Characteristics of the Boreal Mixedwood Forest Associated with Subnivean Access by the American Marten (*Martes americana*)

by
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ABSTRACT

Habitat selection by the American marten (*Martes americana*), in studies throughout its range, has been associated with forest types that offer higher structural complexity. Such structure has been proposed to facilitate predator avoidance and access to the subnivean environment for thermoregulation and food procurement. The purpose of my study was to assess fine-scale habitat characteristics at points of subnivean access, and to use these characteristics to evaluate stands designated as reserved marten habitat according to the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario*. In two study areas near Kapuskasing and near Thunder Bay, Ontario, I used point sampling to measure overhead canopy cover and various attributes of downed wood and dead trees, and plot sampling to describe understory woody vegetation, where 31 subnivean access points had been determined by winter tracking of marten. A case-control design and stepwise logistic regression were used to compare habitat at marten access points to habitat available in adjacent areas, using two or more reference points each 50-100 m from an access point. Overhead canopy cover (P = 0.003), abundance of coarse woody debris (P = 0.020), and deciduous understory stem density (P = 0.030) were positively associated with subnivean access. Total volume of standing dead trees (snags) and coarse woody debris in intermediate stages of decay, identified by loose bark and little to no intact fine branch structure, were negatively associated with subnivean access when estimated as volume within a plot (P = 0.047). In habitat reserves in the Lakehead Forest, near Thunder Bay, the same characteristics were used in a forward stepwise discriminant function analysis comparing sites of used subnivean access and proximally located

control points to stands designated as “good” and “fair” suitable marten habitat within marten cores. The discriminant function analysis was able to distinguish the “good” suitable habitat from the case – control model to a greater degree than the “fair” suitable habitat.

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INTRODUCTION

American marten (*Martes americana*) are found throughout the boreal forest of North America, as well as in some hemi-boreal (temperate) and montane forests (Strickland and Douglas 1987). Marten are generally associated with later stages of forest succession, in forest stands with high (overstory) canopy closure, large amounts of downed wood (i.e., coarse woody debris, CWD), and a large proportion of softwood (Bowman and Robitaille 2005, Allen 1982). Winter is a time when prey acquisition is more difficult than at other times of the year because common prey, such as microtines, are located within the subnivean layer (beneath snow). Access to the subnivean layer is achieved by marten digging through the snow or entering through existing openings, primarily created by CWD and low-hanging conifer branches (Hargis and McCullough 1984). Frequency of subnivean access and success in prey acquisition have both been linked to abundance of prey and CWD (Andruskiw et al. 2008, Sherburne and Bissonette 1994), and both of these variables have been associated with primarily older forests (Payer and Harrison 2004, 1999; Thompson 1994, 1986; Thompson and Harestad 1994). Tree height, as a proxy for forest age, has also been used as a variable for assessing marten habitat.

Having habitat needs that conflict with interests in the industry for mature coniferous forest, marten have received much attention in forest management planning (Bowman and Robitaille 1997). In Ontario, forest management plans from 1996 to 2007 for most of the boreal forest have followed the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario*. The premise for these guidelines was a series of habitat characteristics that were originally outlined by Allen's (1982) Habitat Suitability Index (HSI) model and can be estimated from Forest Resource Inventory (FRI) maps. Throughout a managed forest in Ontario, stand-scale management designates FRI stand polygons as "good," "fair," or "poor" marten habitat and further organized into marten "core areas", required to be between 30 and 50 km^2 in size with a higher proportion (>75%) of "good" and "fair" marten habitat than in the remainder of the managed forest (Watt et al. 1996). Stands designated as "good" habitat are typically mature to old-growth forest with 25 to 80% conifer composition and must have at least 50% canopy closure. Such stands are usually rich in CWD, snags, and structural diversity. They also typically have a diverse herb and shrub understory to support prey species (Racey et al. 1989). Stands designated as "fair" habitat are lacking at least one facet of "good" habitat, while "poor" habitat generally has low conifer composition and/or low structural diversity. This designation is based on habitat interpretation at the stand level, and is delineated among vegetation types in Northwestern Ontario's Forest Ecosystem Classification by Racey et al. (1989), based on Racey and Hessey (1989). Thus, this delineation is directly related to an ecosystem classification and is indirectly related to forest structure. In this thesis, the structural characteristics identified as important to marten habitat (i.e., canopy cover, forest composition, and abundance of CWD, snags, and shrub understory) were directly explored as they were available in winter conditions in Northwestern Ontario's boreal forest.

The ultimate objective of this study was to evaluate forest stands designated as "fair" and "good" suitable marten habitat in marten "core areas" of the Lakehead Forest, near Thunder Bay. Ontario. This evaluation was done by first identifying which forest structural characteristics at the localized scale are important to subnivean access, as a representation of suitable winter habitat characteristics. A localized scale was considered the area in direct view of a marten attempting subnivean access. These structural characteristics were investigated by point and plot sampling where 31 subnivean access points had been determined by winter tracking of marten in two areas near Kapuskasing and Thunder Bay, Ontario. I hypothesized that FRI types designated by forest managers as “fair” and “good” suitable marten habitat would have forest structural characteristics more similar to those at sites of subnivean access than control points. I also expected that the “good” suitable habitat areas will exhibit these characteristics at higher levels than the “fair” suitable habitat, based on the premise that the delineation of vegetation types by Racey et al. (1989) both predicts and distinguishes marten habitat well. Finally, I expected that the abundance of dead wood, canopy cover, and understory coniferous growth would be the most important variables in discriminating subnivean access and thus be most important in the evaluation of reserved marten habitat. I rationalized the expected order of importance of these features based on past research, which has unanimously identified CWD as important (Payer and Harrison 2004; Bowman and Robitaille 1997; Chapin et al. 1997; Drew 1995; Sherburne and Bissonette 1994; Corn and Raphael 1992; Allen 1982), whereas preference for higher levels of canopy is common (Smith and Shaefer 2002; Bowman and Robitaille 1997; Hargis and McCullough 1984; Allen 1982), but with exceptions (Chapin et al. 1997; Sherburne and Bissonette 1994), and the link between subnivean access and understory coniferous growth has been identified (Hargis and McCullough 1984), but has not received much attention. Trends and interactions pertaining to the characteristics discriminating subnivean use in this study were also explored.

METHODOLOGY

Site Selection

Subnivean access by marten was observed from backtracking in the Gordon Cosens Forest licence area near Kapuskasing (KAP) in the winters of 2006 and 2007 (I. Thompson, J. Fryxell, and J. Baker, pers. comm.) and in Sibley Provincial Park (SPP) near Thunder Bay in winter 2009 (by the author). A total of 31 access points were recorded as GPS co-ordinates, and these points were revisited in summer 2010 to compare (as "case" points) to control points in adjacent forest, using a case-control design (Keating and Cherry 2004). A total of 93 control points were randomly located from 50 to 100 m away, using random number tables to determine azimuth and distance from the access points.

Fair suitable habitat (FSH) and good suitable habitat (GSH) was then selected from three Lakehead Forest marten "core areas," based on ease of accessibility by boat or truck. A total of 60 plots were located in FSH and GSH from random distances and azimuths from landforms identifiable on maps and on the ground (e.g., water crossings, unique forest edge, or road shape).

Measurement of Forest Structural Characteristics

A fixed circular plot of 50 m^2 was established with a 3.99 m radius around each used and control point and at each FSH and GSH plot. A total of 24 variables was measured either at plot centres or in the plots (Table 1).

Canopy cover was estimated at the plot centres using a convex spherical densiometer to reflect winter conditions by taking measurements prior to bud flush or ignoring deciduous foliage. Canopy tree composition was estimated by basal area, using a metric wedge prism with a basal area factor of 2. Understory stems and CWD above the average snow depth, determined by historical weather data and estimating the effect of canopy cover (D'Eon 2004), were tallied for each plot. CWD was tallied by species, diameter, length class (1 - 2 m, 2 - 4 m, and >4 m), decay class and orientation (degree of lean) above the ground (using 10 degree increments). Decay class was evaluated using a three-category classification method adapted from Maser et al. (1979). Stems with little to no sign of decay, with all bark and fine branches intact, were "decay class 1." Stems with intermediate sign of decay, with few to no fine branches, intact or loosening bark and solid wood were "decay class 2." Stems with extensive signs of decay, minimal to no branches or bark and stem decay were "decay class 3." More advanced stages of decay are characteristic of CWD in the duff layer, and thus below the estimated snow level and not considered in this study. Dead wood was further classified as CWD (0 - 60^{o}) or snags (70 - 90^{o}). All dead wood variables were expressed as stem counts and also as approximate volume within plots. Approximate volume was calculated by multiplying stem diameter by length class. Length classes 1- 2 m, 2 - 4 m and >4 m were represented by fixed lengths of 1.5 m, 3 m, and 6 m, respectively.

All sub-canopy woody vegetation (1 - 6 m in height) was tallied by species and height class (1 - 2 m, 2 - 4 m, and 4 - 6 m). These data were then grouped by vegetation type (coniferous and deciduous) and height class. Coniferous understory growth consisted of black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), eastern white cedar (*Thuja occidentalis*), jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*). Deciduous understory growth consisted of trembling aspen (*Populus temuloides*), balsam poplar (*Populus balsamifera*), white birch (*Betula papyrifera*), 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*). Larch was grouped with deciduous shrubs due to seasonal senescence of its foliage. Deciduous species growing in clumps of ≥10 stems originating from a communal root source were tallied together. Total deciduous understory growth was calculated by combining single stemmed and clumped individuals on a plot and multiplying a constant factor of 6 to clumped individuals. This factor was based on field observations comparing the average relative ground cover and structure of clumped individuals to single-stemmed individuals.

Basal area of overstory trees was calculated by multiplying the stem count (achieved by prism sweep) by the basal area factor. Conifer basal area included black spruce, white spruce, balsam fir, eastern white cedar, jack pine, white pine, and red pine and total basal area grouped all species.

Table 1. Description of forest structural variables collected in this study. This list was later reduced to remove correlated variables.

Structural Variable	Description
1 - 2 m Conifer	Conifer stem count in 1 - 2 m height class
2 - 4 m Conifer	Conifer stem count in 2 - 4 m height class
4 - 6 m Conifer	Conifer stem count in 4 - 6 m height class
Total Conifer	Conifer stem count in 1 - 6 m height class
1 - 2 m Deciduous	Deciduous stem count in 1 - 2 m height class

Table 1. (Continued)

Structural Variable	Description
2 - 4 m Deciduous	Deciduous stem count in 2 - 4 m height class
4 - 6 m Deciduous	Deciduous stem count in 4 - 6 m height class
Total Deciduous Single Stems	Deciduous stem count (1 - 6 m height class)
Total Deciduous Understory Growth	Deciduous stem count in 4 - 6 m height class
Overhead Canopy Cover	Tree canopy cover in winter conditions
CWD Stem Count	Dead wood stem count with a 0 - 60^o orientation
Snag Stem Count	Dead wood stem count with a 70 - 90^o orientation
Total Dead Wood Stem Count	Total stem count of CWD and snags
Dead Wood in Decay Class 1 Stem Count	Dead wood stem count in decay class 1
Dead Wood in Decay Class 2 Stem Count	Dead wood stem count in decay class 2
Dead Wood in Decay Class 3 Stem Count	Dead wood stem count in decay class 3
CWD Volume	Volume of dead wood with a 0 - 60^o orientation
Snag Volume	Volume of dead wood with a 70 - 90^o orientation
Total Dead Wood Volume	Total volume of CWD and snags
Volume of Dead Wood in Decay Class 1	Volume of dead wood in decay class 1
Volume of Dead Wood in Decay Class 2	Volume of dead wood in decay class 2
Volume of Dead Wood in Decay Class 3	Volume of dead wood in decay class 3
Conifer Basal Area	Basal area of coniferous species (excluding larch)
Total Basal Area	Basal area of all species combined

Data Analysis

Square-root and log transformations were tested on all variables. The transformation (or lack thereof) yielding the greatest Shapiro-Wilk (W) statistic was used in subsequent analyses and, with this option, all 24 variables were normally distributed ($W > 0.7$). Square-root transformations were used in 17 cases, log transformation in 6 cases and untransformed in 1 case (APPENDIX I). Boxplots were used to ensure homogeneity of variance-covariance matrices (APPENDIX II).

Kendall's tau (τ) rank correlation coefficients were used to test independence among variables, using only the case-control data from KAP and SPP. The number of variables used in the first step of analysis was reduced to those with rank correlation coefficients of $-0.4 < \tau < 0.4$, but retaining all variables for which significant differences were estimated between case and control points. Significance in difference was tested by Student's *t*-test or, following Levene's test for equality of variances ($P > 0.05$), by a *t*-test for unequal variances with an adjusted degrees of freedom. A variable was removed if it was correlated to a variable with a higher *t* value calculated from the difference between case and control.

A forward conditional (stepwise) multinomial logistic regression was first used on the KAP and SPP data to determine the forest structural characteristics most associated with subnivean access points. Model parsimony was assessed with Akaike's Information Criterion (AIC). Starting with all of the previously screened variables, the main effects model was reduced to the model with the lowest AIC. A full factorial model was then constructed using the main effects model and all possible interactions, reducing again to the model with the lowest AIC. Means of significant forest structural characteristics and a reduced Kendall's tau correlation matrix were used to interpret results. In a final step, a forward stepwise DFA was then conducted on the FSH and GSH data together with the KAP and SPP data, using variables that were found to be significant to subnivean access by the first logistic regression model on KAP and SPP data alone. A variable entry level of $\alpha = 0.10$ was used to ensure all variables deemed important to subnivean access were used in the DFA. Discriminant function plots from variables entering the DFA were used to interpret these results.

RESULTS

Means of canopy cover, CWD stem count, and conifer basal area were significantly different in case and control plots ($P < 0.05$). These three variables and an additional seven that were not significantly correlated entered the first logistic regression model (Table 2, APPENDIX III).

Table 2. Means, standard deviations (used and control) and *t*-test results for variables used in logistic regression after correlated variables were removed by use of *t*-test and a Kendals' tau correlation matrix. Unequal variance *t*-test used adjusted degrees of freedom (*df*) to determine equality of means.

Structural Variable	Case		Control		*t*-test for Equality of Means		
	Mean	Std. Dev.	Mean	Std. Dev.	*t*	*df* (adj.)	*P*
Overhead Canopy Cover	38.64	9.90	32.87	12.06	−2.70	69	0.01
CWD Stem Count	1.88	2.77	0.86	1.27	−2.32	46	0.02
Conifer Basal Area	14.30	8.13	11.36	8.93	−2.29	72	0.03
Total Deciduous Understory Growth	7.61	10.08	5.62	6.61	−1.15	52	0.25
Volume of Dead Wood in Decay Class 3	0.03	0.07	0.03	0.12	1.15	54	0.26
Snag Stem Count	3.91	3.11	3.30	2.82	−0.93	55	0.36
Volume of Dead Wood in Decay Class 2	0.02	0.05	0.11	0.75	−0.73	60	0.47
Total Dead Wood Volume	0.09	0.18	0.16	0.75	−0.70	69	0.49
Volume of Dead Wood in Decay Class 1	0.04	0.18	0.02	0.08	−0.55	62	0.59
Total Conifer	7.55	7.13	7.48	7.37	−0.01	56	0.99

The most parsimonious logistic regression model (lowest overall AIC), without interactions, included overhead canopy cover, CWD stem count, total deciduous understory growth, and volume of dead wood in decay class 2 as significant predictors of subnivean access (Table 3). Of these, all but volume of dead wood in decay class 2 were associated with higher levels near points of subnivean access. The log transformation used to normalize volume of dead wood in decay class 2 yielded a positive regression coefficient, in fact related to a negative influence of this variable (in values <1) on subnivean access. Total deciduous understory growth, comprised of single- and multi-stemmed individuals, was most correlated with the number of single deciduous stems ($\tau = 0.906$). CWD stem count was negatively correlated with CWD volume ($\tau = -0.577$). Volume of dead wood in decay class 2 was the fourth significant predictor of subnivean access. This variable had a higher correlation with snag volume ($\tau = 0.396$) than with CWD volume ($\tau = 0.137$) and was negatively correlated with snag stem count ($\tau = -0.186$) and with stem counts of dead wood in decay class 2 ($\tau = -0.265$). Conifer basal area was significantly different between case and control plots (Table 2) and did not enter the most parsimonious logistic model, due to its correlation with canopy cover ($\tau = 0.536$).

Table 3. Akaike's Information Criterion (AIC), parameter coefficients (β), standard errors, Chi-square (χ^2) significance tests with *p*-values, and the exponent of β for parameters in the most parsimonious main effects logistic model ($\alpha = 0.05$) predicting subnivean access by marten.

Effect	AIC	β	Std. Error	χ^2	*P*	Exp (β)
Overhead Canopy Cover	142.1	0.063	0.023	7.29	0.003	0.939
Total Deciduous Understory Growth	138.2	0.300	0.142	4.46	0.030	0.740
CWD Stem Count	138.9	0.630	0.276	5.21	0.020	0.533
Volume of Dead wood in Decay Class 2	137.5	0.433	0.223	3.76	0.047	0.649

The most parsimonious logistic regression model, including interactions, linked overhead canopy cover ($\chi^2_{1,28} = 6.4$, $P = 0.012$) and the interactions between canopy cover and CWD stem count ($\chi^2_{1,28} = 6.1$, $P = 0.013$), between canopy cover and volume of dead wood in decay class 2 ($\chi^2_{1,28} = 10.4$, $P = 0.001$), and among canopy closure, total deciduous understory growth and volume of dead wood in decay class 2 ($\chi^2_{2,28} = 7.9$, $P = 0.005$) to subnivean access. Both canopy cover and CWD stem count were more likely to be higher at points of subnivean access than at control points (Fig. 1). Use of subnivean access was more frequent in areas with a low volume of dead wood in decay class 2, especially where canopy cover was limited (Figs. 2 - 4). When deciduous understory growth was incorporated, use of subnivean access was generally restricted to higher levels of canopy cover in its absence. Conversely, subnivean access sites occurred over a greater range of canopy cover when deciduous understory growth was present. The proportion of used subnivean access points to control points was much higher when deciduous understory growth was present (31% in plots with 1 - 9 stems and 30% for plots with 10+ stems) vs. only 16.7% when absent. Finally, subnivean access was less likely in areas with a high volume of dead wood in decay class 2.

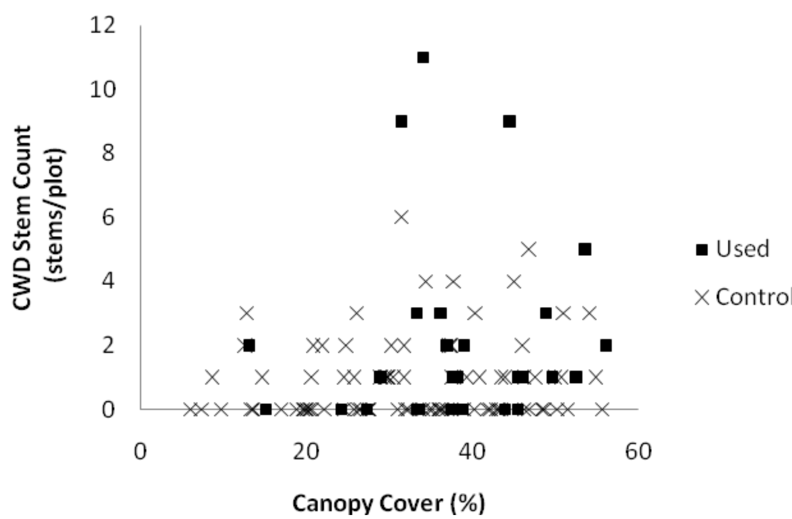

Fig. 1. Overhead canopy cover and coarse woody debris (CWD) stem count in areas of used subnivean access by marten and near control points in KAP and SPP.

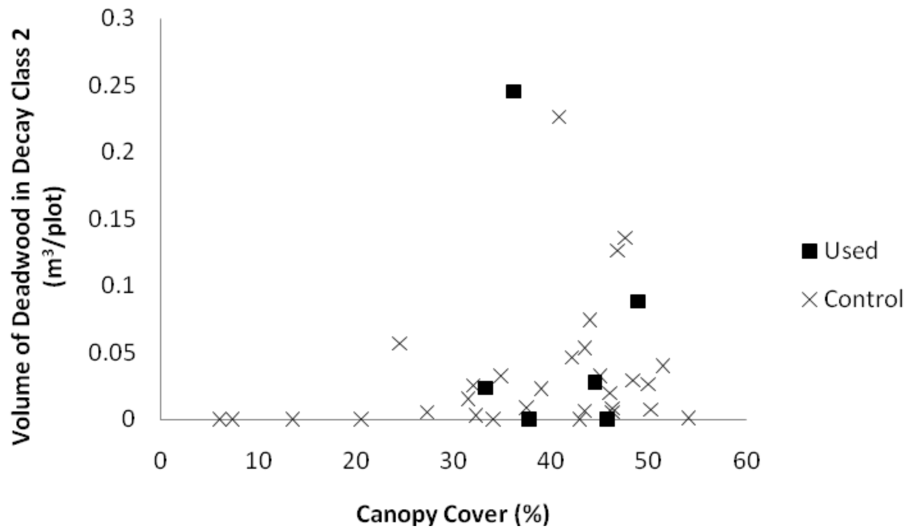

Fig. 2. Overhead canopy cover and volume of dead wood in decay class 2 at subnivean access points used by marten and near control points in KAP and SPP, where deciduous understory growth is absent.

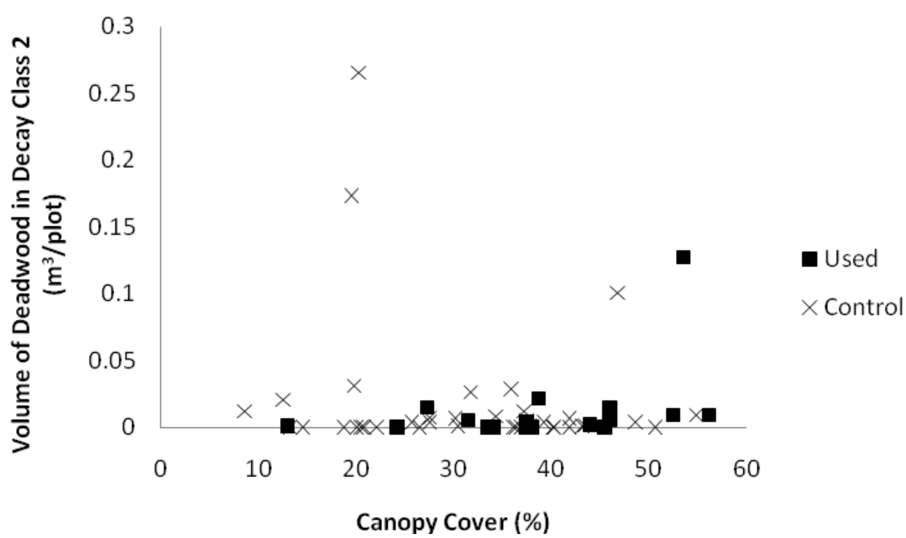

Fig. 3. Overhead canopy cover and volume of dead wood in decay class 2 at subnivean access points used by marten and near control points in KAP and SPP, where deciduous understory growth is low (1- 9 stems/plot).

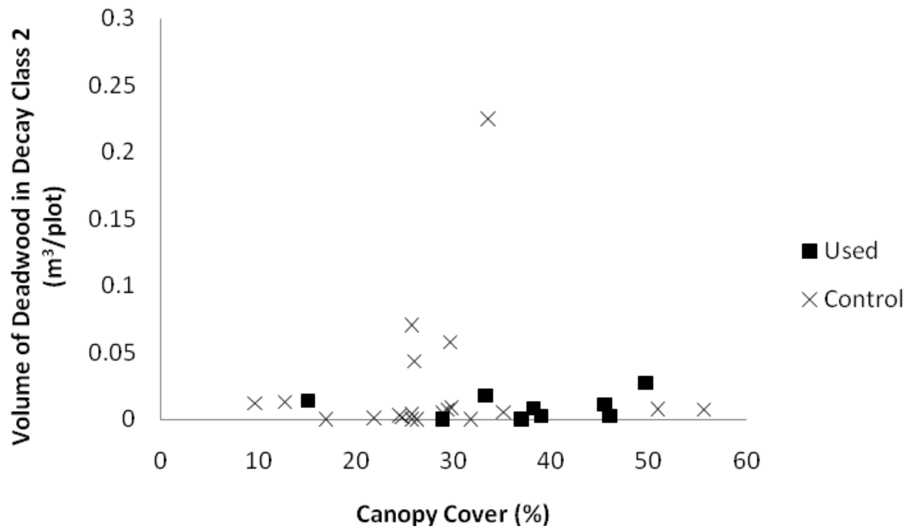

Fig. 4. Overhead canopy cover and volume of dead wood in decay class 2 at subnivean access points used by marten and near control points in KAP and SPP, where deciduous understory growth is high (10+ stems/plot).

Reserved marten habitat (both FSH and GSH) was more similar to habitat at subnivean access points than at nearby control points (Fig. 5). Discriminant functions 1 and 2 accounted for 69.4 and 16.9%, respectively, of the variance across all four variables in the DFA (Table 4). Axis 1, which represents discriminant function 1, places the mean score for both FSH and GSH plots with the mean score for subnivean access points (Fig. 5). Total deciduous understory growth occurred at significantly higher levels at both FSH and GSH sites than at control points (Table 5). Canopy cover at FSH, but not GSH, was higher than at control points. Axis 2, which represents discriminant function 2, distinguished FSH from GSH (Fig. 5). Although none of the variables associated with the DFA differed significantly between FSH and GSH (Table 5), the scores in table 4 show that the distinction might be higher canopy cover in FSH and higher CWD stem count and volume of dead wood in decay class 2 in GSH.

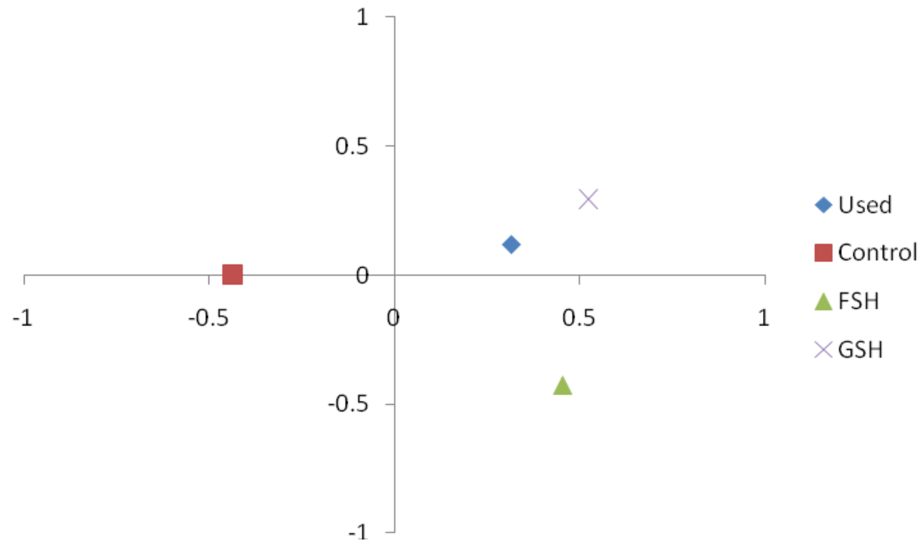

Fig. 5. Scores, means and standard deviations of discriminant functions 1 (*x*-axis) and 2 (*y*-axis) ($\alpha = 0.10$).

Table 4. Factor loadings of forest structural characteristics on discriminant functions for subnivean access points, control points, and reserved marten habitat (FSH and GSH).

Structural Variable	Discriminant Function	
	1	2
Total Deciduous Understory Growth	0.666	−0.173
Overhead Canopy Cover	0.319	−0.445
CWD Stem Count	0.332	0.329
Dead Wood in Decay Class 2 Stem Count	0.178	0.792

Table 5. Structural variables in the most parsimonious main effects logistic model explaining marten subnivean access, Wilks' Lamda for the partial effect of each variable, and its mean for case points, control points, and reserved marten habitat (FSH and GSH). For each variable, means with the same letter are not significantly different (p>0.05) by multiple comparisons using Student's *t*-test with Bonferroni correction.

Structural Variable	Wilks' Lambda	Group Means			
		Used	Control	FSH	GSH
Overhead Canopy Cover	0.755	38.64[a]	32.87[b]	38.57[ac]	33.13[abc]
Total Deciduous Understory Growth	0.907	14.76[a]	10.88[a]	16.07[ab]	16.9[ab]
CWD Stem Count	0.748	2.12[a]	1.24[b]	1.47[abc]	1.87[abc]
Volume of Dead Wood in Decay Class 2	0.745	0.02[a]	0.11[ab]	0.02[ab]	0.04[a]

DISCUSSION

The most important structural feature in predicting subnivean access by marten in KAP and SPP was overhead canopy cover, a variable that differed significantly between subnivean access sites and control sites, and entered the most parsimonious logistic regression model, both as a main effect and within all significant interactions in an expanded model. The importance of canopy cover as a component of marten habitat is consistent with previous studies, but differs from other studies that revealed that CWD, but not canopy cover, is important to subnivean access (Chapin et al. 1997; Sherburne and Bissonette 1994). It has been suggested that horizontally oriented CWD may be more important than leaning snags (I.D. Thompson pers. comm.), but the sample size used in this study did not allow for the two components of dead wood to be distinguished in this study, which grouped them as CWD. Bait-box experimentation has shown no link between canopy cover and habitat use when complex woody structure is present (Drew 1995), suggesting correlations between overhead canopy cover and marten subnivean access may be more directly linked to the stem structure associated with preferred habitat. The importance of dead and fallen trees to marten has been widely accepted. Further classification of dead trees and branches by their orientation on the ground and level of decay allowed this study to identify CWD as positively correlated with subnivean access and volume of dead wood in decay class 2 as negatively correlated. Unlike the findings by Hargis and McCullough (1984), that marten selected dense cover <3 m above snow level, coniferous understory growth was not significantly different between case and control sites in KAP and SPP. On the other hand, total deciduous understory growth was important to subnivean access. In discriminating points of known marten subnivean access in this study, areas with no deciduous understory were used only if overhead canopy cover was >30%. This relationship has not previously been reported for marten.

The behaviour of marten in winter is thought to be influenced by three needs: thermoregulation, acquisition of prey, and avoidance of predators (Godbout and Ouellet 2010; Drew and Bissonette 1997; Drew 1995; Thompson and Colgan 1994; Brown and Lasiewski 1972). The thermally inefficient morphology of mustelids incurs a higher metabolic cost for thermoregulation relative to most other mammals (Brown and Lasiewski 1972). As a result, subnivean refuge is a common practice for marten in cold temperatures. Accessing this refuge is facilitated by forest understory structure (particularly CWD), which provides breaks in the snow (Corn and Raphael 1992). Further, the low thermal conductivity of partially decomposed wood is expected to incur important thermal benefits at subnivean resting sites, by allowing for a more thermoneutral environment and less conductive heat loss to snow, which may lead to melting and consequent wetting of marten fur (Buskirk et al. 1989). Thus, increased quantity of dead wood may influence the likelihood of subnivean access through an increase in opportunity and/or quality of rest sites, potentially explaining the strong relationship of CWD stem count abundance to subnivean access in this study.

Continual acquisition of food is important to compensate for the metabolic cost of the thermal inefficiency associated with marten morphology, especially in cold-stressed environments (Brown and Lasiewski 1972). Excessive thermal costs result in the need for marten to maximize hunting efficiency, while minimizing supranivean exposure. Andruskiw et al. (2008) found that dead wood abundance enhanced the hunting efficiency of marten when preying on small rodents, which have been found to account numerically for 60 - 70% of their diet in northeastern Ontario (Thompson and Colgan 1987). Total deciduous understory growth, in a fashion similar to CWD, could facilitate hunting, especially of snowshoe hares (*Lepus americanus*), which have been found to contribute up to 85% of the caloric intake of marten during periods when hare were abundant (Thompson and Colgan 1994). Pietz and Tester (1983) found a strong correlation between intensity of hare activity and the abundance of shrubs >1 m tall. Studies in Alaska and Minnesota found that hare occurred most commonly in snow-laden alder, willow, spruce, and tamarack branches (Pietz and Tester 1983; O'Farrell 1965).

Models have suggested that animals will exhibit nearly optimal behaviour when present in the environment in which they evolved (McFarland and Houston 1981); those in an environment with high predation risk will exhibit better anti-predator behaviour relative to those evolved in environments with less predation risk (Bouskila and Blumstein 1992). All forest structural characteristics positively linked to subnivean access points in this study may be associated with anti-predatory strategies. Overhead canopy cover acts as concealment from avian predators. Further, canopy cover in winter is highly correlated to the abundance of coniferous trees, which serve as arboreal refuge from terrestrial predators and provide marten tight branching structure to hide them from avian predators (Pullainen 1981; Drew 1995). Though it does not provide concealment in winter, deciduous understory growth also provides subcanopy structure that may inhibit aerial ambushes. Marten morphology has been linked to an increase in manoeuvrability in tight spaces (Brown and Lasiewski 1972). Although this adaptation is usually described as beneficial to hunting efficiency, e.g. facilitating entry and manoeuvrability in escape habitats of rodents, it may be similarly beneficial in marten themselves evading predation, e.g. from red fox (*Vulpes vulpes*). Dense stem structure resulting from a high density of deciduous understory stems and/or CWD should facilitate escape by marten from terrestrial predators (Chapin et al. 1997; Hodgman et al. 1997).

The evaluation of marten habitat reserves, as outlined by the *Forest Management Guidelines for the Provision of Marten Habitat in Ontario*, showed that the delineation of stands by vegetation type does predict the occurrence of the stand-scale forest structural characteristics that were associated with subnivean access. “Good” suitable habitat exhibited higher levels of structural characteristics that discriminate subnivean access than “fair” suitable habitat, with the exception of average canopy cover. The lower average level for canopy cover may be, in part, due to the designation of several vegetation types within the “Aspen Hardwood and Mixedwood” treatment unit as “good” suitable habitat (Racey et al. 1989). Though this treatment unit does include vegetation types that offer a diverse understory and overhead structural complexity, canopy cover is lacking in winter due to foliar senescence, especially in hardwoods. This study used canopy cover as a measure of winter foliar cover and did not represent overhead structural complexity, thus unable to distinguish between a defoliated stand and an open canopy. The discriminant function analysis was able to distinguish the “good” suitable habitat from the case – control model to a greater degree than the “fair” suitable habitat. Furthermore, my results were not able to significantly distinguish between “good” and “fair” suitable habitat. This indicates that both “good” and “fair” suitable habitat exhibit the characteristics associated with subnivean access at adequate levels to facilitate survival in winter.

Further study relating forest structural complexity to subnivean use by marten should focus on the comparison of used subnivean access to unused subnivean access points within 1 meter of a marten’s track. Analysis of canopy cover should also be sensitive to structural gaps, rather than just foliar gaps. Further, data should be collected that tracks individual marten to determine variation in habitat preferences associated with individuals.

CONCLUSIONS

Subnivean access by marten is predicted by small-scale forest structural characteristics. As overhead canopy cover, deciduous understory growth and near-ground dead wood amounts increase, a marten’s likelihood of subnivean access also increases. It is no surprise that studies of marten conclude that an important variable predicting subnivean access is CWD, as it facilitates optimal habitat use for the three main life requisites for winter survival. Canopy cover and deciduous understory growth are also important components of forest structural complexity.

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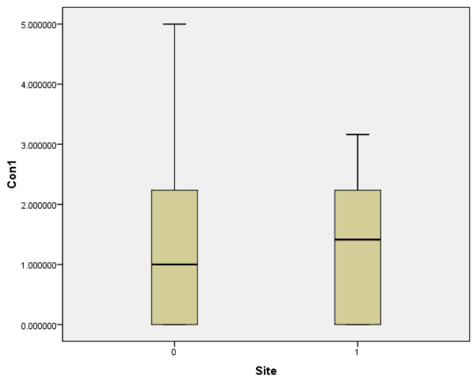
APPENDICES

APPENDIX I. Normality testing (*W*) of all variables for use in the selection of the most appropriate transformation for further analysis.

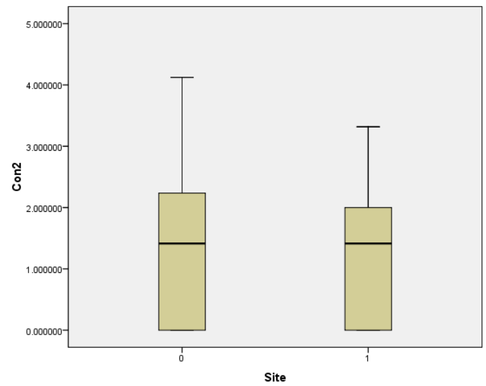
Structural Variable	No Trans	SQRT Trans	LOG Trans
1 - 2 m Conifer	.754	.887	.803
2 - 4 m Conifer	.832	.897	.818
4 - 6 m Conifer	.769	.847	.739
Total Conifer	.889	.934	.877
1 – 2 m Deciduous	.718	.836	.714
2 – 4 m Deciduous	.759	.843	.760
4 – 6 m Deciduous	.660	.703	.467
Total Deciduous Single	.831	.907	.859
Total Deciduous Understory Growth	.778	.921	.877
Overhead Canopy Cover	.978	.947	.879
CWD Stem Count	.634	.805	.570
Snag Stem Count	.908	.950	.900
Total Dead Wood Stem Count	.883	.971	.932
Dead Wood in Decay Class 1 Stem Count	.526	.785	.489
Dead Wood in Decay Class 2 Stem Count	.781	.914	.845
Dead Wood in Decay Class 3 Stem Count	.799	.816	.654
CWD Volume	.349	.584	.767
Snag Volume	.166	.545	.969
Total Dead Wood Volume	.184	.595	.981
Volume of Dead Wood in Decay Class 1	.263	.538	.786
Volume of Dead Wood in Decay Class 2	.106	.395	.914
Volume of Dead Wood in Decay Class 3	.278	.595	.821
Conifer Basal Area	.920	.978	.938
Total Basal Area	.961	.978	.914

**Highlighting indicates how variable was treated within the model.

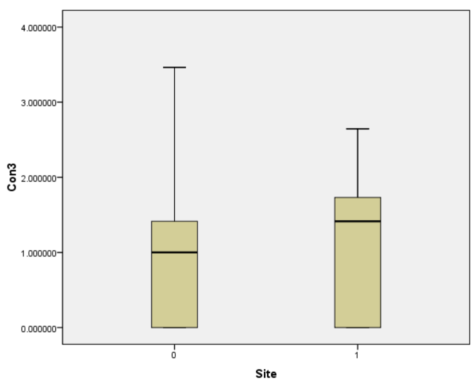
APPENDIX II. Boxplots showing that all variables meet the requirement of homogeneity for use in logistic regression.



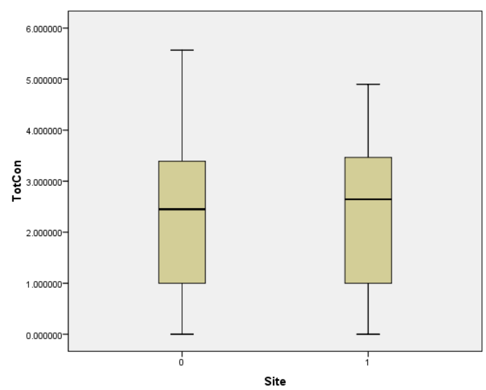
1 – 2 m Conifer



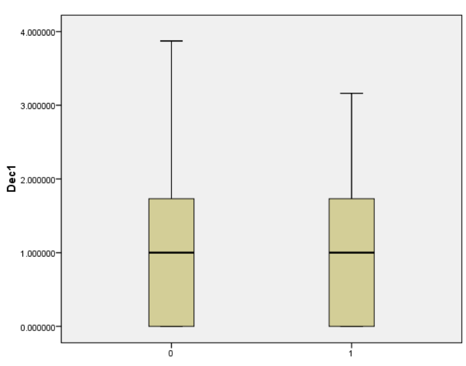
2 – 4 m Conifer



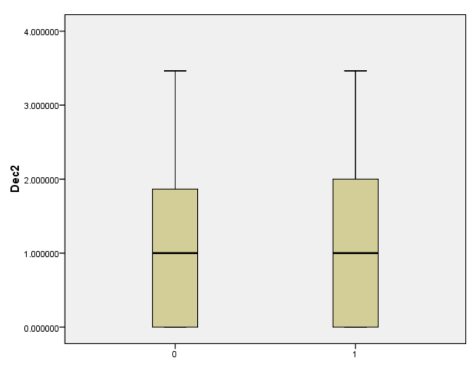
4 – 6 m Conifer



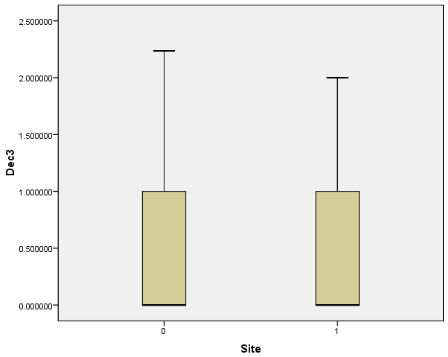
Total Conifer



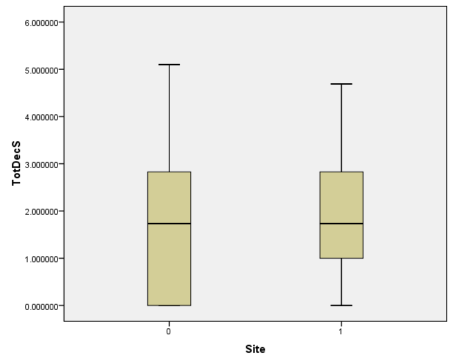
1 – 2 m Deciduous



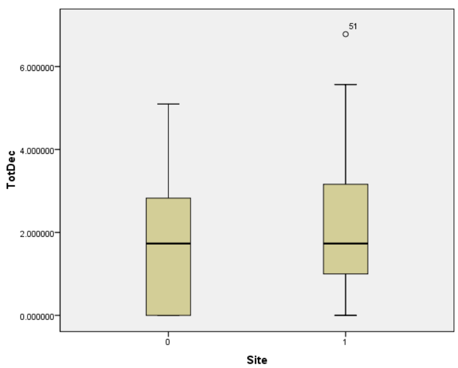
1 – 2 m Deciduous



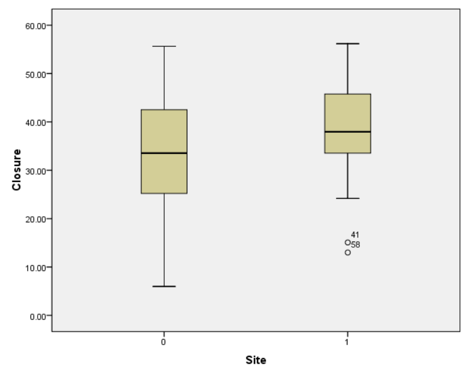
4 – 6 m Deciduous



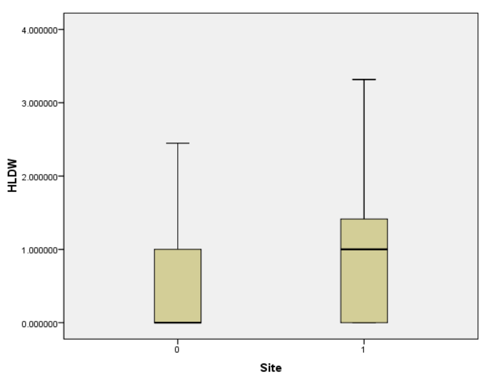
Total Deciduous Single



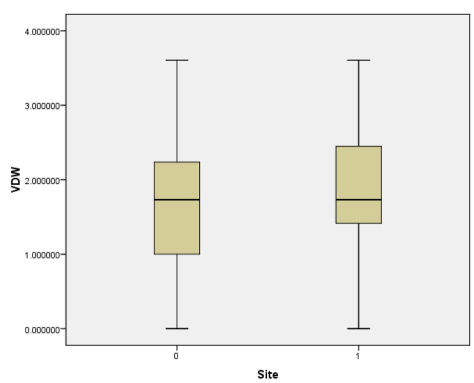
Total Deciduous Understory Growth



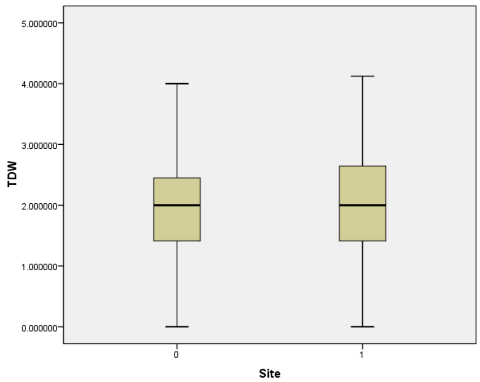
Overhead Canopy Cover



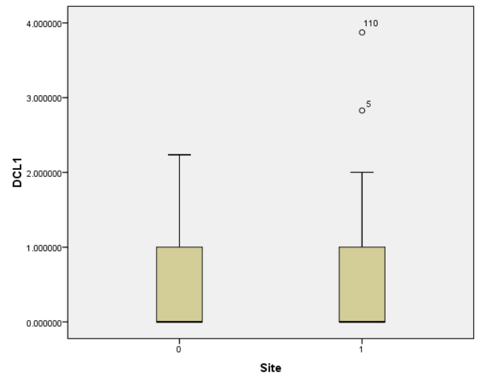
CWD Stem Count



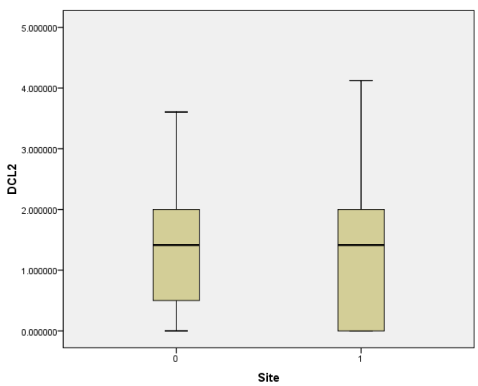
Snag Stem Count



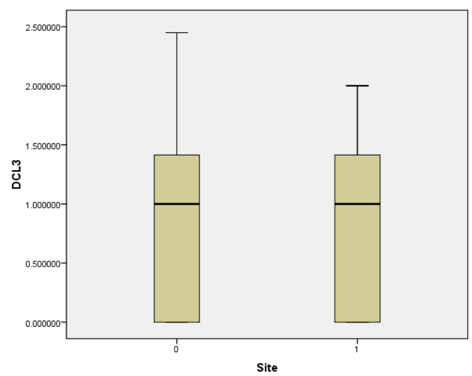
Total Dead Wood Stem Count



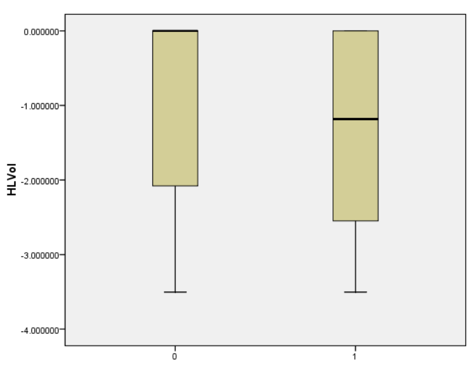
Dead Wood in Decay Class 1 Stem Count



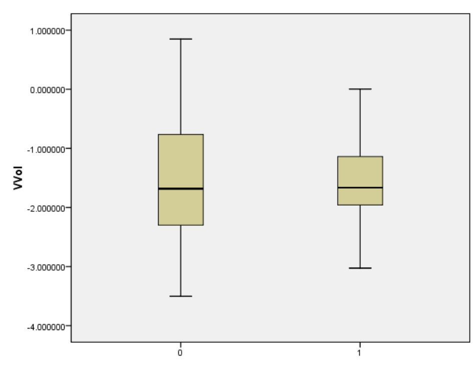
Dead Wood in Decay Class 2 Stem Count



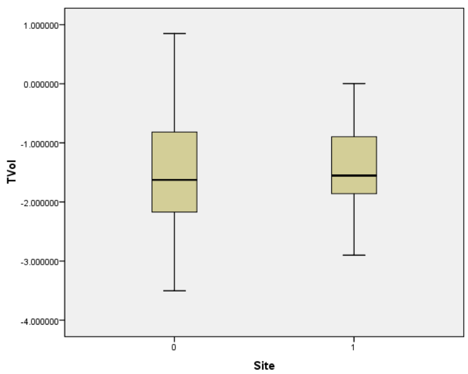
Dead Wood in Decay Class 3 Stem Count



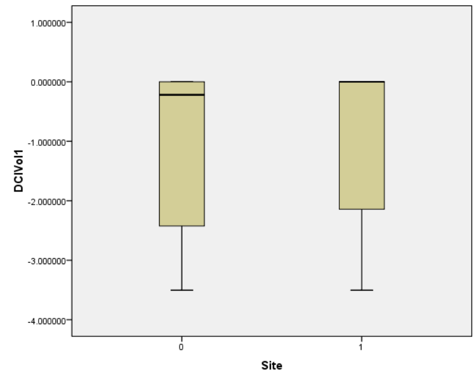
CWD Volume



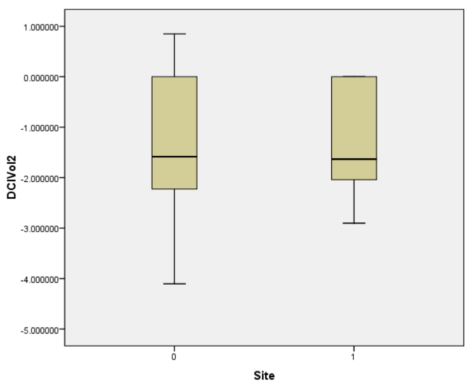
Snag Volume



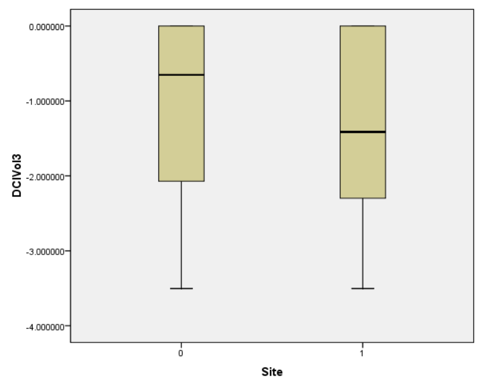
Total Dead Wood Volume



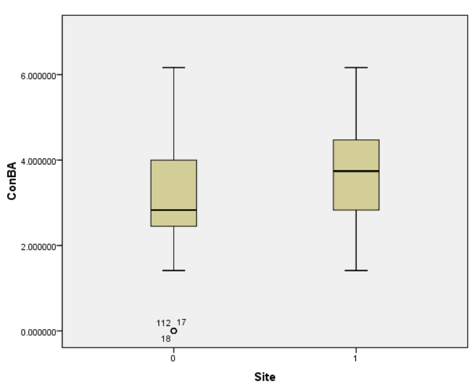
Volume of Dead Wood in Decay Class 1



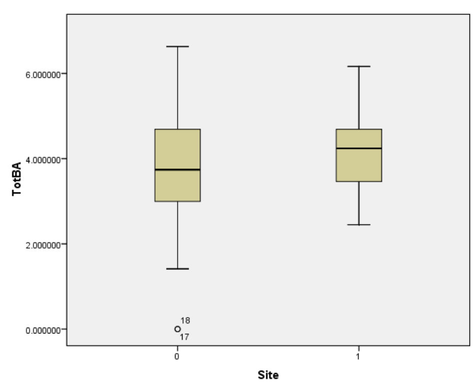
Volume of Dead Wood in Decay Class 2



Volume of Dead Wood in Decay Class 3



Conifer Basal Area



Total Basal Area

APPENDIX III. Correlations of variables used in logistic regression to all measured forest characteristics by a Kendal's tau correlation matrix (R).

Correlation Matrix	Canopy Cover	1 - 6 m Conifer	Total Deciduous Understory Growth	Conifer Basal Area	CWD Stem Count
Canopy Cover	1.000	-0.157	-0.190	0.536	0.143
1 - 2 m Conifer	-0.271	0.725	0.100	-0.220	-0.094
2 - 4 m Conifer	-0.111	0.774	0.084	-0.182	-0.052
4 - 6 m Conifer	0.074	0.555	-0.032	-0.030	0.037
1 - 6 m Conifer	-0.157	1.000	0.084	-0.187	-0.053
1 - 2 m Deciduous *	-0.175	0.084	0.672	-0.174	0.076
2 - 4 m Deciduous *	-0.224	0.146	0.735	-0.189	0.053
4 - 6 m Deciduous *	-0.088	0.153	0.403	-0.204	-0.065
1 - 6 m Deciduous *	-0.228	0.145	0.906	-0.226	0.036
Total Deciduous Understory Growth	-0.190	0.084	1.000	-0.184	0.030
Conifer Basal Area	0.536	-0.187	-0.184	1.000	0.116
Total Basal Area	0.361	-0.322	-0.206	0.608	0.107
CWD Stem Count	0.143	-0.053	0.030	0.116	1.000
Snag Stem Count	0.316	-0.220	-0.147	0.240	0.150
Total Dead wood Stem Count	0.305	-0.211	-0.096	0.227	0.425
CWD Volume	-0.161	0.033	-0.007	-0.216	-0.577
Snag Volume	0.041	-0.136	-0.072	0.029	-0.104
Total Dead wood Volume	0.059	-0.136	-0.118	0.015	-0.004
Volume of Dead wood in Decay Class 1	-0.201	0.124	0.103	-0.193	-0.107
Volume of Dead wood in Decay Class 2	-0.129	0.023	-0.139	-0.062	-0.108
Volume of Dead wood in Decay Class 3	-0.107	0.041	-0.049	-0.075	-0.151
Dead wood in Decay Class 1 Stem Count	0.287	-0.229	-0.146	0.248	0.238
Dead wood in Decay Class 2 Stem Count	0.237	-0.155	-0.043	0.169	0.299
Dead wood in Decay Class 3 Stem Count	0.165	-0.126	0.012	0.137	0.211

* refers to single stemmed individuals

APPENDIX III (continued).

Correlation Matrix	Snag Stem Count	Total Dead Wood Volume	Volume of Dead Wood in Decay Class 1	Volume of Dead Wood in Decay Class 2	Volume of Dead Wood in Decay Class 3
Canopy Cover	0.316	0.059	-0.201	-0.129	-0.107
1 - 2 m Conifer	-0.292	-0.098	0.219	0.093	0.074
2 - 4 m Conifer	-0.184	-0.145	0.090	-0.019	0.033
4 - 6 m Conifer	0.007	-0.141	-0.034	-0.094	-0.068
1 - 6 m Conifer	-0.220	-0.136	0.124	0.023	0.041
1 - 2 m Deciduous *	-0.153	-0.062	0.096	-0.155	-0.049
2 - 4 m Deciduous *	-0.104	-0.153	0.086	-0.161	-0.063
4 - 6 m Deciduous *	-0.003	-0.111	0.010	-0.154	-0.022
1 - 6 m Deciduous *	-0.126	-0.135	0.101	-0.167	-0.036
Total Deciduous Understory Growth	-0.147	-0.118	0.103	-0.139	-0.049
Conifer Basal Area	0.240	0.015	-0.193	-0.062	-0.075
Total Basal Area	0.321	0.054	-0.227	-0.025	-0.048
CWD Stem Count	0.150	-0.004	-0.107	-0.108	-0.151
Snag Stem Count	1.000	0.117	-0.254	-0.186	-0.184
Total Dead wood Stem Count	0.830	0.125	-0.253	-0.198	-0.191
CWD Volume	-0.134	0.088	0.106	0.137	0.200
Snag Volume	0.037	0.726	0.138	0.396	0.148
Total Dead wood Volume	0.117	1.000	0.107	0.363	0.158
Volume of Dead wood in Decay Class 1	-0.254	0.107	1.000	0.101	-0.014
Volume of Dead wood in Decay Class 2	-0.186	0.363	0.101	1.000	0.145
Volume of Dead wood in Decay Class 3	-0.184	0.158	-0.014	0.145	1.000
Dead wood in Decay Class 1 Stem Count	0.421	0.105	-0.593	-0.064	-0.015
Dead wood in Decay Class 2 Stem Count	0.685	0.075	-0.159	-0.265	-0.043
Dead wood in Decay Class 3 Stem Count	0.314	0.065	-0.047	-0.064	-0.597

APPENDIX IV. Comparison of study areas (KAP and SPP) using DFA (α = 0.15). Data were separated by study area (KAP and SPP) and marten usage to show variation using a DFA. Means and standard deviations of discriminant scores were used to visualize the discrimination between study areas (see Fig.). Discriminant functions 1 and 2 (x and y axes respectively) collectively describe 92.5% of the variance and are quantified by the accepted variables (see Table).

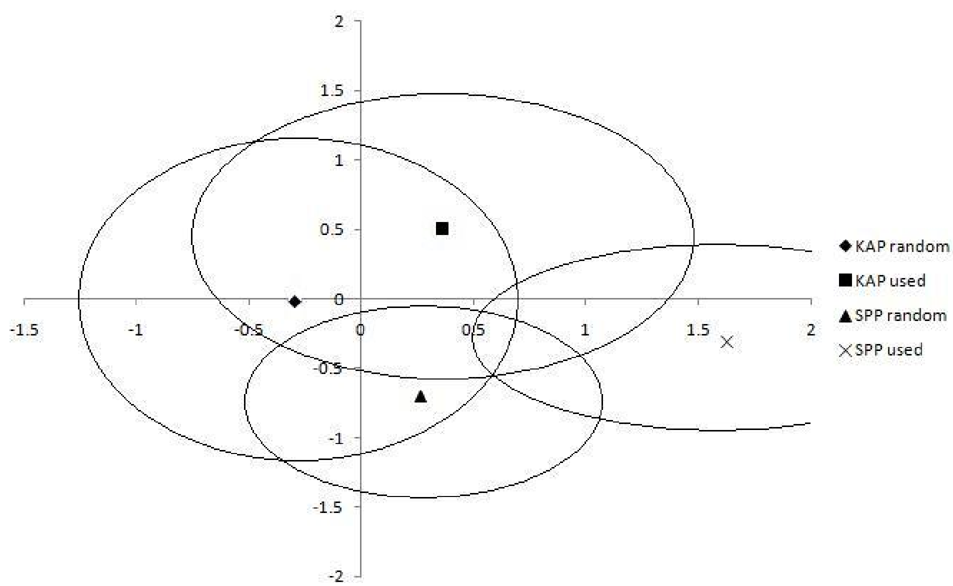


Fig.: Means and standard deviations of discriminant scores used to discriminate study areas.

Table: Variables accepted to discriminate between KAP and SPP (α = 0.15) and corresponding influences on discriminant functions 1 and 2.

Variable Accepted	DF 1	DF 2
Volume of Dead wood in Decay Class 2	0.773	-0.176
CWD Stem Count	0.758	-0.020
Overhead Canopy Cover	0.404	0.585
Total Deciduous Understory Growth	0.142	0.672
4 - 6m Conifer	-0.076	0.546