ÉCOSCIENCE
20 (4): 383–390 (2013)

Characteristics of the boreal mixedwood forest associated with the use of subnivean access points by American martens[1]

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Abstract: Habitat for American martens (*Martes americana*) is associated with forest types that offer fine-scale structural complexity in part used to access the winter subnivean environment, which is used for food procurement, predator avoidance, and rest. We assessed habitat characteristics associated with points of subnivean access by martens from winter tracking in a boreal mixedwood forest in northern Ontario. We then assessed areas designated as reserved marten habitat according to *Forest Management Guidelines for the Provision of Marten Habitat in Ontario* with respect to these characteristics. Coarse woody debris counts were positively associated with subnivean access. We found some evidence that subnivean access points differed in a transition from patches of coniferous to mixedwood forest, defined by tree basal area. Especially in mixedwood patches, deciduous shrub density may also facilitate subnivean access. Development of guidelines to protect features associated with fine-scale structural complexity important in winter to martens should be a research priority.
Keywords: American marten, boreal mixedwood forest, coarse woody debris, forest management, habitat reserve, *Martes americana*, Ontario.

Résumé: L'habitat de la martre d'Amérique (*Martes americana*) est associé aux types de forêt qui offrent une complexité structurale à fine échelle, cette complexité étant utile aux martes entre autres en hiver pour accéder à l'environnement subnival dans le but de s'alimenter, d'éviter les prédateurs et de se reposer. Nous avons évalué les caractéristiques de l'habitat associées aux points d'accès subnival grâce à un suivi hivernal des pistes de martres dans une forêt boréale du nord de l'Ontario. Nous avons ensuite évalué ces mêmes caractéristiques dans des secteurs désignés comme réserves d'habitat pour la martre selon les directives ontariennes d'aménagenent forestier pour la conservation de l'habitat de la martre. La quantité de débris ligneux grossiers était associée de façon positive à l'accès subnival. Certains résultats indiquaient que les points d'accès subnival différaient dans la transition entre des parcelles de conifères et de forêt mixte (le type de forêt étant défini par la surface terrière d'arbres). Dans les parcelles mixtes en particulier, la densité d'arbustes feuillus peut faciliter l'accès subnival. L'élaboration de directives pour protéger les caractéristiques forestières associées à une complexité structurale à fine échelle importante pour les martres en hiver devrait constituer une priorité de recherche.
Mots-clés: aménagement forestier, débris ligneux grossiers, forêt boréale mixte, *Martes americana*, martre d'Amérique, Ontario, réserve d'habitat.

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

Introduction

American martens (*Martes americana*) are found throughout the boreal forest and in some temperate and foothills forests of North America (Strickland & Douglas, 1987). They have received considerable attention in forest management planning in Canada (Thompson, 1991; Watt *et al.*, 1996), and are considered a featured or indicator species of sustainable forestry in British Columbia (Stordeur, 1986), Ontario (Watt *et al.*, 1996), Quebec (Potvin, Courtois & Bélanger, 1999), and Newfoundland and Labrador (Sturtevant, Bissonette & Long, 1996). Although martens are considered specialists of old-growth, coniferous forests (Buskirk & Powell, 1994), their wide range actually incorporates considerable variability not only in available habitat, but also in apparent habitat selection (Hearn *et al.*, 2010). As an explanation for this variability, Godbout and Ouellet (2010) proposed and concluded that selection may be stronger and more consistent at finer scales than at the landscape and home-range scales historically approached in studies that generalize to associate marten habitat selection with old-growth, coniferous forest. Documenting the importance of fine-scale forest structural elements to martens can explain their persistence in a range of landscapes and may assist forest managers with their recovery in younger forests.

Learning about their fine-scale habitat selection is also a way to gain insights into marten behaviours (Thompson, Fryxell & Harrison, 2012). Certain fine-scaled features such as den sites and resting habitats are important for parturition and thermoregulation (Smith & Schaefer, 2002; Payer & Harrison, 2003; 2004; Porter, St. Clair & de Vries, 2005; Godbout & Ouellet, 2010). Fine-scale selection is

[1]Rec. 2013-08-27; acc. 2014-02-21.
Associate Editor: Louis Imbeau.
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DOI 10.2980/20-4-3634

also associated with gaining access to the winter subnivean zone, where frequency of access is linked to success in prey acquisition (Andruskiw *et al.*, 2008). Selection operating at fine scales should be expected for a mammal generally weighing <1 kg (Clark *et al.*, 1987), and, as suggested by Godbout and Ouellet (2010) and by Thompson, Fryxell, and Harrison (2012), forest structural elements can be classified as serving ecological functions that variably provide 1) opportunities for detecting prey, 2) means for protection from or avoidance of predators, and 3) areas for rest, denning, and efficient thermoregulation.

Godbout and Ouellet (2010) inferred that martens hunt in areas supporting higher prey detection and abundance and found that summer and winter habitat selection models built on forest structural elements they associated exclusively with this function, as opposed to the other 2 listed above, were prioritized: martens selected areas of higher coniferous tree canopy closure, higher shrub lateral cover, and more abundant coarse woody debris (CWD) on the forest floor. Other winter habitat selection models discussed by Godbout and Ouellet (2010) broadened to include the other 2 functions: avoiding predators and finding resting spots in areas of higher total tree density and tree basal area (Chapin *et al.*, 1997; Payer & Harrison, 2003). A coarser-scale habitat classification available on forestry maps includes estimates like canopy closure and tree basal area, so these maps can actually perform well in predicting finer-scale elements of winter habitat selection by martens (Godbout & Ouellet, 2010).

In this paper, we explore fine-scale, winter habitat selection using multimodel inference (Burnham & Anderson, 2002) and a data set originating from the identification of subnivean access points in forest used by martens in northern Ontario, Canada. Our study differs from other work because it focuses on boreal mixedwood forest. This forest type is dominated by trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) in early succession, black spruce (*Picea mariana*) or white spruce (*P. glauca*) in old growth, and balsam fir (*Abies balsamea*) in very late succession if there is no wildfire (McClain, 1981). We predicted that, perhaps uniquely to the boreal mixedwood forest, clusters of deciduous shrubs, which persist in treefall gaps into old-growth stages, can provide points of access below the snow to martens additional to those provided by the CWD and low-hanging, conifer branches more typically associated with subnivean access (Corn & Raphael, 1992; Sherburne & Bissonette, 1994; Thompson & Colgan, 1994; Andruskiw *et al.*, 2008). We used the same set of 3 functions adopted by Godbout and Ouellet (2010) and later by Thompson, Fryxell, and Harrison (2012) to compare models of fine-scale selection associated with prey availability, predator avoidance, and finding resting areas, as identified by structural elements of the tree and shrub strata and the forest floor. We then surveyed selected fine-scale structural elements in habitat reserves delineated following the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario* (Watt *et al.*, 1996). These guidelines categorize stands from forestry maps as poor, fair, or good marten habitat according to general winter habitat characteristics (Racey, Whitfield & Sims, 1989). The guideline authors (Watt *et al.*, 1996) further associate the presence of snags (vertical CWD or standing dead trees) as a component of good marten habitat, so we built and compared models explaining access to the subnivean zone with CWD counts and volumes, coniferous tree canopy closure, tree basal area, and coniferous and deciduous shrub and snag density.

Methods

Study areas

Our study areas were defined by 1) backtracking along the routes taken by 12 radio-collared, adult female martens in the Gordon Cosens Forest (49°25'N, 82°25'W), near Kapuskasing (KAP), Ontario, Canada in the winters of 2006 and 2007 and 2) following the tracks of 3 additional, unmarked martens in Sleeping Giant Provincial Park (SGP; 48°20'N, 88°45'W), near Thunder Bay, Ontario, Canada in winter 2009. We added a third area by 3) assessing habitat in marten reserves in the Lakehead Forest (LKH; 48°23'N, 89°15'W), also near Thunder Bay. All areas are boreal mixedwood forest in a variety of mid- to late- successional stages with <20% of the landscape in younger stands. The forest at KAP was fire-originated, with numerous insect infestations and a history of horse-logging, followed by fire suppression, which have together created an uneven age structure. The topography of the region is flat with largely clay soils and dotted with numerous small lakes and other wetlands. The climate is typified by long, cold winters, a January mean temperature of −18.9 °C, and total snowfall from October through April of 266 cm. The forest in SGP was affected by a maritime climate and less affected by fire, but was otherwise similar in disturbance history, structure, and composition to the KAP forest. A protected area (244 km^2) since 1944, SGP has not been logged since the 1950s, resulting in a mature forest. Topography comprises gently sloping hills and very thin soil overlying Lake Superior sedimentary rocks with many bare outcrops. The climate in Thunder Bay is milder than in KAP, with a January mean temperature of −14.8 °C and total snowfall from October through April of 185 cm. The LKH forest has a climate, topography, and forest structure and composition similar to SGP, except that there is a history of extensive disturbance by logging and agricultural development, such that mature forest is less common on the landscape. Post-logged forest encompasses the designated marten reserves.

Study design

In summer 2010, we examined 31 flagged areas identified in a previous winter as marten subnivean access points, defined as holes observed in the snow large enough (≥10 cm diameter) and deep enough for a marten to enter to the forest floor (Andruskiw *et al.*, 2008). Such points were marked with flagging tape during the backtracking exercises in the winters of 2006, 2007, and 2009. These points numbered 21 in KAP and 10 in SGP, and were widely enough dispersed to ensure that they represented habitat use by most of the tracked martens. They were considered case points in a case-control design (Keating & Cherry, 2004) in which we located a further 3 points 50−100 m from each case point, using random numbers to determine azimuth and distance. The resulting 93 control points were considered to be in areas potentially used by martens, but not tracked specifically to the point of subnivean access during our back-tracking exercise. They increased our sample size to $n = 124$ to assist with model comparisons.

In the marten reserves, we separated habitat into the fair and good categories identified in the provincial guidelines by Watt *et al.* (1996). There, we established an additional 60 points, 10 in fair and 10 in good habitat in each of 3 LKH reserves or marten core areas, as these are referred to in the guidelines document. These core-area points were located at random distances and azimuths from landforms identifiable on maps and on the ground. We did not sample stands designated as poor habitat within or outside the marten core areas, because this category implies a wide range of unsuitable habitats.

Measurement of forest structural characteristics

We established a circular plot of 50 m^2 (3.99 m radius) around each case, control, and core-area point, where we assessed forest structures defined by 20 variables (Table I). At each plot centre, we estimated coniferous canopy closure with a convex, spherical densiometer. We estimated canopy tree basal area with a metric 2-factor prism held at the plot centre and calculated separately the coniferous component. We separately estimated snag density from counts of dead trees within each plot and calculated snag volume by multiplying stem diameters (at breast height, ≥10 cm) by their length. Volume is overestimated this way. Stems of dead trees with a lean of ≤60° from horizontal were considered CWD, and standing stems with a lean of >60° from horizontal were considered snags. In order to test our idea that clusters of shrubs might also be associated with marten subnivean access, we estimated heights and density of shrubs ≥1 m tall, again separating the coniferous component and identifying species. We used average February snow depth from climate normals for Kapuskasing and Thunder Bay and estimated the effect of canopy cover for each plot on a virtual snow depth following D'Eon (2004); this process to approximate midwinter conditions was used to further separate shrub counts into classes of 1.0−1.9 m, 2.0−3.9 m, and ≥4.0 m height above the virtual snow surface. We tallied shrubs growing in clumps of ≥10 stems from a common root, typical for some of the deciduous species, as 1 individual, but adjusted density for these shrubs by multiplying the tally by a constant factor of 6. This factor was based on the average observed cover associated with clumped deciduous stems relative to single stems within a similar height class and similar growing conditions. We categorized portions of CWD within the plot and ≥1 m in length or height above our imaginary snow surface by diameter (>1 cm), length class (1–2 m, 2–4 m, and >4 m), and decay class. Decay class for CWD, including snags, was adapted from Maser *et al.* (1979): CWD with little to no sign of decay and with all bark and fine branches intact fell into decay class 1; CWD with intermediate signs of decay and with few to no fine branches, intact or loosening bark, and solid wood fell into decay class 2; CWD with extensive signs of decay and with minimal to no branches or bark fell into decay class 3. We did not separately consider logs in more advanced stages of decay because these mostly occurred below the imaginary snow surface. We calculated CWD volumes by multiplying stem diameters by their length, converting recorded classes of 1–2 m, 2–4 m, and >4 m into fixed lengths of 1.5 m, 3.0 m, and 6.0 m. Again, volume is overestimated this way.

TABLE I. Forest structural variables measured in this study as a candidate list determining fine-scale winter habitat selection by American martens.

Variable set description	Number of variables	Likely function to martens [a]
Tree stratum		
Coniferous canopy closure	1	Prey
Total basal area	1	Rest
Coniferous basal area [b]	1	Rest, predator
Snag density (CWD [c] 60–90° from horizontal) [b]	1	Prey, rest
Snag volume [b]	1	Prey, rest
Shrub stratum		
Deciduous shrub density [d]	4	Prey
Coniferous shrub density [d]	4	Prey
Ground stratum		
CWD count [e]	2	Prey, rest
CWD volume [e]	5	Prey, rest

[a] Prey = prey abundance and detectability; predator = predator protection and avoidance; rest = rest, denning, and thermoregulation; adapted from Godbout and Ouellet (2010).

[b] Variables are additional to the set tested by Godbout & Ouellet (2010).

[c] CWD = coarse woody debris.

[d] We separated shrubs by height in classes of 1.0−1.9 m, 2.0−3.9 m, and ≥4.0 m above estimated average snow depth and included a fourth variable, total shrub density.

[e] Excluding snags, *i.e.*, CWD is 0–60° from horizontal; we added 3 variables that separated CWD counts and volume each into 3 decay classes (Maser *et al.*, 1979; Andruskiw *et al.*, 2008). We added, for both total CWD count and total CWD volume, a second variable that included snags, *i.e.*, CWD in all orientations.

Data analysis

We followed the approach of Godbout and Ouellet (2010) to develop and subsequently compare a series of models of marten habitat selection, entering a series of the forest structural variables into conditional logistic regressions in the NOMREG procedure (IBM Corp., 2012). We first tested square-root and log transformations on all variables and used transformations in subsequent analyses if they yielded a greater Shapiro–Wilk (W) statistic. We thus adjusted our data to a normal distribution ($W > 0.70$) with square-root transformations for 13 variables and log transformations for 6 variables, leaving 1 data array, coniferous canopy closure, without transformation ($W = 0.98$). We used boxplots to ensure homogeneity of variance–covariance matrices, and Kendall's tau (τ) rank correlation coefficients to explore relationships among variables. We eliminated 1 variable in each correlated pair ($\tau < -0.6$ or $\tau > 0.6$), retaining variables for which averaged differences between case and control points were higher, and continued this process until no correlations ($-0.6 < \tau < 0.6$) remained in the data matrix.

We compared conditional logistic regression models based on 1 to 3 variables, associated wherever possible with just 1 or 2 potential functions to martens (Table I), in order to understand how fine-scale winter habitat selection might be best described, particularly with respect to subnivean access; where all 3 functions were associated with a combination of model variables, it was in order to include all models with 2 variables and all 3-variable models with deciduous shrub density as a unique component of the boreal mixedwood forest. We did not allow variable interactions to enter into any model. We used Akaike's Information Criterion (AIC) corrected for small samples to assess model parsimony.

Because of our particular interest in less conifer-dominated areas of the boreal mixedwood forest, we developed 3 subsets of the combined data, including the LKH marten habitat reserves together with the KAP and SGP case-control data, separating the data set into what we defined *post hoc* as coniferous and mixedwood patches. First, we divided coniferous basal area by total basal area at each case, control, and core-area point and considered the point to be in a mixedwood patch if the ratio was ≤ 0.7 and in a coniferous patch if the ratio was >0.7. Then we entered variables from among the best-fit set of conditional logistic regressions into an analysis of variance at $\alpha = 0.05$ with Bonferroni corrections for multiple comparisons. We compared case and control points to core-area points of fair and good habitat in the marten reserves separately for coniferous and mixedwood patches for a small subset of variables.

Results

Seven non-correlated forest structural variables were entered into the logistic regression model set (Table II). Variables not in this list included total basal area, which was correlated with coniferous basal area ($\tau = 0.608$); all shrub densities by height class, each correlated with the corresponding totals in the deciduous and coniferous categories; total coniferous shrub density, negatively correlated with snag density ($\tau = -0.620$); and CWD total count, correlated with snag density ($\tau = 0.830$). We chose not to include any CWD counts by decay class, which were more correlated one to the next than were CWD volumes by decay class. CWD volume in decay class 2 was the least cross-correlated among other decay classes; it was the only measure of decay included among the variables in the modeled set related to CWD (Table II). For this and the remaining 6 variables, 19 models were compared to allow all combinations of variables associated with CWD and snags, to include all models associated just with prey acquisition and rest as structural functions, and to add deciduous shrub density as an additional variable to all models linked to prey acquisition.

The most parsimonious model predicting subnivean access included only CWD count (Table III). There is a >99% probability that this forest structural element alone best defines winter subnivean access among the model set we tested. Where martens accessed the subnivean layer, there were 71% higher CWD counts than at associated control points (Table II). Due to limitation of the *post hoc* analysis with respect to sample sizes and the number of tests, only for coniferous patches were case ($n = 24$) and control ($n = 54$) points significantly different in CWD counts (Figure 1). Core-area points corresponding to good ($n = 21$) and fair ($n = 16$) habitat in the coniferous patches of the LKH reserves could not be distinguished, nor could they be distinguished from case and control points with respect to CWD counts. In mixedwood patches, case ($n = 9$), control ($n = 35$), and the good ($n = 7$) and fair ($n = 14$) points in the marten core areas followed trends similar with respect to CWD counts to those in coniferous patches, but no significant differences were found among the point categories.

Among the models with just 1 structural variable, significant support based on the χ^2 approximation of Wald's statistic was found for CWD count, but also for coniferous basal area, a variable we associated with predator avoidance as well as rest (Table III). Among other 1-variable models, weak support in explaining marten subnivean access was found for snag density, which was 18% higher at access points, and deciduous shrub density, which was 36% higher at access points than at surrounding control points (Table II). Neither CWD volume in decay class 2 nor total CWD volume could be selected from the model-building exercise as important to defining subnivean access. CWD count was weakly and negatively correlated with CWD total volume ($\tau = -0.577$). In neither coniferous nor mixedwood patches were significant differences found comparing case, control, and core-area points with respect to snag density, although in mixedwood patches, snag density was 38% higher at subnivean

TABLE II. Forest structure at marten subnivean access points ($n = 31$) and control points ($n = 93$) along snow tracks in northwestern Ontario. The variable set is formed by removing correlated variables from the list in Table I and retaining variables with the higher mean difference between access and control points. Estimates of coarse woody debris (CWD) and all density estimates are measures within a 50-m^2 plot.

Variable	Access points		Control points		Likely function to martens [a]
	Estimate	SE	Estimate	SE	
Coniferous canopy closure (%)	38.60	1.80	32.90	1.20	Prey
Coniferous basal area ($m^2 \cdot ha^{-1}$)	14.30	1.50	11.40	0.90	Rest, predator
Snag density	3.90	0.60	3.30	0.30	Prey, rest
Deciduous shrub density	7.60	1.80	5.60	0.70	Prey
CWD count	2.12	0.50	1.24	0.13	Prey, rest
Total volume CWD and snags (m^3)	0.09	0.03	0.16	0.08	Prey, rest
CWD volume in decay class 2 (m^3)	0.02	0.01	0.11	0.08	Prey, rest

[a] Defined in Table I.

access points than surrounding control points (Figure 1). Differences in deciduous shrub density were only significant in mixedwood patches, and then only in a comparison between random points in the KAP and SPG study areas and the core-area points in fair habitat in the LKH forest, where they were about 2.3 times as high; subnivean access points were about 78% higher in deciduous shrub density than were control points. Among the 2-variable models in Table III, higher support from the AIC occurred when snag density and when deciduous shrub density were added to CWD count, and a higher χ^2 was estimated for the case where coniferous basal area was added to CWD count.

Discussion

Fine-scale forest structural characteristics important to martens

As in earlier studies where CWD count was declared to be a more important element than any others in determining winter marten habitat selection (Sherburne & Bissonette, 1994; Chapin, Harrison & Phillips, 1997), our analysis in the boreal mixedwood forest prioritized this variable and did not find the support that Godbout and Ouellet (2010) found for higher coniferous tree canopy closure and the lateral cover provided by conifer shrubs in explaining marten winter habitat selection. Our results also suggest that martens selected subnivean access points where locally high coniferous basal area occurred. Deciduous shrubs do not appear to increase the likelihood of subnivean access unless considered together with CWD counts. Fine-scale forest structural elements selected by martens to gain subnivean access should be related to success of prey acquisition (Andruskiw *et al.*, 2008), but the 2 most important variables in our modelling exercise for boreal mixedwood appear equally relatable to predator avoidance and rest (Godbout & Ouellet, 2010). Contrary to the suggestion by Watt *et al.* (1996), the role of snags (CWD with ≤40° lean) was less important than that of fallen woody materials. However, in the boreal mixedwood forest, unlike the mature, coniferous forest emphasized by the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario*, large aspen in intermediate stages of decay abound as snags or large fallen logs, and this structure is probably much less important to martens for access to the subnivean layer than the complex structure afforded by leaning coniferous CWD and other types of lateral cover.

Occurring with higher frequency in mixedwood relative to coniferous patches, and especially common in the LKH marten reserves, is the potential structure afforded by deciduous shrubs, a diverse part of the boreal mixedwood forest understory representing >15 woody species in our surveys; in order of decreasing frequency, the most common were trembling aspen, balsam poplar (*Populus balsamifera*), white birch, black ash (*Fraxinus nigra*), mountain maple (*Acer spicatum*), green alder (*Alnus viridis* spp. *crispa*), speckled alder (*Alnus rugosa*), willow (*Salix* spp.), beaked hazel (*Corylus cornuta*), serviceberry (*Amelanchier* spp.), choke cherry (*Prunus virginiana*), pin cherry (*Prunus pensylvanica*), honeysuckle (*Lonicera* spp.), mountain ash (*Sorbus* spp.), and larch (*Larix laricina*). We suggest that factors explaining marten subnivean access may vary with transitions in local tree dominance (basal area) from coniferous to mixedwood patches. This conclusion is not unlike that of Bowman and Robitaille (2005), who found eastern white cedar (*Thuja occidentalis*) trees, not generally associated with marten habitat, important to winter habitat selection where this species becomes more frequent in northeastern Ontario. Similarly, just as the branch structure of some shrub species is more likely than that of others to create a gap in the snow that facilitates subnivean access by martens, the negative correlation between snag and coniferous shrub density found in our study might

TABLE III. Conditional logistic regression models comparing subnivean access points by martens (cases) along snow tracks to nearby random (control) points. The likeliest difference between case (n = 31) and control (n = 93) points is the CWD count. Models are listed in order of increasing Akaike Information Criterion corrected for small sample size (AIC_c). The Chi-square (χ^2) approximation of the Wald statistic, ΔAIC, and AIC weights (w_i) assisted in model comparisons.

Variables included in the model	Likely function to martens [a]	K	χ^2	AIC_c	ΔAIC	w_i
CWD count	Prey, rest	1	8.3	26.946	0.000	0.994
Snag density	Prey, rest	1	0.7	37.154	10.208	0.006
Deciduous shrub density	Prey	1	0.7	50.060	23.114	0.000
Coniferous basal area	Rest, predator	1	4.6	50.877	23.931	0.000
CWD count, snag density	Prey, rest	2	8.3	73.576	46.630	0.000
CWD count, deciduous shrub density	Prey, rest	2	9.1	86.590	59.644	0.000
Coniferous basal area, CWD count	All three	2	12.1	90.145	63.199	0.000
CWD volume in decay class 2	Prey, rest	1	0.5	95.514	68.568	0.000
CWD count, CWD volume in decay class 2	Prey, rest	2	9.8	105.778	78.832	0.000
Coniferous basal area, deciduous shrub density	All three	2	7.7	116.376	89.430	0.000
CWD total volume	Prey, rest	1	0.4	116.673	89.727	0.000
Coniferous canopy closure	Prey	1	6.2	118.877	91.931	0.000
CWD count, CWD volume in decay class 2, snag density	Prey, rest	3	10.1	121.890	94.944	0.000
Coniferous basal area, CWD count, deciduous shrub density	All three	3	15.0	122.341	95.395	0.000
Coniferous canopy closure, CWD count	Prey, rest	2	12.2	127.734	100.788	0.000
Coniferous canopy closure, CWD count, deciduous shrub density	Prey, rest	3	15.0	135.336	108.390	0.000
Coniferous basal area, coniferous canopy closure	All three	2	6.6	136.113	109.167	0.000
Coniferous canopy closure, deciduous shrub density	Prey	2	9.1	137.780	110.834	0.000
Coniferous canopy closure, CWD total volume	Prey, rest	2	6.4	143.242	116.296	0.000

[a] Defined in Table I. These functions were used to guide selection of the model set to be compared (see text).

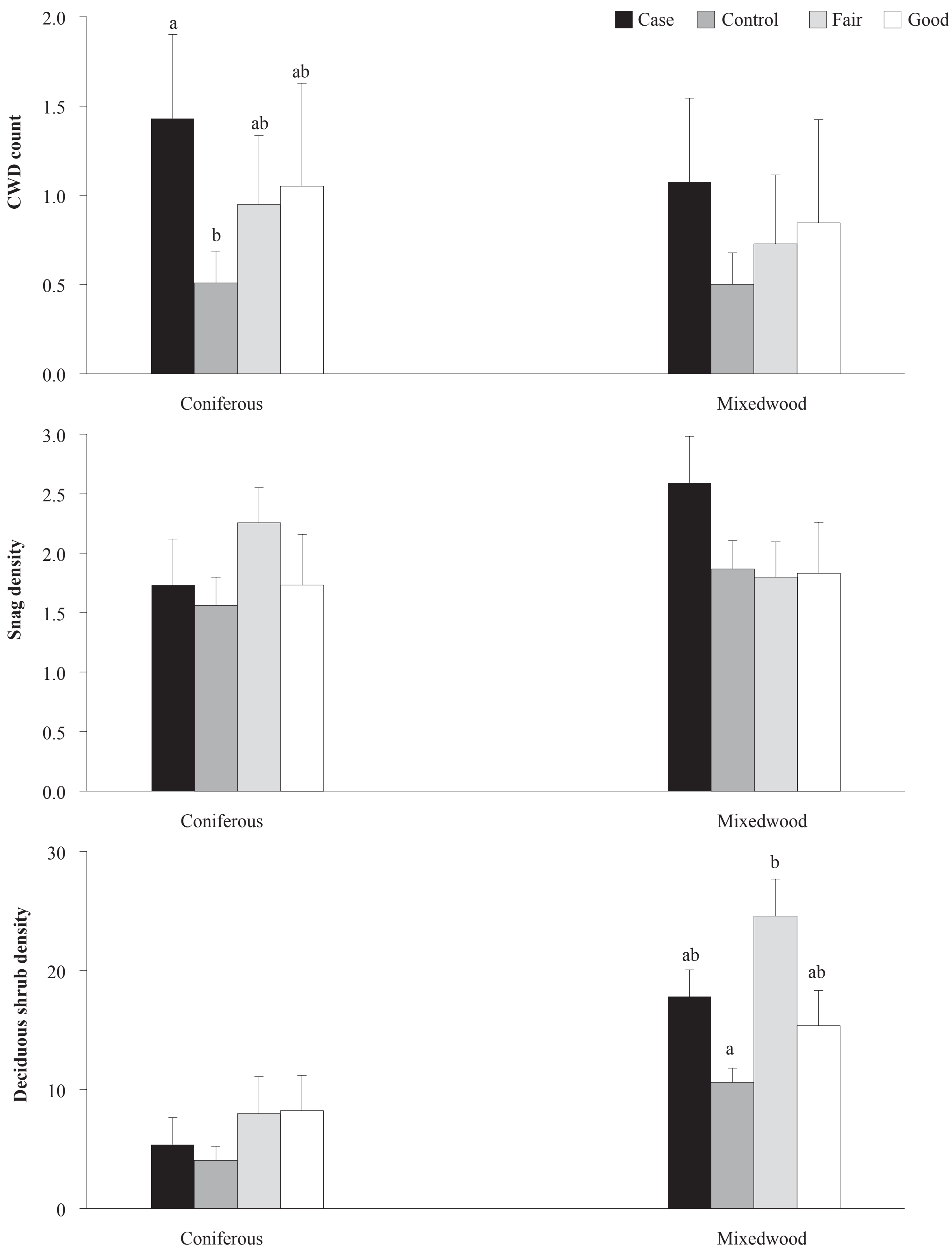

Figure 1. Coarse woody debris (CWD) counts, snag density, and deciduous shrub density at marten subnivean access points (n = 31) and control points (n = 93) along snow tracks in northern Ontario and at points in fair (n = 30) and good (n = 30) habitat designated in Lakehead Forest marten reserves, near Thunder Bay, Ontario. The terms counts and density are identical and localized to 50-m^2 forest plots. Plots were separated into coniferous and mixed-wood patches based on coniferous basal area. Error bars show mean + SE and matching lower case letters show cases where *post hoc* multiple comparisons in an analysis of variance (ANOVA) were not significantly different. Where letters do not appear, significant differences were not found among the point categories.

indicate that facilitation of marten activity by typically upright coniferous shrubs, in contrast to deciduous shrubs, is more likely as they die and subsequently become snags and then leaning CWD.

Management implications

Our study, like that by Godbout and Ouellet (2010), illustrates that a coarser-scale management approach may miss some of the fine-scale features of habitat required by martens, including the potential usefulness of deciduous shrubs for accessing subnivean habitat. Further research on fine-scale habitat use by martens will increase the sophistication of existing forest management beyond coarse scales, even as our approach to coarse-scale habitat management becomes increasingly sophisticated (Hearn *et al.*, 2010). We recommend forestry practices such as those found in the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario*, which preserve patches of high coniferous tree basal area and a continuous supply of partially decomposed CWD ≥ 10 cm in diameter. We suggest that subnivean access by martens is best facilitated in mixedwood forest by management practices that offer a dense understory structure provided both by fallen and leaning CWD and by patches of dense deciduous shrubs that usually occur in small gaps created by single fallen trees. These habitat elements are less important than are snags, and can be maintained as mixedwood forests mature. We suggest that future research investigate the maintenance of patches of both coniferous and deciduous understory shrubs in the understory of mature boreal mixedwood forest. Maintenance of such structure through all forest stages is likely related to patterns of tree mortality and variation in drainage.

Acknowledgements

This study was supported by Lakehead University. Data on marten locations were provided from a project conducted jointly by the Ontario Ministry of Natural Resources, University of Guelph, and Canadian Forest Service. The volunteer efforts of J. Willoughby and L. Palka in data collection were vital to the completion of the study. An earlier draft of this manuscript was the Master's thesis of the second author, who was assisted by the comments of J.-F. Robitaille, Laurentian University. We are grateful for the comments of two anonymous reviewers and the associate editor of Écoscience in improving our original submission.

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