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Author: Mowat, Garth

Source: Wildlife Biology, 12(1) : 51-61

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2006)12[51:WHAOAM]2.0.CO;2

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Winter habitat associations of American martens *Martes americana* in interior wet-belt forests

Garth Mowat

Mowat, G. 2006: Winter habitat associations of American martens *Martes americana* in interior wet-belt forests. - Wildl. Biol. 12: 51-61.

I systematically sampled American marten *Martes americana* presence in two large study areas in the Selkirk and Purcell Mountains of southwest Canada using hair removal traps and tracks in snow. Both study areas were mostly forested and contained a broad cross-section of stand ages including abundant early seral and mature forest. I extracted measures of forest structure and dominant tree species, climax ecosystem types and human use from digital resource databases and used multiple logistic regression to model habitat selection of martens. I summarized data in windows of 100 m to 10 km in radius around each sample location to investigate the effect of varying data resolution on habitat selection. Marten detection at hair sites was positively related to temperature and trap duration and negatively related to snowfall while the trap was set. Martens were detected in all habitats sampled including recently logged areas, regenerating stands, dry Douglas-fir *Pseudosuga menziesii* forest and subalpine parkland. Overall selection was mildly greater using mean habitat values in 100 m and 2 km radius windows for both study areas. Martens selected for greater crown closure and older stands at the finer resolution; no selection for forest structure was detected at the larger resolution except that martens selected against increased overstory heterogeneity as measured by the standard deviation of crown closure (within the window). Martens preferred coniferous stands over deciduous dominated stands and were more abundant in wetter than in dryer ecosystems. Selection for ecosystems and stand types was stronger in the larger window size. At the intensity sampled in this study, neither road density nor logging appeared to affect marten habitat selection when I accounted for variation in ecosystems and stand structure. This study examined habitat selection at relatively coarse scales; stronger associations with forest structure may be expected at finer scales. In addition, roads or logging may influence habitat selection below the scale of my analysis.

Key words: British Columbia, Canada, habitat selection, Martes americana, spatial scale

Garth Mowat, Aurora Wildlife Research, RR 1, Site 14, Comp 8, Crescent Valley, BC, V0G 1H0, Canada - email: garth.mowat@gov.bc.ca*

** Present address: BC Ministry of Environment, Suite 401, 333 Victoria St. Nelson BC, V1L 4K3, Canada*

Received 29 December 2003, accepted 11 October 2004

Associate Editor: Piero Genovesi

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Martens *Martes americana* are found in coniferous and mixed coniferous forests throughout North America and are typically considered denizens of mature forest stands (Strickland & Douglas 1987). Buskirk & Powell (1994) suggested that the physical structure of the stand is more important than tree species composition, although other authors have suggested that spruce and fir stands are favoured by martens (Clark et al. 1987, Buskirk & Powell 1994). Huggard (1999) found that martens used wetter ecosystems more than xeric ones in high elevation Engelmann spruce *Picea engelmannii*-subalpine fir *Abies lasiocarpa* forest, and Buskirk & Ruggiero (1994) suggested that martens avoid dryer forests and ecosystems. Martens avoid openings, especially in winter, and select stands with higher cover (Clark et al. 1987). Structure on the ground such as woody debris provides access to the sub-nivean environment and sheltered resting places (Buskirk & Ruggiero 1994, Coffin et al. 1997). Horizontal structure may also provide increased habitat quality for voles, the principal prey of martens in most areas (Clark et al. 1987, Buskirk & Ruggiero 1994). The direct effect of human alterations to forests on marten habitat quality, beyond removal of the canopy, is unclear; the fragmentation of forest stands caused by settlement, logging and road building appears to have a negative effect on martens (Chapin et al. 1998, Hargis et al. 1999).

What is the causal relationship between marten habitat selection and fitness? Overstory species and stand age have no clear relationship with fitness. Stand structure may directly affect predation risk and hence fitness (Buskirk & Powell 1994). Wetter ecosystems have greater primary productivity which directly influences food abundance. All the above variables may be correlated to prey abundance. Human impacts to forests affect their structure and floristics and therefore predation risk and probably prey abundance; local human influences on primary productivity are less likely. Additionally, the scale or resolution of analysis may reflect the influence of factors that operate at different scales (May 1994, Powell 1994). For example, fine scales of analysis may measure behavioural decisions related to forage preference or predator avoidance by individuals, while coarse scales of analysis likely measure differences in species density among sample units. The effect of scale can be investigated by examining habitat relationships across a range of scales (Chapin et al. 1997, Meyer et al. 1998) or selecting scales *a priori* (Bowers et al. 1996, Pedlar et al. 1997). In this study I selected scales based on the strength of the relationship between habitat and response variables (Nams et al. 2005).

I wanted to know if broad-scale anthropogenic changes in forest structure and floristics were related to the distribution of martens. I was also interested in the relationship between distribution and more static variables such as climax ecosystems which index broad-scale productivity. I selected independent variables based on previously established, or hypothesized, habitat relationships and chose to do my analysis at two levels of resolution because I felt that individual behaviour would influence selection at fine resolution, and variation in density would be more influential at coarser resolution. My goal was to test the association between various habitat measures and marten occurrence and to explain my results in terms of their influence on fitness or density.

Study areas

The Selkirk study area covered 797 km^2 of the central Selkirk Mountains in southeastern British Columbia (BC). Biogeoclimatic (BEC) zones, each with distinct vegetation and soils, assume climate is the principle factor influencing ecosystem development (Meidinger & Pojar 1991). BEC mapping is intended to map various scales of climax ecosystems which are assumed to be relatively stable. Different plant species associations may dominate various seral stages but the plant community will succeed to a stable climax ecosystem. Three BEC zones occurred in the Selkirk study area: interior cedar-hemlock (ICH), Engelmann spruce-subalpine fir (ESSF) and alpine tundra (AT). These zones are divided into subzones based on variation in rainfall and growing season. In this area, cedar-hemlock forests occur < 1,400 m a.s.l., where western hemlock *Tsuga heterophyla*, western redcedar *Thuja plicata*, Douglas-fir *Pseudosuga menziesii* and spruce hybrids *Picea* spp. are the dominant overstory species. Engelmann spruce-subalpine fir forests are found between roughly 1,400 and 2,300 m a.s.l., where Engelmann spruce and subalpine fir dominate the canopy, although many early seral stands are dominated by lodgepole pine *Pinus contorta*. Extensive areas of alpine tundra are found above about 2,300 m. We did not sample in the alpine tundra, but we did sample in the treed portion of the subalpine zone.

The Purcell study area was a 1,059 km^2 region in the Central Purcell Mountains of southeast BC. The diversity of ecosystems was greater in the Purcell study area than the Selkirk study area. Along with the three zones described above, two dryer zones occurred in this area: interior Douglas-fir (IDF) and montane spruce (MS). The IDF zone was dominated by Douglas-fir, lodgepole pine, and western larch *Larix occidentalis* stands. Engelmann spruce and lodgepole pine were the dominant can-

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opy species in the MS ecosystem. The north and west side of each study area were moist environments that graded to much dryer forests in the southeast of the study area.

Logging occurred throughout both areas, mostly within the last 30 years, however significant amounts of mature forest remained in both areas. Road networks were extensive, all main drainages had all-weather roads and only a couple of side drainages in each area contained no road. Other human impacts included back-country recreation (including snowmobiling and alpine skiing), mining and hydroelectric lines. There were < 10 year-round human residents living on either study area. Private land with rural housing bordered the lower elevation, eastern edge of both study areas.

Methods

Field methods

I collected detection data using baited glue traps to remove hair from animals. I assessed the presence of martens in a 100-m radius of a capture site, using snow tracking, both during the setting and removal of sites. Hair traps were fashioned after the design described by Foran et al. (1997). Sampling was distributed systematically across both study areas. The Selkirk study area was divided into 9-km^2 square cells and each cell was sampled on four separate occasions for 14.6 days on average (SD = 3.14) between 15 January and 14 March 1997. Trap sites were usually moved after each trapping occasion (Mowat & Paetkau 2002), and repeated trapping events at the same site were not used in habitat analyses. Because the primary objective for the Selkirk study was to estimate marten population size, field personnel were instructed to install sites where they felt it would be most likely to detect martens within the cell, to increase capture success. Sites were mostly set in patches of mature forest, thus habitat was not sampled randomly or in proportion to availability. Further details on the methods for the Selkirk area are described in Mowat & Paetkau (2002).

The primary study goal in the Purcell study area was to examine the influence of commercial forestry on marten distribution and greater effort was made to locate sample sites randomly. I divided the Purcell study area into 265 5-km^2 square cells and used a GIS to randomly locate one sample site in each cell. Cells located along the study area boundary which were < 5 km^2, or those which were predominantly glacier or alpine tundra were not sampled. If there was a road in or within < 500 m of a cell then I restricted the trap location to within 500 m of the road. If there was no road within 500 m of the cell, then the location was randomly located. In practice many sites were too difficult or dangerous to access, and these sites were moved closer to accessible roads. Cells with no road within 500 m were accessed using a helicopter. In that case I placed the site 50-100 m from the closest landing site to the sample point. In both study areas, I attempted to locate sites > 1 km apart to minimize multiple detections of the same individual (Zielinski & Kucera 1995). I set one hair trap in each of 194 cells between 31 January and 26 March 2001; one cell was sampled twice in different locations. Each site was active for 15.0 days (SD = 2.63) and not visited again until it was removed. Martens usually removed the bait from the trap during their first visit making it unlikely the trap would detect another individual or species. In contrast, short-tailed weasels *Mustela erminea* were sometimes unable to remove the bait and so martens may be detected at a site which has already detected weasels. Because weasels often removed the bait and deterred a marten from entering a trap, I removed sites that detected a weasel from the database but not those where both marten and weasel were detected.

I identified species detected in hair traps based on hair morphology and tracks at the site (Mowat & Paetkau 2002). Weasels have short white hair during winter, whereas both red squirrels *Taimiasciurus hudsonicus* and flying squirrels *Glaucomys sabrinus* have short red-brown to gray hair with little difference between the length of the guard and underfur. Fishers *Martes pennanti* did not occur in either study area (Cowan & Guiguet 1965, Gibilisco 1994) and, during winter, minks *Mustela vison* were rare in the upland areas we sampled (Mowat & Paetkau 2002). Visual identification was not certain for 57 samples from the Selkirk study area and 27 samples from the Purcell study; these I sent to a commercial genetics lab (Wildlife Genetics International, Nelson, BC, Canada) for species testing. Of these samples, six visually classified as weasel were marten (18%), and two samples classified as marten were weasel (4%). When the classification was uncertain, all weasel and all marten samples were genetically tested, therefore errors in species assignment were likely to be few. All 22 weasel samples were short-tailed weasel; no long-tailed weasels *M. frenata* were detected.

I interviewed fur trappers working in both areas and asked them how many and where they trapped marten. Twelve martens of an estimated population of 225 (Mowat & Paetkau 2002) were taken on the Selkirk study area during the November-December (1996) previous to my work. On the Purcell study area, 115 martens and six weasels (species unknown) were trapped on the study

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area during November-December 2000, 2-3 months previous to my fieldwork. I felt that the number of marten killed on the Selkirk study area were too few to measurably affect the outcome of habitat analyses. For the Purcell area, I scored trapping effort by fur trappers as a binary variable. Any cell where a trapper killed a marten was considered trapped, all other cells were considered untrapped. Kyle et al. (2003) genotyped 60 samples taken from different sites across the two month sampling period and all 60 samples were different individuals. This suggests that considerably more than 60 martens were present on the Purcell area during our work.

Statistical analysis

I derived habitat information from GIS databases. BC Forest Cover data map forest structure and floristics based on overstory species at a scale of 1:20,000. This mapping system differs from BEC mapping because the primary focus is to map stands based on stand type (overstory species associations) and current vegetation. These stands may change rapidly across time while the ecosystems mapped in the BEC mapping are assumed to be static. Seral stage changes within BEC ecosystems often involve a change in stand type hence stand types mapped in Forest Cover mapping are loosely nested within BEC zones and subzones. Forest Cover mapping is based on interpretation of 1:15,000 scale black and white air photos and ground plots for truthing (Resources Inventory Branch 1995). Structural values are averages for visually mapped polygons. Polygons are usually > 2 ha in size and average in the tens of hectares, depending on forest complexity.

I investigated the effect of habitat resolution by calculating mean habitat values in circular windows of eight discrete sizes around sample sites (Table 1). Window sizes varied from 0 m (point extraction) to 10 km in radius. The systematic distribution of sample points, and the fact that habitat values were averaged across windows means that habitat measures, though not strictly randomly chosen, probably reflect all habitat available across the study area when windows are several km in radius (Nams et al. 2005), especially in the Purcell area. I summarized habitat selection across stand age by dividing the percent use of a category by the percent available; this relative measure of selection is termed W by Manly et al. (1993).

Table 1. Habitat measures and sources of data. Areas were transformed to a proportion of the window area when data were rescaled. All habitat information came from public access databases and measures were extracted using a GIS. BEC = biogeoclimatic zones which are an ecosystem classification system designed to map climax ecosystems regardless of current vegetation cover (Meidinger & Pojar 1991).

Habitat Variables	Units	Source
Ecosystem type (up to 4)	% in window	BC digital BEC mapping
Stand age	Mean years	BC Forest Cover Mapping
Crown closure	Mean percent	BC Forest Cover Mapping
Crown closure	Standard deviation	BC Forest Cover Mapping
Douglas-fir and larch	Mean % in overstory	BC Forest Cover Mapping
Spruce and subalpine fir	Mean % in overstory	BC Forest Cover Mapping
Cedar and hemlock	Mean % in overstory	BC Forest Cover Mapping
Pine	Mean % in overstory	BC Forest Cover Mapping
Deciduous	Mean % in overstory	BC Forest Cover Mapping
Length of roads	Meters	BC Forest Cover Mapping
Logged land	Proportion of area	BC Forest Cover Mapping

I used logistic regression to test the relationship between various habitat variables and the probability of detecting a marten. I used the logit function and tested assumptions regarding residuals. I tested for relationships among variables using Spearman rank correlation analysis to avoid including highly correlated variables in the same model. I compared model fit using Akaike's Information Criteria (AIC) values and the rescaled r^2, and classification accuracy using c. AIC is a relative measure of model fit which is discounted as the number of parameters in the model increases; reductions in AIC of two or more are considered significant improvements in model fit and parsimony (Burnham & Andersen 1998). An increase in AIC suggests the model is less parsimonious than the global model. AIC weights are also given for comparisons of multiple models. The rescaled r^2 measures the proportional reduction in the log-likelihood measure and is analogous to the familiar r^2 of linear regression (Menard 1995). Overall classification accuracy of the data in the model is measured by c; c of 1.0 means that all observations in the data set were correctly classified by the model.

I included variables that indexed parameters that may affect detection success such as temperature, precipitation, trapping effort and the length of time a trap was set, to reduce the influence of measurement errors. I measured the effect of resolution of habitat data by comparing the fit of a global model, which included forest structure, stand types and ecosystems as explanatory variables, and variables that controlled for measurement error, for each window size. I used SAS™ Version 8 (SAS Institute Inc., Cary, NC, USA) software for microcomputers for data manipulation and analysis.

Results

For marten habitat analysis in the Selkirk area I removed 1) one site for which I could not identify the hair sample, 2) 19 sites that detected weasels in the hair trap, and

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Table 2. Multivariate logistic regression analysis of marten habitat selection in the Selkirk Mountains with habitat data summarized in 100 m radius circular windows. All models include the variables temperature, snowfall and trap duration to account for their influence on detection success. ω_i = AIC weight.

Model no	Variables in model	AIC	ΔAIC	Parameters	ω_i	Corrected R^2	c
1	Subzones, stand types & structure (global model)	306.0	1.1	14	0.218	0.16	0.71
2	Stand types and structure	313.1	8.2	11	0.006	0.10	0.66
3	Subzones and structure	311.2	6.3	9	0.016	0.09	0.65
4	Subzones and stand types	305.6	0.7	12	0.266	0.15	0.70
5	Subzones, stand types & crown closure	307.5	2.6	13	0.103	0.15	0.70
6	Subzones, stand types & stand age	304.9	0	13	0.378	0.16	0.71
7	Covariates only	311.8	6.9	4	0.012	0.03	0.58
	Human use variables						
8	Model 6 & SE of crown closure	306.3	1.4	14		0.16	0.72
9	Model 6 & roads	305.8	0.9	14		0.17	0.72
10	Model 6 & logging < 10 years old	305.9	1.0	14		0.17	0.71
11	Model 6 & logging < 20 years old	306.4	1.5	14		0.16	0.71
12	Model 6 & all logging	306.5	1.6	14		0.16	0.71
	Measurement errors (covariates)						
13	Model 6 minus duration	303.6	-1.3	12		0.16	0.71
14	Model 6 minus temperature	305.7	0.8	12		0.15	0.70
15	Model 6 minus snow	305.2	0.3	12		0.15	0.70

3) 33 sites that had been previously hair-trapped. Of the remaining 257 sites, 177 (69%) detected marten based on hair traps (166) and tracks near the site (11). Marten detection rate was positively related to mean temperature and negatively related to snowfall, but weakly related to trap duration (compare models 13-15 to model 6 in Table 2).

In the Purcell area I removed 15 sites which detected weasels; martens were detected at 117 of 187 sites (63%) based on hair traps (105) and snow tracks (12). Marten detection was related to trapping effort by fur trappers, mean temperature and trap duration, while there was little support for the influence of snowfall on detection success (compare models 12-15 to model 1 in Table 4).

Marten hair traps performed equally well in the Purcell and Selkirk study areas. The proportion of hair trap approaches (based on negative hair trap results and tracks in snow near the trap) that failed to detect a marten was similar between study areas (8% in the Selkirks vs 3% in the Purcells; Mowat & Paetkau 2002). Temperatures were at times much colder during the Purcell work (as low as -28°C), yet the glue patches worked well.

The relationship between explanatory variables and marten detection varied little with resolution (the global model which included all independent variables was used for this analysis), although it was greatest when data were summarized for 100 m and 2,000 m radius windows (Fig. 1). Therefore I did all further analyses at these two window sizes to attempt to separate habitat related behavioural preferences of individuals and differences in species density across the study area.

In the Selkirk mountains, ecosystem, stand type and structure were all related to marten habitat selection at the 100 m window size as can be seen by the increase in AIC and decrease in r^2 when these variables were removed (models 2-5) and compared to the global model (model 1) in Table 2 . Only crown closure was not related to marten habitat selection at this resolution as demonstrated by the reduction in AIC in model 6 with respect to the global model (ΔAIC = -1.1) and higher AIC weight for model 6 than for model 1. Stand types had similar fit to BEC subzones (compare models 2 and 3 in Table 2). At the larger window size, BEC subzone contributed less to model fit than stand type, and both crown closure and stand age contributed little to the relationship (Table 3). None of the human use variables

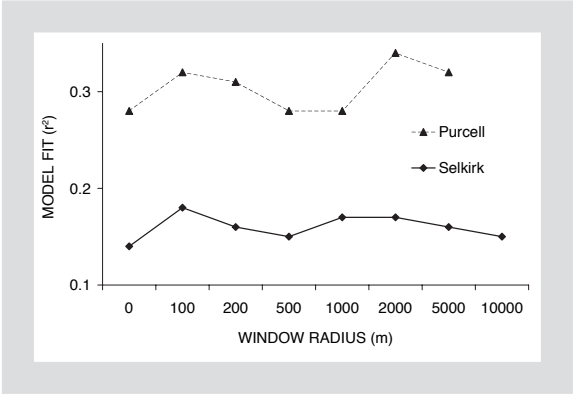


Figure 1. Relationship between marten presence at hair trap sites and mean habitat values across window size for the Selkirk and Purcell study areas. Model fit is measured by the corrected r^2. All descriptive habitat variables are included in each model; i.e. the global model from Tables 2-5.

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Table 3. Multivariate logistic regression analysis of marten habitat selection in the Selkirk Mountains with habitat data summarized in 2,000 m radius circular windows. All models include the variables temperature, snowfall and trap duration to account for their influence on detection success. ω_i = AIC weight.

Model no	Variables in model	AIC	ΔAIC	Parameters	ω_i	Corrected R^2	c
1	Subzones, stand types & structure (global model)	305.2	3.6	14	0.079	0.17	0.71
2	Stand types and structure	306.0	4.4	11	0.053	0.13	0.69
3	Subzones and structure	310.3	8.7	9	0.006	0.09	0.65
4	Subzones & stand types	301.6	0	12	0.477	0.16	0.71
5	Subzones, stand types & crown closure	303.6	2	13	0.176	0.16	0.71
6	Subzones, stand types & stand age	303.3	1.7	13	0.204	0.17	0.71
7	Covariates only	310.8	9.2	4	0.005	0.03	0.59
	Human use variables						
8	Model 4 & SE of crown closure	303.6	2	13		0.16	0.71
9	Model 4 & roads	300.5	-1.1	13		0.18	0.72
10	Model 4 & logging < 10 years old	302.3	0.7	13		0.17	0.71

improved model fit above the best fit model at either resolution (see Tables 2 and 3). There was a mild improvement in fit when roads were added to the model at the larger window size (ΔAIC = -1.4; see Table 3), but the relationship with roads was positive and likely related to greater selection for wetter ecosystems or lower elevations (where roads are often located) than selection for roads by martens.

The most striking difference for the Purcell Mountains was that model fit (r^2) was greater than for the Selkirk Mountains. Structure, stand type and BEC subzone were all related to marten preference. There was little difference between the improvement in fit generated by stand type or BEC subzone (Tables 4 and 5), probably because these variables were strongly correlated with one another. At the smaller window size both stand age and crown closure were related to selection (see Table 4) however, at the larger window size structure only mildly improved model fit (see Table 5). I retained the structure variables to test the human use variables at the larger window size because I wanted to account for the variation in structure (see Tables 4 and 5). Like the Selkirk data, these data did not support the hypothesis that roads or logging negatively affected marten presence when other habitat factors were accounted for (see Tables 4 and 5). The addition of the standard error of crown closure to the global model increased model fit (see Table 5: model 8) which suggests that greater fragmentation of the overstory leads to a reduction in marten presence even when differences in overstory are accounted for.

Although the difference in model fit between the two resolutions I analyzed was small (see Fig. 1), the pre-

Table 4. Multivariate logistic regression analysis of marten habitat selection in the Purcell Mountains with habitat data summarized in100 m radius circular windows. All models include the variables temperature, snowfall, trapping effort and trap duration to account for their influence on detection success. ω_i = AIC weight.

Model no	Variables in model	AIC	ΔAIC	Parameters	ω_i	Corrected R^2	c
1	Subzones, stand types & structure (global model)	227.6	0	14	0.133	0.31	0.79
2	Stand types and structure	226.1	-1.5	11	0.282	0.28	0.77
3	Subzones and structure	225.0	-2.6	10	0.488	0.28	0.77
4	Subzones and stand types	240.1	12.5	12	0.000	0.21	0.73
5	Subzones, stand types & crown closure	231.4	3.8	13	0.020	0.27	0.76
6	Subzones, stand types & stand age	228.7	1.1	13	0.077	0.29	0.77
7	Covariates only	242.9	15.3	5	0.000	0.10	0.67
	Human use variables						
8	Model 1 & SE of crown closure	228.5	0.9	15		0.31	0.79
9	Model 1 & roads	226.1	-1.5	15		0.33	0.80
10	Model 1 & logging < 10 years old	228.9	1.3	15		0.31	0.79
11	Model 1 & logging < 20 years old	229.5	1.9	15		0.31	0.79
12	Model 1 & all logging	229.5	1.9	15		0.31	0.79
	Measurement errors (covariates)						
13	Model 1 minus trapping	230.3	2.7	13		0.28	0.77
14	Model 1 minus duration	230.2	2.6	13		0.28	0.77
15	Model 1 minus temperature	231.1	3.5	13		0.28	0.77
16	Model 1 minus snow	226.5	-1.1	13		0.30	0.79

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Table 5. Multivariate logistic regression analysis of marten habitat selection in the Purcell Mountains with habitat data summarized in 2,000 m radius circular windows. All models include the variables temperature, snowfall, trapping effort and trap duration to account for their influence on detection success. ω_i = AIC weight.

Model no	Variables in model	AIC	ΔAIC	Parameters	ω_i	Corrected R^2	c
1	Subzones, stand types & structure (global model)	228.9	0	14	0.195	0.30	0.79
2	Stand types and structure	231.7	2.8	11	0.048	0.25	0.76
3	Subzones and structure	233.8	4.9	10	0.017	0.22	0.74
4	Subzones & stand types	229.1	0.2	12	0.177	0.28	0.77
5	Subzones, stand types & crown closure	230.6	1.7	14	0.083	0.28	0.77
6	Subzones, stand types & stand age	227.1	-1.8	13	0.480	0.30	0.78
7	Covariates only	242.9	14	5	0.000	0.10	0.68
	Human use variables						
8	Model 1 & SD of crown closure	224.9	-4	15		0.33	0.80
9	Model 1 & roads	229.8	0.9	15		0.31	0.79
10	Model 1 & logging < 10 years old	230.7	1.8	15		0.30	0.79
11	Model 1 & logging < 20 years old	230.9	2	15		0.30	0.79
12	Model 1 & all logging	230.9	2	15		0.30	0.79

dictive power of each group of independent variables changed across window sizes. Selection for stand structure was greater at the smaller window size in both areas while selection for stand types and ecosystems was greater at the larger window size.

In the Selkirk area, martens preferred spruce-fir, cedar-hemlock and pine stands to Douglas-fir-larch and deciduous dominated stands. Selection for the ICH and ESSF zones was similar. In the Purcell Mountains, martens preferred coniferous stands over deciduous dominated stands and wetter ecosystems were preferred over dryer ones. In all cases where stand structure variables generated measurable predictive power, martens selected for greater crown closure and older stands. Selection for stand age was weaker in the Selkirks, where rainfall was relatively high and even, compared to the Purcells, where there was large variation in rainfall within the study area (Fig. 2). The greatest avoidance was for stands < 10 years of age in the Purcells; this was not seen in the Selkirks because few sites were set in stands < 10 years of age. In summary, martens were detected more often in wetter ecosystems, and within ecosystems they preferred wetter coniferous stands. At the finer resolution, they avoided younger stands with less overstory.

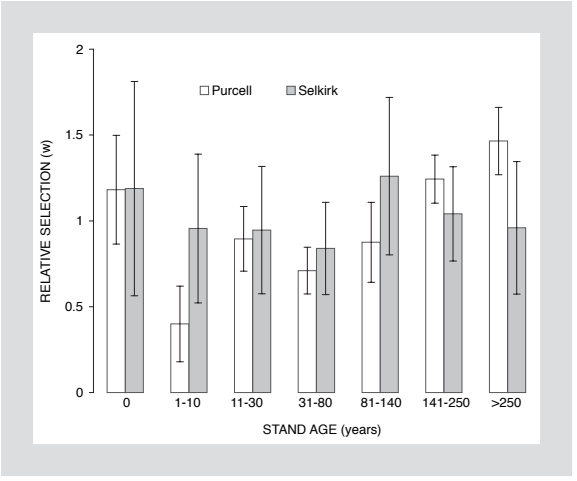


Figure 2. Marten selection for stand age (in years) at hair detection sites for the Selkirk and Purcell study areas in southeastern British Columbia. Selection is measured by percent use divided by percent available. Stands with age zero are non-commercially forested stands with no or sparse overstory. Error bars indicate 95% confidence intervals.

Discussion

I demonstrate that climax ecosystems and stand types are more important in describing marten habitat selection at broader scales while stand age and crown closure (which are correlated with one another) are more important at the finer scale. The finer resolution analysis was still relatively coarse and was unlikely to detect behavioural decisions regarding resting or denning sites. Greater selection for forest structure may be expected at finer scales of resolution than analyzed here. Ecosystems and stand types are related to primary productivity and ultimately affect food abundance and population density. Martens have broad diets and select food from all seral stages (Buskirk & Ruggiero 1994, Clark et al. 1987, Cumberland et al. 2001); therefore, coarse measures of ecosystem productivity such as rainfall likely affect marten density in a general fashion. My data suggest that wetter ecosystems and stand types support greater marten numbers. Stand structure affects predation risk; presumably greater cover reduces predation risk (Buskirk & Ruggiero 1994). Therefore, cover may affect local movements and hence foraging opportunities (Lofroth 1993, Buskirk & Powell 1994, Krohn et al. 1997). Cover may also influence prey abundance (Coffin

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et al. 1997). I suggest that forest overstory influences individual fitness by increasing predation risk when overstory is low.

My work was in winter during the period of maximum snow depth. Preferences for structure may be relaxed in summer when deciduous vegetation has leaves. The differences in abundance among ecosystems occurred at large scales and are unlikely to vary among seasons.

Similar to Krohn et al. (1997) in California and Chapin et al. (1997) in Maine, I did not find strong selection among stand types when I controlled for variation due to structure and ecosystem type. Nor was selection for stand types consistent between areas. Like Lofroth (1993), I observed consistent selection against deciduous stands. I observed selection against Douglas-fir stands in the Selkirk area but not in the Purcell area. Selection against Douglas-fir-larch stands in the Selkirks is not surprising because these were the driest stand types in the ICH and ESSF ecosystems. Douglas-fir and larch were more abundant in the Purcell area and occurred in all ecosystems. Selection against the dryer Douglas-fir-larch stands in the Selkirks was probably based on moisture regime rather than on overstory species. My observations, like those of Chapin et al. (1997), support the suggestion by Buskirk & Powell (1994) that tree species composition is less important to martens than the physical structure of the stand.

Selection against deciduous stands may also be driven by lack of physical structure because crown closure in BC forest cover mapping is measured in summer and is therefore overestimated in deciduous stands in winter. The consistent selection against deciduous stands, even when the variation in structure is accounted for, may be due to inaccuracy in the structural data during winter, rather than to selection against a stand type *per se*. Payer & Harrison (2003) point out that martens occur in almost pure deciduous stands in parts of their range. Poole et al. (2004) have shown that a medium density resident population of marten exists in predominantly deciduous forest in northeastern BC.

My data do not support the hypothesis that human use of a landscape, as indexed by roads and logging, reduce habitat quality for martens beyond the change in forest structure caused by logging. My analysis was a rather coarse-scale test of this hypothesis in an area with relatively low road and logging density; human use of both areas was low, especially in winter. Robitaille & Aubry (2000) presented data that suggested that road traffic caused martens to avoid forest in close proximity to roads, but they did not measure whether this avoidance might reduce habitat quality at a larger scale.

Results from the Purcell study area support the hypothesis that broad-scale fragmentation of the forest canopy (as measured by the standard deviation of overstory closure) negatively affects marten habitat (Thompson & Harestad 1994:359). Several detailed analyses have recently demonstrated the negative effect of forest fragmentation on martens (Chapin et al. 1998, Hargis et al. 1999, Potvin et al. 2000) although not all researchers controlled for habitat loss (as caused by forest removal) explicitly in their analyses. I found that broad-scale fragmentation of the canopy reduced habitat selection even when I explicitly controlled for habitat loss by including stand age and crown closure in the model. As forest fragmentation increases, some suitable habitat fragments become difficult to access, and hence are not used (Chapin et al. 1998), presumably because martens are reluctant to travel through open habitat to access the remaining patches.

Thompson & Harestad (1994) suggested that all seral stages younger than and including mature forest will receive less use by martens than old growth. My data do not support this suggestion because I detected martens in all stand ages even open cut-blocks, and selection across stand age was relatively weak (see Fig. 2). The relatively weak influence of stand age, or its correlate crown closure, suggests that the influence of seral stage on marten habitat quality was not so profound in the forests I worked in. Baker (1992) and Mowat et al. (2000) found that only the most open cut-blocks (< 10 years old) received markedly less use by martens than older stands in coastal British Columbia. Lofroth (1993) demonstrated that only stands with < 20% overstory closure received less marten use than more closed stands in a wet subboreal region of central British Columbia. Bowman & Robitaille (1997) found that marten used second growth spruce/fir stands in Ontario and that martens selected for greater structure in mid-seral stands, as they do in mature stands. Payer & Harrison (2003) showed that martens used second-growth conifer and deciduous stands in Maine and again, they selected for greater structure in regenerating areas. Canopy closure is achieved rapidly in wet forests and the above observations suggest that regenerating stands can reach the stage where overstory structure is no longer limiting in about 10 years. In addition, logging methods used in wetter areas often leave large volumes of debris in the logged area (Mowat et al. 2000, McCleary & Mowat 2002), hence short-term limitation of downed wood is unlikely (Payer & Harrison 2003). Further, Cumberland et al. (2001) suggested that martens may depend on snowshoe hares *Lepus americanus*, grouse and red squirrels for a much greater portion of their diet than previously assumed. Hares and grouse both use closed regenerating stands during win-

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ter (Krebs et al. 2001). I suggest that marten habitat use is less associated with forest age in wet forests than in dryer forests.

The methods used in my study present several limitations. First, selection for structure at the fine resolution in the Selkirk area may have been weak because we did not sample in many forest openings. Alternatively, we may have observed reduced selection for structure because the Selkirk area was relatively wet, and regeneration was likely faster than on much of the Purcell study area. The influence of stand age and crown closure may be small in wet areas because vegetation closure recovers rapidly. The systematic nature of the sampling on both areas means that stand types and ecosystems were likely sampled across the entire range of variation. Also, stands mapped as non-forested are given zero values for age and overstory but are often sparsely treed. These stands do not support commercial forests based on the definition of the mapping system. Martens used these sparsely treed stands which confounded the relationship between stand age and marten presence, especially for the Purcell area (see Fig. 2). The influence of non-forested areas on regression results was likely to have been small because these areas were few and their influence was reduced when habitat values were averaged across windows.

Other mapping errors may have influenced the relationship among independent variables. Forest age is updated regularly following the original mapping or the harvest of an area. Crown closure is updated less often and, while this variable probably changes little in a mature forest over 20-30 years (the age of mapping I used), major changes occur in young stands. For young stands, age is probably a better index of crown closure in my data. My data for the Purcell area suggest little use of stands < 10 years of age, however, the ultimate limiting factor may be lack of overstory. Finally, the forest mapping data are averaged across hectares and bait sites attract animals from tens and perhaps hundreds of meters. My data measure marten association with stand structure, not site level structural features. Other inaccuracies in the GIS data such as misclassification of tree species and spatial errors in polygon boundaries likely created noise in the habitat data and reduced model fit; bias was less likely.

Weasels may have reduced marten detection in the sites where the two species co-exist, but the number of sites where I detected weasels was relatively small. Weasels were found in all forest types, but occurred more in open sites and stands than martens (Mowat & Poole 2005).

I demonstrated that trap duration, temperature and snowfall can affect trap success in a winter environment. Zielinski & Stauffer (1996) demonstrated that trap duration was the major variable affecting trap success using baited track plates for martens and fishers. Duration did not affect detection success during the Selkirk fieldwork because there was little variation in duration (Mowat & Paetkau 2002) compared to the Purcell work. The total snowfall while the trap was active had little relationship to trap success in the Purcells where snowfall averaged 8 cm and was never > 10 cm during a trapping episode. In the Selkirks, where snowfall averaged 38 cm per episode and was > 1 m during some episodes, this variable negatively influenced detection success. In both areas temperature was the most important covariate affecting trap success. I know of no other studies demonstrating this effect with carnivores, but fur trappers have often noted the influence of temperature on trapping success. White et al. (1982) pointed out that temperature can be an important variable affecting trap success for small mammals.

Acknowledgements - funding for this work was provided by Forest Renewal British Columbia and Slocan Forest Products, Tembec, and the Arrow IFPA. I thank K. Stuart-Smith, D. Stanley, P. Frasca, G. Richardson, R. Serrouya, P. Cutts, M. Panian, C. Strobeck, C. Davis and D. Underwood. D. Fear, S. Petrovic, M. Petrovic, P. Cutts and C. Shurgot helped with fieldwork. D. Paetkau, M. Paradon, M. Watt, K. Stalker and C. Kyle assisted with DNA analysis. M. Buchanan, D. Pritchard and K. Poole did GIS mapping and data extraction. S. Minta and K. Heinemeyer kindly shared their knowledge about hair removal of marten. Thanks to V. Nams, I. Adams, K. Poole, P. Genovesi and several anonymous referees for their reviews of the manuscript.

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