 WELS and T5 R11 WELS; 460211.85 N, 690910.62 W), Piscataquis County. T4 R11 WELS was open to trapping during 1993–1996 but was closed to trapping during the 1997 and 1998 trapping seasons (late Oct–31 Dec) to protect study animals. T5 R11 WELS was closed to trapping from October 1994–December 1998, as were adjacent townships to the north, east, and west. The area was managed for pulpwood and saw timber, and approximately 56% of the area was clearcut during 1974–1994. Average stand size was 23 ha for second-growth forest types, 61 ha for regenerating forest stands that had been clearcut previously, and 77 ha for partially harvested stands. Forestry activities resulted in a dense, well-distributed network of gravel roads (1.1 km of road/km²).

Second-growth stands had tree heights >9 m (dominant trees >12-m height), canopy closure $\geq 50\%$, and were 80–140-years-old. Second-growth deciduous forests included red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), paper birch (*Betula papyifera*), and yellow birch (*B. alleghaniensis*). Second-growth coniferous forests were composed of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white pine (*Pinus strobus*). Forests regenerating from clearcutting (≤ 24 years old, ≤ 6 m tree height) were primarily composed of paper birch, red maple, balsam fir, red spruce, and raspberries (*Rubus* sp.).

Partial harvesting began in 1992 and included harvest blocks of 73–344 ha. Partially harvested stands were logged with the goal of leaving 1 overstory tree every 4.6 m. One partial cut was harvested with chainsaws, and all other cuts involved single-grip harvesters that felled, delimited, cross-cut, measured to length, and piled logs at the felling site; logs were transported from the stand with forwarders. Partial harvesting resulted in stands of mixed deciduous-coniferous trees.

METHODS

Habitat Sampling of Partially Harvested Stands

We measured habitat characteristics during summer 1998 along transects established in portions of the partially harvested stands that occurred within home ranges of resident martens. We sampled 22 transects (6–8 per harvested stand) that were 250 m, began a random distance 50–100 m from roads, and included 6 plots spaced 50 m apart (132 plots total). Each plot was composed of 2 10-m \times 3-m adjoining subplots in a T formation, randomly oriented from the center point. We used asymmetrical, randomly oriented plots to avoid over-sampling of harvesting trails that were oriented perpendicular to roads. Within each plot we measured mid-point diameter of stumps (≥ 7.6 cm at mid-point diameter, <2.0 m tall) that were $\geq 50\%$ within each plot, and we used these measurements to reconstruct stand structure prior to harvest. We measured overhead canopy closure with a spherical densiometer (Lemmon 1956) centered on the mid-point of the plots and averaged readings from each of the 4 cardinal directions.

We estimated leaf-off season basal area of partially harvested stands during winter 1999 on random-

ly oriented 1-km transects that were within the boundaries of summer 1998 home ranges of resident martens. We sampled 20 plots per transect (427 total plots), spaced at 50 m, and we calculated basal area of live coniferous and deciduous trees, and snags using a 2 m²/ha factor prism (Avery and Burkhart 2002). We also measured overstory canopy closure using a spherical densiometer.

We reconstructed stand structure prior to harvest by estimating pre-harvest basal areas from stumps and live trees. We estimated stump diameter at breast height (dbh) from stump diameter using a relationship developed for the spruce-fir region (Wenger 1984). We then transformed stump diameters to basal area with the formula $B.A. = 0.00545415 * \text{Diameter}^2$ (Wenger 1984). We calculated percent removal of each stand as basal area of stumps divided by basal area of live trees + basal area of stumps.

Trapping and Radiotelemetry of Martens

We livetrapped martens during summer (15 May–4 Jul) and fall (1–31 Oct), 1995–1998. We located traps 200–500 m from roads, spaced at 250–650-m intervals to ensure that each potential marten territory would include >1 trap. We positioned ≥ 6 traps within each partially harvested stand. We systematically placed traps throughout the entire study area so that we could compare ages and home-range sizes of martens with partial harvesting in their home ranges to those without. Capturing and handling procedures for martens and radiotelemetry procedures are described by Fuller (1999). Marten trapping procedures were approved by the Institutional Animal Care and Use Committee, University of Maine.

We located each radiocollared marten 5–7 times per week during summer and once every 4–5 days during winter. Radio-locations were distributed around the clock in the summer to avoid possible bias from temporal patterns of habitat use. We used hand-held, 2-element, H- and yagi-antennas to obtain locations from a vehicle or snowmachine by triangulating from fixed receiving locations on logging roads. We also conducted relocations approximately every 5 days from fixed-wing aircraft (Piper Super Cub) with 2 side-facing H-antennas (Gilmer et al. 1981), and we separated relocations by ≥ 12 hr to ensure temporal independence of observations (Swihart and Slade 1985, Katnik et al. 1994).

We used the program TRIANG (White and Garrott 1984) to determine marten locations and error polygons. Mean angular error of observers

associated with ground-based telemetry was 6° and was estimated as the mean difference between actual and estimated bearings for 60 hidden transmitters located by several observers. We used the mean angular error for each location to estimate the size of error polygon associated with each location. We estimated the error polygon associated with telemetry from aircraft to be 2.7 ha based on the mean difference between actual and estimated locations from 40 hidden transmitters at known locations.

We calculated 95% minimum-convex-polygon (MCP) home ranges (Mohr 1947) of resident (i.e., ≥ 10 locations collected over ≥ 90 days) marten using the program CALHOME (Kie et al. 1994). Probabilistic home-range models such as kernel and harmonic mean can provide reliable home-range estimates, but many more radiolocations would be required to produce stable estimates (Boulanger and White 1990, Seaman and Powell 1996). It was not possible to obtain a sufficient number of radio locations to use probabilistic models because of limited battery life of transmitters, and ≥ 12 hr was needed between locations for independence of observations (Karnik et al. 1994). Boulanger and White (1990) reported that MCP home-range estimates were similar to those obtained from harmonic mean models; thus, we chose the MCP method because of its graphical simplicity (Mohr 1947) and because stable area-observation curves (Odum and Kuenzler 1955) could be obtained for the leaf-on and leaf-off seasons based on the number of independent locations that we obtained (32–80 per marten). All of our analyses were based on the leaf-on and leaf-off seasons. The leaf-on season incorporated late spring, summer, and early fall when leaves are on deciduous trees that provided overhead cover and access to small mammal prey. The leaf-off season incorporated late fall, winter, and early spring when canopy closure was reduced because of deciduous leaf-fall, and access to small mammals was reduced because of snow.

Habitat Selection

Second-growth mixed-stands in Maine were a meaningful benchmark for evaluating habitat quality of partially harvested mixed stands to martens. For example, martens exhibited a trend of greatest selection for second-growth forest stands within home ranges, and selection did not differ significantly among second-growth mixed, deciduous, or coniferous stands in Maine (Chapin et al. 1997). Further, second-growth

mixed stands had the greatest small mammal densities of all mature forest types during summer (Fuller et al. 2004), and thus they offered the greatest prey potential for martens. All of the partially harvested stands were mixed coniferous-deciduous stands prior to harvest; therefore, we used second-growth mixed stands as the benchmark for evaluating habitat selection and prey abundances in partially harvested stands.

Habitat Database.—We used a 1997 forest-type coverage based on stereoscopic interpretation of 1:15,840 color infrared aerial photographs, obtained from Bowater, Inc., Millinocket, Maine. We incorporated overstory types and locational data from martens in a geographic information system (ARC/INFO 7.12, Environmental Systems Research Institute, Redlands, California). The habitat types we used in all analyses included second-growth mixed stands that were partially harvested, second-growth (80–140-years-old, >9 -m tree height) well-stocked closed-canopy forest ($\geq 50\%$ canopy closure) composed of poletimber and sawtimber that had not been harvested since 1974, and early successional stands (≤ 6 -m tree height) of seedlings and saplings that were clearcut during 1974–1994. To maximize statistical power, we combined second-growth deciduous, coniferous, and mixedwood stands into a single second-growth forest type because a companion study by Chapin et al. (1997) did not observe differences in habitat selection among those 3 overstory types for martens in north-central Maine.

Habitat Selection Analyses.—Stand-scale habitat selection evaluated selection for overstory types within home ranges using individual martens as the sampling unit. We used radiolocations with error polygons <10 ha (Chapin et al. 1997) to evaluate stand-scale habitat selection. We used marten monitored for 1 season (marten-season) as the experimental unit for individuals monitored >1 year in all habitat selection analyses because collapsing data across years for individual marten that use high-quality habitat could bias results by under-representing those most commonly used areas, especially if marten had greater survival or fidelity in areas that were repeatedly used. Based on area-observation curves, the minimum number of locations needed to estimate home-range area was 23 during the leaf-on season and 25 during the leaf-off season. In northcentral Maine, Chapin et al. (1997) and Payer (1999) found no difference in stand-scale selection indices between sexes, age classes, or

years; therefore, we pooled across those categories when analyzing stand-scale selection. We calculated a selection index for each forest type for each marten with >10% partial harvesting within their home range as use (U) minus availability (A) divided by availability $([U-A]/A)$; Manly et al. 1993, Chapin et al. 1997). We determined use as the proportion of radiolocations in each forest type and availability as the proportion of each forest type in each marten's home range.

To evaluate stand-scale habitat selection during the leaf-on and leaf-off seasons, we used a multi-response permutation procedure (MRBP; Aebischer et al. 1993) in a complete randomized block design using the program BLOSSOM (Slauson et al. 1994). Randomization procedures are not based on an assumed population distribution (Edgington 1987) because probabilities are based on permutations of the data from randomization theory (Slauson et al. 1994). Such permutation procedures are appropriate for small sample sizes (Slauson et al. 1994) and when missing selection indices are estimated (Aebischer et al. 1993). If $P < 0.10$, we used a series of multi-response permutation procedures (MRPP) to test the 3 possible pairwise comparisons. To control for experimentwise error rate, we adjusted the rejection level by the number of simultaneous comparisons ($\alpha = 0.10/k$), where $k = 3$, resulting in an adjusted α of 0.03.

Seasonal Habitat Selection and Home-range Characteristics.—To evaluate the effect of season on habitat selection, we compared selection indices for partially harvested stands, proportion of partial harvesting in home ranges, and home-range areas of martens with partially harvested stands within their home range between leaf-on and leaf-off periods. We restricted analysis to individual marten that were monitored during consecutive seasons. We used a permutation test for matched pairs (PTMP), a special case of multi-response permutation procedures for randomized blocks where we placed data in 2 groups (leaf-on and leaf-off seasons) and n blocks (number of marten). This test is recommended as a distribution-free statistical test for paired comparisons with small sample sizes (Slauson et al. 1994). If area of home ranges differed between seasons, we determined which overstory types differed by calculating the proportion of each overstory type in the home range for each marten during consecutive seasons, with a PTMP. We also used a PTMP to test whether the proportion of radiolocations in partially harvested stands differed from leaf-on to leaf-off seasons.

Sex-specific differences in home-range areas of martens have been well documented (e.g., Buskirk and McDonald 1989), so we tested for differences in home-range size by season (leaf-on and leaf-off seasons), treatment (marten with >10% partial harvesting within their home range and marten with no partial harvesting in their home range), and the interaction between season and treatment separately for males and females using analysis of variance. No difference in home-range size between years or between yearlings and adults was observed during companion studies (Chapin et al. 1997, Phillips et al. 1998); therefore, we pooled years and ages when comparing home-range areas. We assessed homogeneity of error variances with Levene's test (Milliken and Johnson 1992) and normality with Lilliefors test (Lilliefors 1967). We conducted a square root transformation on home-range area to meet parametric assumptions (Zar 1999).

Age Structure

We compared age distributions of resident, non-juvenile martens that had >10% partial harvesting in their home range to martens that had no partial harvesting in their home range. We compared the distribution of martens in each age class (1, 2, 3+ years) that had partial harvesting in their home range to martens with no partial harvesting in their home range using a likelihood ratio test (Zar 1999).

Snowshoe Hare Density

Fecal pellet-counts provided an index of over-winter abundance of snowshoe hares (Wolff 1980, Litvaitis et al. 1985a, Krebs et al. 1987). We censused hare pellets within 5-m \times 30-cm transects that were oriented randomly on the innermost 12 trap stations on grids that were used to sample small mammals during a companion study (Fuller et al. 2004). Overstory types included second-growth mixed coniferous-deciduous ($n = 7$ grids), second-growth mixed stands that were partially harvested ($n = 7$), second-growth deciduous ($n = 2$), second-growth coniferous ($n = 2$), and regenerating early-successional (clearcut in 1982; $n = 2$) stands. We cleared transects of all pellets during the fall of 1997 and counted pellets deposited during winter prior to emergence of deciduous leaves (19–21 May 1998).

We used the regression formula of hare density/ha = $(0.15979 + 0.0001 \text{ *pellet density/ha/month; } r^2 = 0.87, P < 0.001)$ to transform pellet densities to hare densities (Homyack et al. 2005). We compared density of hares between partially harvest-

ed mixed stands and second-growth mixed stands. We used a Mann-Whitney *U*-test to assess differences in number of snowshoe hares/ha within partially harvested mixed stands vs. second-growth mixed stands.

Food Habits

We collected marten scats at successful trap sites during summer (1991, 1994–1995, *n* = 188), at resting sites (1994–1995, *n* = 17), and while snowtracking radiocollared individual martens (1997–1999, *n* = 14) during winter. When possible, we recorded sex of martens for scats collected. We oven-dried scats at 50°C for 24 hours and examined them macro and microscopically to determine percent occurrence of food items (Erlinge 1968, Jacobsen and Hansen 1996). We made scale impressions by compressing hairs between 2 sheets of clear polyvinyl chloride plastic (0.03-mm thickness) in a steel press (modified from Williamson 1951, Moore et al. 1974) and heated them at 105°C for 2.5–3 hours. We then identified scale impressions from scale casts (Williams 1938, Adorjan and Kolenosky 1969, Moore et al. 1974) using a reference collection of impressions from known species.

RESULTS

Habitat Sampling of Partially Harvested Stands

Live-tree basal area in partially harvested stands averaged 12.8 m²/ha and snag basal area averaged 1.9 m²/ha. The average live-tree basal area in second-growth, mixed stands that were adjacent to partially harvested stands ranged from 18–27 m²/ha. Winter canopy closure in the partially harvested stands ranged from 22–29%, and canopy closure during summer was 62–71%. Canopy closure in second-growth, mixed stands was greater, with a range of 35–41% in winter and 85–92% in summer. Percent basal area estimated to have been removed during harvesting ranged from 52–59% in the partially harvested stands. All of the 7 partially harvested stands that were measured had basal area and canopy closure below the thresholds for marten occupancy recommended by Payer and Harrison (2003, 2004).

Habitat Selection

We based stand-scale habitat selection analyses on 23 marten-years (18 individuals: 9 M, 9 F) during the leaf-on season and 9 marten-years (8 individuals: 6 M, 2 F) during the leaf-off season. We

Table 1. Results of stand-scale habitat selection analyses for martens during the leaf-on (1 May–31 Oct) and leaf-off (1 Nov–30 Apr) seasons in north-central Maine, USA, 1996–1999.

| Season | N ^a | <i>P</i> ^b | Median selection indices ^c for forest types ^d | | |
|-----------------------|----------------|-----------------------|--|----------------------|---------------------|
| | | | Second-growth | Partially harvested | Regenerating forest |
| Leaf-on ^e | 23 | 0.022 | 0.081 ^A | 0.161 ^A | -0.552 ^B |
| Leaf-off ^e | 9 | 0.059 | 0.003 ^A | -0.169 ^{AB} | -1.00 ^B |

^a Number of marten-seasons in stand-scale analysis.
^b From multiresponse permutation tests (MRBP) on selection indices.
^c Selection index = (use-availability)/availability
^d Second-growth = 80–140-years-old, >9.0-m tree height; coniferous, deciduous, and mixed coniferous-deciduous forest; Partially harvested = 13 m²/ha \bar{x} residual basal area; Regenerating forest = ≤6-m tree height, cuts ≤24-years-old.
^e Forest types with different letter superscripts within a season indicate significant pairwise differences using multiresponse permutation procedures (MRPP), Bonferroni-adjusted α = 0.03 (0.10/*k*, where *k* = number of pairwise comparisons).

recorded 982 locations during the leaf-on season (55% from aircraft) and 271 during the leaf-off season (74% from aircraft). We monitored each marten for an average of 56 locations (range = 39–80) during the leaf-on season and 37 locations (range = 32–49) during the leaf-off season. The average size of error polygons used in stand-scale analysis was 2.97 ha, which was 4–13% of the average area of stands. Therefore, the small telemetry errors likely did not introduce substantial bias or decrease efficiency of testing habitat selection (Nams 1989).

During the leaf-on season, martens used forest types disproportionately from availability within their home ranges (MRBP, δ = 0.95, *P* = 0.02; Table 1). Selection indices were greater for second-growth forest types (MRPP, δ = 1.178, *P* = 0.001) and partially harvested stands (MRPP, δ = 1.23, *P* = 0.004) than for regenerating forests (Bonferroni-adjusted α = 0.03; Table 1). There was no difference in selection between second-growth forest types and partially harvested stands (MRPP, δ = 0.57, *P* = 0.67) during the leaf-on season (Table 1).

Martens also used forest types disproportionately from availability during the leaf-off season (MRBP, δ = 1.084, *P* = 0.06; Table 1). Selection indices were similar between second-growth and partially harvested stands (MRPP, δ = 0.51, *P* = 0.44; Table 1). Second-growth stands were selected over regenerating stands (MRPP, δ = 1.28, *P* = 0.004), but there was no significant difference in selection between partially harvested and regenerating stands (MRPP, δ = 1.46, *P* = 0.06; Bonferroni-adjusted α = 0.03; Table 1).

Table 2. Mean 95% minimum convex polygon home-range area (km²; *n*, SE) during leaf-on (1 May–31 Oct) and leaf-off (1 Nov–30 Apr) seasons for martens with and without partial harvesting in their home ranges in T4 R11 and T5 R11 WELS, north-central Maine, USA, 1995–1999.

| | Home-range area | | | |
|-----------------------|-------------------|----------------------|-------------------|----------------------|
| | Males | | Females | |
| | With ^a | Without ^b | With ^a | Without ^b |
| Leaf-on ^c | 4.33 ^A | 4.42 ^A | 2.76 ^A | 2.65 ^A |
| <i>n</i> , SE | 20, 0.50 | 36, 0.33 | 13, 0.30 | 43, 0.18 |
| Leaf-off ^c | 6.29 ^A | 3.45 ^B | 3.10 ^A | 1.70 ^B |
| <i>n</i> , SE | 9, 0.58 | 12, 0.79 | 5, 0.65 | 11, 0.26 |

^a Home ranges of martens with >10% partially harvested stands in home range.

^b Martens with no partial harvesting in home range.

^c Different letter superscript indicates a significant seasonal difference in home-range area within a sex.

Seasonal Habitat Selection and Home-range Characteristics.—Paired analyses of martens (*n* = 8 marten-years; 7 individuals: 6 M, 1 F) monitored in consecutive leaf-on vs. leaf-off seasons indicated that the stand-scale selection index for partially harvested stands did not differ (PTMP, δ = 1.30, P = 0.27) between seasons. However, the proportion of partial harvesting within marten home ranges (*n* = 12 marten-years; 11 individuals: 7 M, 4 F) declined (PTMP, δ = 0.17, P = 0.01) during the leaf-off season; the maximum percent of partial harvesting within home ranges was 73% during the leaf-on season and only 34% during the leaf-off season. Conversely, the proportion of second-growth forest types in marten home ranges (*n* = 12 marten-years; 11 individuals: 7 M, 4 F) increased (PTMP, δ = 0.14, P = 0.07) during the leaf-

off season, and the maximum percent of second-growth forest within home ranges increased from leaf-on (79%) to leaf-off (85%) seasons. Martens maintained home ranges (*n* = 12 marten-years; 11 individuals: 8 M, 3 F) with similar (PTMP, δ = 0.12, P = 0.23) proportions of regenerating forest during the leaf-on and leaf-off seasons. The combined amount of partial harvesting and regenerating forest within marten home ranges during the leaf-off season was 31%, and 7 of 9 marten monitored had <36% of their home range composed of partially harvested and regenerating forest stands.

Home-range area of martens monitored in consecutive seasons (*n* = 12 marten-years; 11 individuals: 7 M, 4 F) were larger (PTMP, δ = 1.99, P = 0.01) during the leaf-off season. Specifically, mean area of home ranges during the leaf-off season for males (6.29 km², *n* = 9) and females (3.10 km², *n* = 5) was larger than home ranges during the leaf-on season (M = 4.33 km², *n* = 20; F = 2.76 km², *n* = 13). There was a treatment * season interaction for females (F = 4.029, P = 0.049) and males (F = 8.124, P = 0.006), indicating that seasonal effects of home-range area differed between treatments (i.e., marten with >10% partial harvesting in their home range compared to martens with no partial harvesting in their home range). Home-range areas of males and females during the leaf-on season were similar between martens that had partial harvesting in their home range (*n* = 33 marten) and marten that did not (*n* = 79 marten; Table 2). During the leaf-off season, however, home ranges of martens that had partial harvesting were up to twice as large as home ranges without partial harvesting (Table 2).

Age Structure

The median age of martens with >10% partially harvested stands in their home range was 2.0 years (*n* = 27) and was identical to the median age of martens without partial harvesting (*n* = 60). The age class distribution of 1, 2, and 3+ year-old marten with and without partial harvesting in their home range also did not differ (*n* = 87, G = 0.11, 2 df, P = 0.95; Fig. 1).

Snowshoe Hare Density

Estimated density of snowshoe hares was greatest in regenerating clearcuts and lowest in partially harvested stands (Table 3). Density of hares in second-growth mixed stands was significantly greater (P = 0.06) than in partially harvested mixed stands (Table 3).

Table 3. Average density of snowshoe hares estimated^a in 5 overstory types^b (number of grids) in T4 R11 and T5 R11 WELS, north-central Maine, USA, during the leaf-off season (Oct–Apr), 1997–1998. Statistical comparisons are only presented for mixed coniferous-deciduous vs. partially harvested stands.

| | Overstory type | | | | |
|----------------------------|------------------------|------------------------|------------------------|------------------------|-----------------------|
| | REG (<i>n</i> = 2) | CON (<i>n</i> = 2) | DEC (<i>n</i> = 2) | MIX (<i>n</i> = 7) | PH (<i>n</i> = 7) |
| Hares/hectare ^c | 1.64 | 0.24 | 0.17 | 0.23 ^A | 0.17 ^B |
| SE | 0.87 | 0.03 | 0.00 | 0.03 | 0.01 |

^a Estimates were derived from pellet counts using the relationship of hare density/ha = 0.15979 + 0.0001 * pellet density/ha/month (Homyack et al. 2005).

^b REG = regenerating (<6-m tree height) forest (clearcut 1982), CON = second-growth (80–140-years-old, >9-m tree height) coniferous, MIX = second-growth mixed coniferous-deciduous, DEC = second-growth deciduous, PH = partially harvested mixed stands (>9-m tree height, 13 m²/ha \bar{x} residual basal area).

^c Different letter superscript indicates significant (P < 0.10) Mann-Whitney U difference between partially harvested (PH) and mixed coniferous-deciduous (MIX) stands (P = 0.06).

Food Habits

We quantified percent occurrence of food items for 188 individual marten scats during the leaf-on season (May–Oct) and for 41 scats during the leaf-off season (Nov–Apr; Table 4). Red-backed voles (*Clethrionomys gapperi*) occurred most frequently, appearing in 58.5% of leaf-on season scats and 46.3% of leaf-off season scats. The second most frequent mammal remains in scats was deer mice (*Peromyscus maniculatus*; 33.5% leaf-on, 41.5% leaf-off; Table 4). Snowshoe hares had the greatest change in percent occurrence from leaf-on to leaf-off seasons; hares occurred in only 6.9% of leaf-on season scats, but occurred in 29.3% of scats during the leaf-off season. Red squirrels (*Tamiasciurus hudsonicus*) were also prevalent in marten scats (22%) during the leaf-off season. Additional food items in marten scats included shrews (*Blarina brevicauda* and *Sorex cinereus*), jumping mice (*Napaeozapus insignis*), meadow voles (*Microtus pennsylvanicus*), white-tailed deer (*Odocoileus virginianus*), birds and insects, and seeds including *Rubus* spp., *Pyrus* spp., *Lonicera* spp., and *Prunus pensylvanica* (Table 4). All food items were found in marten scats of both sexes, with the exception of white-tailed deer that only occurred in scats deposited by a single female marten and was likely carrion provided by trappers using road-killed deer as bait to snare coyotes.

DISCUSSION

Partially harvested stands had basal areas (13 m²/ha) below thresholds previously defined as suitable for martens (18 m²/ha; Payer and Harrison 2003, 2004), suggesting that partial harvests may be below the threshold of vertical structure required by martens to avoid predation (Payer and Harrison 2000), which is the principal non-human related cause of marten mortality in Maine (Hodgman et al. 1994, 1997; Payer 1999). Fishers are a principal arboreal predator of martens in Maine, and we hypothesize that martens prefer stands with complex vertical structure to avoid being captured by fishers, which are less agile in trees and have difficulty moving from tree to tree in the forest canopy.

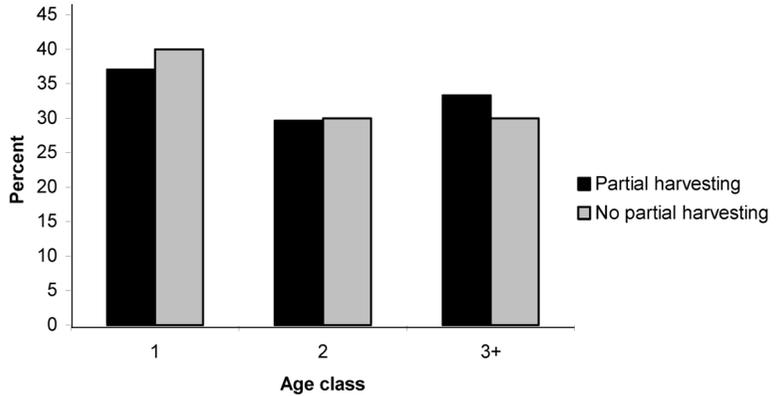


Fig. 1. Age class distribution of resident martens with >10% partial harvesting (n = 27) and with no partial harvesting (n = 60) in their home range, north-central Maine, USA, 1996–1999.

Canopy closure in partially harvested stands (26%) was also below previously defined thresholds for martens during winter, but it was adequate during summer (67%). Sufficient overhead canopy closure may be especially important to martens during winter to decrease risk of predation (Hargis and McCullough 1984, Buskirk and Ruggiero 1994, Hodgman et al. 1997), as they typically avoid stands with <30% canopy closure (Spencer et al. 1983, Thompson and Harestad 1994). Increasing the basal area of partially harvested stands by selectively retaining large conifer trees could increase the canopy closure during

Table 4. Percent occurrence of food items in 229 marten scats in T4 R11 and T5 R11, WELS, north-central Maine, USA, collected during the leaf-on (1 May–31 Oct) and leaf-off (1 Nov–30 Apr) seasons, 1991 and 1994–1999.

| Food items | Leaf-on (n = 188) | Leaf-off (n = 41) |
|--------------------------------|-------------------|-------------------|
| Mammals | | |
| <i>Clethrionomys gapperi</i> | 58.5 | 46.3 |
| <i>Peromyscus maniculatus</i> | 33.5 | 41.5 |
| <i>Soricidae</i> ^a | 16.0 | 17.1 |
| <i>Tamiasciurus hudsonicus</i> | 24.5 | 22.0 |
| <i>Lepus americanus</i> | 6.9 | 29.3 |
| <i>Napaeozapus insignis</i> | 13.3 | 2.4 |
| <i>Microtus pennsylvanicus</i> | 1.6 | 0 |
| <i>Odocoileus virginianus</i> | 0 | 7.3 |
| Unidentified | 4.8 | 0 |
| Birds | 6.9 | 9.8 |
| Insects | 6.9 | 0 |
| Seeds | | |
| <i>Rubus</i> spp. | 12.8 | 7.3 |
| <i>Pyrus</i> spp. | 8.0 | 26.8 |
| <i>Prunus pensylvanica</i> | 8.0 | 0 |
| <i>Lonicera</i> spp. | 7.5 | 0 |
| Unidentified berries | 27.7 | 29.3 |

^a *Soricidae* = *Blarina brevicauda* and *Sorex cinereus*.

winter to approach the thresholds recommended by Payer and Harrison (2003, 2004).

During the leaf-on season, martens selected partially harvested and second-growth forest stands relative to regenerating stands. Partially harvested stands probably retained sufficient mature forest characteristics by way of horizontal and vertical structure and canopy closure to receive substantial use by martens during the leaf-on season. During the leaf-off season, however, martens exhibited lower selection for partially harvested stands and greater selection for second-growth forest types; second-growth stands had canopy closure and basal areas above published thresholds (Payer and Harrison 2003, 2004). Consequently, martens decreased the proportion of partial harvesting within their home ranges (i.e., 53% decline in maximum percentage) and increased the proportion of second-growth forest during the leaf-off season. In contrast, Payer (1999) did not document a seasonal change in home-range composition of martens that inhabited home ranges without partially harvested stands, suggesting that partially harvested stands may have lower habitat quality than second-growth stands during the leaf-off season.

Choice of forest stands by martens may be more closely associated with prey abundance and availability than with overstory type (Douglass et al. 1983). Abundance of mice and voles were similar between second-growth mixed and partially-harvested mixed stands during summer (Fuller et al. 2004); this suggests that partially harvested stands provided foraging habitat of comparable quality to second-growth stands during the leaf-on period when mice and voles were the primary prey of martens. Snowshoe hares were an important prey item for martens during the leaf-off season, occurring in 29% of scats, compared to 7% during the leaf-on season. However, percent occurrence of indigestible remains in scats underestimates the caloric importance of hares because higher proportions of indigestible remains occur in smaller prey (Lockie 1959, Cumberland et al. 2001). Snowshoe hares comprised 44% of the caloric intake for martens during early winter (22 Nov–7 Dec) in adjacent areas of New Brunswick, but they only represented 8% of the diet based on percent occurrence (Cumberland et al. 2001). Martens may select larger prey items in winter because of higher digestibility and energy per unit volume than smaller prey (Zielinski 1986).

Snowshoe hare densities during the leaf-off season were lowest in partially harvested stands

(0.17/ha) and greatest in regenerating clearcut stands (1.64/ha) and probably contributed to reduced use of partially harvested stands by martens during winter. Despite high densities of snowshoe hares in regenerating stands, these stands do not maintain the required tree height, basal area, or canopy closure; these structural characteristics are all potentially important for marten to escape predation (Hargis and McCullough 1984). Partially harvested stands may provide suitable foraging habitat during summer but appear to be less valuable in winter. Thus, silvicultural changes that could maintain densities of hares in partially harvested stands comparable to mixed stands might benefit martens by providing increased winter prey, while still providing overhead cover.

Home ranges of males and females during the leaf-off season were up to twice as large for martens whose home ranges included partial harvesting than for those that did not, providing further evidence that habitat quality is reduced in partially harvested stands. Martens have larger home ranges in harvested landscapes than in uncut areas (Thompson and Colgan 1987, Potvin and Breton 1997), indicating a link between reduced habitat quality, forest harvesting, and larger home-range requirements. Although it has been proposed that female martens may be limited in their ability to increase home-range area during periods of resource scarcity because of their body size, which is smaller than that of males (Harestad and Bunnell 1979), we observed that females and males that occupied partially harvested stands increased their home-range areas during the leaf-off season. Low availability of snowshoe hares in partially harvested stands may have caused martens to expand home-range boundaries during the leaf-off season to meet food requirements. Expansions of home ranges by martens that inhabited partially harvested areas during the leaf-off season may indicate attempts to mitigate declines in habitat quality of partially harvested stands during periods of energetic stress.

Although martens responded to partial harvesting at the stand scale, landscape-level considerations should also be considered (i.e., martens may not respond in the same manner if partially harvested stands occupy a substantial portion of the available landscape). We hypothesized that martens had opportunities to shift home ranges during the leaf-off season because of the mosaic of forest types that occurred on the landscape. Our study area was composed of >56% regener-

ating clearcuts, which were distributed in large, irregularly spaced aggregations. Martens positioned territories so that the majority of their home range included second-growth forest. During the leaf-off season, martens were able to shift home ranges to include additional second-growth forest because the second-growth forest surrounding the partially harvested stands was unoccupied by other martens due to fragmentation by clearcuts (Chapin et al. 1998). If all suitable habitat had been occupied however, martens may have been unable to shift home ranges during the leaf-off season, resulting in low productivity or survival and the potential for sink habitat (Pulliam 1988) in partially harvested stands. Additionally, partial harvesting did not alter age structures of resident animal populations, but population-level density could be reduced because of increased spatial requirements associated with reduced prey availability or avoidance of areas without adequate levels of vertical and horizontal structure during winter. Martens were able to increase home-range area to include proportionally less partially harvested and proportionally more second-growth forest types during the leaf-off season, but if marten densities were greater, martens may have been unable to make home-range shifts because of social constraints associated with territoriality (Katnik et al. 1994).

Partial harvesting reduced the quality of the habitat during the leaf-off season, as indicated by increased home-range areas, shifts in home-range location, and selection indices more similar to those of regenerating forest stands. The combination of basal area below threshold levels, reduced snowshoe hare density, and avoidance of areas with overhead canopy closure <30% probably reduced habitat quality for martens in partially harvested stands during the leaf-off season.

MANAGEMENT IMPLICATIONS

When partially harvesting, we recommend that a basal area of live trees and snags ≥ 8 m²/ha be kept to maintain canopy closure >30% during summer and winter. This provides martens with escape cover, with complex horizontal and vertical structure, and with attributes that prevent seasonal expansion of home ranges during the leaf-off period. These suggestions corroborate sub-stand scale recommendations provided by Payer and Harrison (2003, 2004).

The size and position of partially harvested stands on the landscape are important considerations when planning partial harvesting on a large

scale. As the area of suitable habitat on the landscape decreases, animal populations are influenced by increased isolation (Andron 1994); thus, the individual size and distribution of harvests on a landscape could affect habitat selection by martens (Hargis and Bissonette 1997, Chapin et al. 1998). Previous studies (Hargis and Bissonette 1997, Chapin et al. 1998, Potvin et al. 2000) suggested that habitat occupancy declines when 25–40% of the landscape is composed of regenerating forest; our results corroborate those findings and suggest that the effects of heavy partial harvesting may be additive to the effects of clearcutting at the landscape scale. Partial harvesting requires that more area be managed to achieve fiber objectives; therefore, partial harvesting could lead to greater habitat fragmentation than by harvesting the same volume of fiber via traditional clearcutting practices.

We suggest that landscape-scale recommendations for partial harvesting consider the combined effects of partial harvesting and regeneration following clearcutting. We recommend that partially harvested stands be positioned within a mature forest mosaic to allow for seasonal shifts in home ranges. Partial harvests that are positioned adjacent to large stands of mature forest would provide opportunities for seasonal shifts or expansions in home ranges, if not all mature forest habitat was included in marten territories. Responses of martens to partial harvesting will likely depend on the residual basal area within the harvested stand, the landscape mosaic in which the harvest is positioned, and the extent that adjacent habitat is saturated with marten territories.

ACKNOWLEDGMENTS

This project was funded by the Maine Cooperative Forestry Research Unit, the Maine Department of Inland Fisheries and Wildlife, by Federal Aid in Wildlife Restoration Project No. W-82-R-11-368, the Maine Agricultural and Forest Experiment Station, and the Department of Wildlife Ecology at the University of Maine. Bowater, Inc. provided aerial photographs, overstory coverages, and unlimited access to their lands. We thank field technicians S. Becker, J. Berube, T. Gorman, M. Loud, J. Martin, A. McCue, G. Orth, L. Thompson, A. Weik, N. Wildman, and G. Zimmerman. We thank D. Payer and H. J. Lachowski for data collection prior to this study and telemetry pilot J. McPhee (deceased). This is Scientific Contribution 2737 of the Maine Agricultural and Forest Experiment Station.

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Associate Editor: Morrison.