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Using radio telemetry, we examined within home range habitat selection by the Eurasian pine marten *Martes martes* (11 males and eight females; 1,495 locations) in managed forest in two study areas, the Varaldskogen Wildlife Research Area, Norway, and the Grimsö Wildlife Research Area, Sweden, near the southern limit of the boreal forest zone. Pine martens preferred spruce-dominated forest with large (≥20 m tall) trees and avoided clearcuts and open habitats. Males and females used similar habitats and habitat use was little influenced by year, season and activity mode (active vs inactive). When habitat types were ranked in order of use, stands dominated by large spruce trees were preferentially selected over the lowest-ranked habitats, i.e. pine-dominated stands with trees <20 m tall, clearcuts, open areas and deciduous stands, but were used similar to other spruce-dominated categories and pine-dominated stands ≥20 m tall. Although pine martens exhibited selection and avoidance of certain habitat types, they were able to exploit a wide range of successional stages in forests with a long history of exploitation.

Key words: Eurasian pine marten, habitat selection, Martes martes, Scandinavia

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In Scandinavia, the Eurasian pine marten *Martes martes* is often considered a habitat specialist, dependent on tracts of natural, spruce-dominated old forest and avoiding open areas such as clearcuts, bogs and fields (e.g. Bjärvall, Nilsson & Norling 1977, Wabakken 1985, Brainerd 1990, Storch, Lindström & de Jounge 1990). Concordantly, pine marten densities have been found to be higher in contiguous, mature forests relative to areas fragmented by modern clearcutting forestry practice (Bjärvall et al. 1977, Bjärvall & Lindström 1991, Gundersen 1995). On the other hand, Brainerd, Helldin, Lindström & Rolstad (1994) found that pine martens displayed a generalised use of forest habitat types relative to age, concluding that forest structure, rather than age, probably influences pine marten selection of habitat. In North America older seral stages of coniferous forests are regarded as important, if not critical, for the closely related American marten *Martes americana* (e.g. Steventon & Major 1982, Buskirk & Powell 1994, Thompson 1991, 1994). However, similar to that reported for the Eurasian pine marten (Brainerd et al. 1994), Chapin, Harrison & Phillips (1997) found that American martens exhibited no apparent selection of a variety of habitats during winter in the northeastern United States, although their study area was little influenced by forestry. They concluded that vertical and horizontal structure may be more important habitat components than age or species composition of the forest overstorey.

Scandinavian boreal forests have a long history of exploitation (Tenow 1974), with industrial forestry during the past 300 years having virtually eliminated old-growth forests in the southern boreal zone (Esseen, Ehnström, Ericson & Sjöberg 1992). The disturbance regime of primeval boreal forest was fire-driven, creating a landscape mosaic of different successional stages. Fire suppression during the past 100 years has effectively eliminated early post-fire seres, but commercial clearcutting has replaced fire as the principal disturbance agent creating the landscape mosaic (Zackrisson 1977, Niklasson & Granström 2000). Forestry practices in this region are among the most mechanised and efficient in the world, with almost all forest land now used for timber and pulp production (Gamlin 1988, Esseen et al. 1992). Although both primeval and intensively managed forests are composed of mosaics of different seral classes, the vertical structure of stands is more complex in uneven-aged primeval stands than in their managed, even-aged counterparts (Swenson & Angelstam 1993, Angelstam 1998).

In a previous paper we rejected the hypothesis of old-growth dependency based on our findings that martens did not select for the oldest forest stands (Brainerd et al. 1994). In this paper we investigate the influence of forest structure on habitat selection, and hypothesise that Eurasian pine martens prefer mature, spruce-dominated forest and conversely avoid clearcuts, bogs and other areas devoid of overhead cover year-round. The primary rationale for this hypothesis is that: 1) mature, spruce-dominated habitats harbour a greater variety of prey species due to their inherently higher site productivity and cover coefficient compared to pine-dominated stands (Wabakken 1985, Eide 1995, Gundersen 1995), and 2) open areas afford little escape cover for pine martens, which can be preyed upon in our study areas by red fox *Vulpes vulpes* (Lindström, Brainerd, Helldin & Overskaug 1995), lynx *Lynx lynx* (Linnell, Odden, Pedersen & Andersen 1998), golden eagle *Aquila chrysaetos* (Nyholm 1970, Pulliainen 1981b, Korpimäki & Norrdahl 1989), and eagle owl *Bubo bubo* (Nyholm 1970, Pulliainen 1981b).

The objective of our study was to examine habitat selection relative to forest structure, season, year, activity mode (active vs inactive/resting) and sex in two managed Scandinavian boreal forests. We restrict our analysis to within home range selection, pertaining to the usage of various habitat types compared to availability within the home ranges of the radio-marked martens (third-order selection, *sensu* Johnson 1980).

A vast body of literature concerns the lack of consistent terminology in habitat selection studies (see Garshelis 2000 and Jones 2001 for recent reviews). Here we follow Manly, McDonald & Thomas (1993: 3) when examining habitat selection, and use the terms 'preference' and 'avoidance' to indicate that certain habitats are utilised significantly more or less than their respective proportions of availability within marten home ranges (see also White & Garrott 1990). From this analysis, we infer that martens are indeed selecting for or against certain habitats if they exhibit marked statistical preference or avoidance of these.

Study areas

We conducted our research in two managed forests near the southern limit of the boreal zone (Ahti, Hämet-Ahti & Jalas 1968) of Sweden and Norway. The Grimsö Wildlife Research Area (59°40'N, 15°25'E) is situated in south-central Sweden, and our efforts were restricted to the southern portion (75 km^2) of the 140-km^2 study area. The Varaldskogen Wildlife Research Area (60°10'N, 12°30'E) is located on the Norwegian-Swedish border, 175 km west of Grimsö, and covers approximately 100 km^2. Grimsö is relatively flat (75-125 m a.s.l.), whereas Varaldskogen is more hilly, varying between 200 and 400 m a.s.l. The areas have similar forest composition, dominated by commercial stands of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* (Table 1). Stands dominated by deciduous trees are rare, but white birch *Betula pubescens*, grey alder *Alnus incana*, and aspen *Populus tremula* are sometimes present as an admixture in coniferous stands. A few deciduous stands occur at abandoned pastures. Lakes and rivers comprise 5% of both study areas. Rocky glacial till, with fields of large boulders in many places, dominates the substrate. For a detailed description of the study areas see Brainerd et al. (1994).

In both study areas timber resources have been inten-

Table 1. Composition (in %) of habitat types according to tree heights within the study areas at Varaldskogen, Norway, and Grimsö, Sweden. The habitat types are: CC = clearcut, DECID = deciduous forest, OPEN = open habitat except water bodies, P = pine forest, S = spruce forest. For pine and spruce forests the tree heights are given.

Habitat type	Varaldskogen	Grimsö
CC 0-1 m	5.2	3.8
DECID	0.1	0.8
OPEN	8.1	26.6
P 1-10 m	19.8	15.1
P 10-20 m	26.0	14.0
P ≥ 20 m	3.8	8.8
S 1-10 m	15.9	4.9
S 10-20 m	13.3	16.4
S ≥ 20 m	7.9	9.6

sively utilised since the mid-1600s, culminating in the late 1800s, when most of the available large-timbered tracts had been exploited. Beginning about 1950, clearcutting and replanting of 5-50 ha units has become the dominant forestry method. Clearcuts and plantations often adjoin, creating contiguous regenerating stands of several hundred ha, comprising >80% of the total productive forest area. This history of use has created a mosaic landscape of even-aged, one-layered stands up to about 80 years of age and multi-layered old forest stands that have naturally rejuvenated after intensive logging at Varaldskogen (Rolstad & Wegge 1989) or burns at Grimsö (Angelstam 1992).

Methods

Data collection and sampling

We captured martens in wooden box-traps (40 × 40 × 60 cm) baited primarily with honey or visceral organs of cervids. The martens were immobilised with a combination of ketamine hydrochloride and xylazine hydrochloride, the dosages for ketamine and xylazine being 10 and 2 mg/kg body weight (drug concentrations 100 mg/ml), respectively. We affixed a small plastic roto-tag and a metal ear-clip in each ear, and attached 2-stage neckband transmitters (Televilt AB, Bandygatan 2, S-711 34 Lindesberg, Sweden) equipped with either metal loop or whip antennas. Size of radio-packages reflected dimorphism between sexes, with male radios (40 g) weighing more than those of females (25 g), about 2.5% of body weight in both cases. Transmitter life averaged nine and six months for males and females, respectively. Although we estimated ages of some of our animals at Grimsö (Helldin 1997), this was not possible with all individuals. Therefore we do not differentiate between age categories in this paper.

We used data collected on eight males and five females captured during four winters at Grimsö (1986/87 and 1988/89-1990/91) and three males and three females captured during two consecutive winters at Varaldskogen (1989/90-1990/91). Two females at Grimsö and two males at Varaldskogen were monitored for more than one year, and habitat analyses were based on their total home ranges used during this period (see below). Subsamples of these data have been used in earlier publications (Storch, Lindström & de Jounge 1990, Brainerd et al. 1994, Brainerd, Helldin, Lindström, Rolstad, Rolstad & Storch 1995).

Radio-locations included triangulations, cross bearings, close-tracking (≤100 m from the animal), and visual observations. In this analysis we included only triangulations with the longest side of error polygons being ≤250 m, and cross-bearings with the longest bearing distance being ≤200 m. The angle between the respective bearings was ≥45° for triangulations and 45-135° for cross-bearings. Error polygons (≤3 ha) were considered acceptable in our study areas, where habitat units were usually >10 ha (see Cederlund & Lemnell 1979, Cederlund, Dreyfert & Lemnell 1979).

Home range centres for independence analyses were computed using the RANGES IV software (Kenward 1990). Altogether, 1,495 radio-locations from Grimsö (N = 1,045) and Varaldskogen (N = 450) were used in this paper. Martens were often continuously radio-tracked for 3-12 hour periods. Hence, we used only independent locations (Swihart & Slade 1985) to minimise autocorrelation and to standardise data across individuals and between study areas. We applied this method to locations <12 hours apart. However, for some pine martens, i.e. denning females, the independence criterion could not be achieved. In such instances, we considered locations ≤12 hours apart as independent samples. This analysis was split into two seasons: winter (16 October-15 April), and summer (16 April-15 October). Locations were equally distributed between winter (N = 724) and summer (N = 772), and active locations comprised 41 and 44% of winter and summer locations, respectively.

We determined habitat use by plotting locations on detailed forest habitat maps provided by the Swedish and Norwegian Forest Services. Habitat availability was measured within the total home range (95% minimum area convex polygon (MCP; Mohr 1947), N ≥ 30 locations (Kenward 1992)) for each individual. Maps with associated forestry plans provided the background material to define habitat types (see Table 1). Mean 24-hour temperatures were recorded daily at weather stations within 50 km of each study area throughout the year, ranging from -18°C to 27°C for the study period.

Snow coverage varied greatly between years, reaching maximum depths of 40 cm during winter 1986/87 at Grimsö and 30 cm during winter 1990/91 at Varaldskogen. The winters of 1988/89, 1989/90 and 1990/91 at Grimsö and 1989/90 at Varaldskogen were virtually snow-free, since periods of snowfall were immediately followed by warm, wet periods that melted the snow.

Analysis of habitat selection

We discerned nine habitat types and categorised them as follows: clearcut with a dominant tree height of 0-1 m (CC 0-1 m), deciduous stands (DECID), open areas including bogs, meadows, or agricultural fields (OPEN), stands dominated by pine (P) and spruce (S). The two latter types were divided into three categories based on the dominant tree height: 1-10 m, 10-20 m, and ≥20 m. Lakes, rivers and other bodies of water were excluded from the analysis.

Initially we pooled all radio locations across individuals and employed the log-likelihood χ^2-test statistic (Sokal & Rohlf 1981) to determine if active selection of habitats was occurring at the study area level (Neu, Byers, Peek & Boy 1974, White & Garrott 1990: 186-191, McClean, Rumble, King, & Baker 1998). We then compared the proportion of habitat use relative to its availability within individual home ranges (the Design III procedure of Thomas & Taylor 1990, McDonald, Reed & Erickson 1991, and Manly et al. 1993). The proportions that describe habitat composition sum to 1 over all habitat types (the unit-sum constraint; Aitchison 1986). To avoid the problem of non-independent proportions, we transformed the compositional data sets using their log-ratios prior to statistical analysis (Aebischer, Robertson & Kenward 1993).

We estimated individual selection coefficients for the sample population (X_i) for each habitat type ($i = 1\text{-}9$) as the ratios of means of proportion used and proportion available habitat for all animals, thereby incorporating individual variation into the standard errors. The ratio of means generally has less bias and variance than the mean of ratios (Manly et al. 1993: 55). Selection coefficients and their associated standard errors were ln-transformed to overcome the unit-sum constraint and to obtain more robust confidence intervals (hereafter referred to as log-ratio selection coefficients; $\ln X_i$). Logarithmic transformation required that each animal used all habitat types, which was not the case for all martens. In these cases we substituted zero values with $\ln(0.01) = -4.61$, being smaller than the lowest recorded non-zero value of -2.97 (Aebischer et al. 1993). To keep the Type I error low, Bonferroni joint confidence intervals were constructed to test the hypothesis that each habitat was used in proportion to its availability within home ranges. We rejected the null hypothesis when values did not intersect zero. Since pine martens were territorial, we took a conservative approach and analysed habitat selection within total 95% MCP ranges.

Possible differences between seasons, years, sexes and activity modes were inferred by comparing the log-ratio selection coefficients for each habitat type between and among the different categories. The data were tested for normality using Kolmogorov-Smirnov test on the multivariate residuals for each habitat type. The assumption of normality was violated for some habitats, and we therefore employed two-tailed ($\alpha = 0.05$) nonparametric procedures (Mann-Whitney U- and Kruskal-Wallis H-tests) to test the null hypothesis that habitat types were used as available within or between different data categories. Correlation was checked with Spearman's rank (r_s) test. We subjectively included only pine martens with ≥10 locations for each comparison.

To rank the habitat types in order of use, we compared selection ratios for the total sample population between habitat types in a pairwise fashion for all possible pairs of habitat types. There were $k' = 36$ possible comparisons between pairs of these ratios, and we set α at $0.10/36 = 0.003$, which gave individual confidence limits of 99.7% (Aebischer et al. 1993, Manly et al. 1993: 60).

Results

Habitat selection did not differ between study areas except for OPEN habitat, which was used less at Varaldskogen ($\ln X_i = -2.10 \pm 0.05$ SE) than at Grimsö ($\ln X_i = -0.96 \pm 0.12$ SE; $U = 36.0$, $N_G = 13$, $N_V = 3$, $Z = 2.22$, $P = 0.026$). However, OPEN habitat was strongly avoided in both study areas ($P < 0.001$, see below). Habitat selection did not differ between sexes, neither when tested on a combined data set, nor when tested within years, seasons or activity modes ($P > 0.05$ for all comparisons). To increase the sample size, we therefore combined data from both sexes and study areas for further analysis.

Log-likelihood χ^2-tests revealed significant departure from a random selection of habitats both in winter (active: $\chi^2_8 = 66.45$, $P < 0.001$; inactive: $\chi^2_8 = 181.02$, $P < 0.001$) and summer (active: $\chi^2_8 = 84.40$, $P < 0.001$; inactive: $\chi^2_8 = 164.30$, $P < 0.001$). For active locations during both seasons, low expected values for DECID ($N = 3$) violated the condition that expected frequencies should be ≥5 for each category. Although such results should be treated with reservation, we decided to include

DECID in the habitat selection analyses since the statistics indicated a strong departure from random use.

The log-ratio compositional analysis of habitat selection within home ranges showed that pine martens avoided CC 0-1 m when inactive, and OPEN in both activity modes, and that they preferred S 10-20 m when inactive and S ≥ 20 m in both activity modes (Fig. 1). Winter selection ratios did not differ between activity modes. During summer, pine martens avoided CC 0-1 m while inactive. They avoided OPEN and preferred S ≥ 20 m in both activity modes (see Fig. 1). Although CC 0-1 m and OPEN were avoided, these habitats were used more often when pine martens were active than inactive (CC 0-1 m; U = 90.0, $N_a = 10$, $N_i = 12$, Z = 1.98, P = 0.047; OPEN; U = 91.5, $N_a = 11$, $N_i = 11$, Z = 2.04, P = 0.042). Active pine martens used OPEN more often during summer than during winter (U = 98.5, $N_a = 11$, $N_i = 12$, Z = 2.00, P = 0.046).

Pine martens used habitats similarly in all years (P > 0.05), except for active locations during winter when they varied in use of P ≥ 20 m from year to year (H = 9.19, N = 3, 4, 7, 5, df = 3, P = 0.03). We checked whether this variation was related to snow depth, which appeared not to be the case ($r_s = -0.05$, N = 19, P > 0.20).

The pairwise comparison of selection ratios revealed that pine martens selected S ≥ 20 m more often than most lower ranking habitats, but similarly to S 1-10 m, S 10-20 m, and P ≥ 20 m (Table 2). S 10-20 m and P ≥ 20 m were selected more often than CC 0-1 m, DECID and OPEN habitats, but similarly to lower-ranking conifer-dominated seres. S 1-10 m and P 10-20 m were selected more often than CC 0-1 m, and P 10-20 m was selected more often than OPEN habitat.

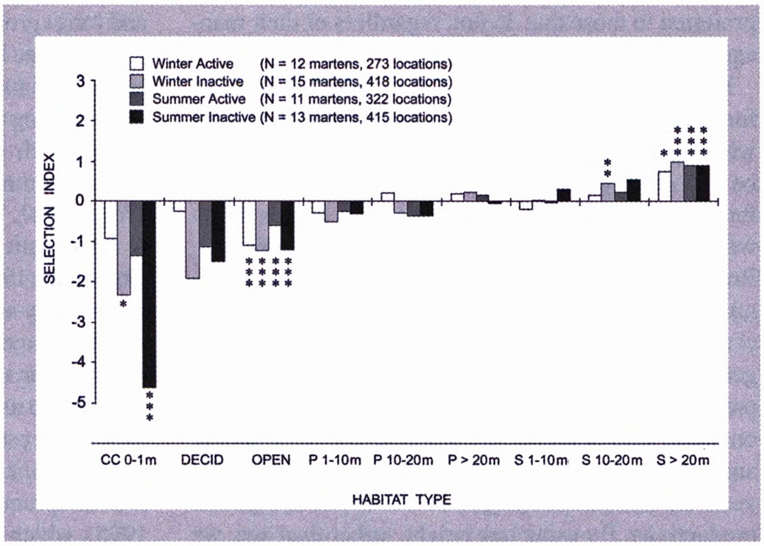

Figure 1. Ln-transformed estimated probabilities of selection (ln X_i) for different habitat types by pine martens in relation to season and activity at the Grimsö (during 1986-1991) and Varaldskogen (during 1989-1991) Wildlife Research Areas. Symbols indicate level of significance: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Discussion

In our study, Eurasian pine martens used a variety of habitat types within their home ranges in a forest landscape with a long history of human exploitation. We know that pine martens are capable of using various habitats from Mediterranean shrublands (Clevenger 1993), montane forests in Switzerland (Marchesi 1989), mesic pine and lowland mixed deciduous forests in Poland (Fedyk, Gebczynska, Pucek, Raczynski & Sikorski 1984, Jedrzejewski, Zalewski & Jedrzejewska 1993), to coniferous-dominated boreal forests in Fennoscandia and Russia (Grakov 1972, Pulliainen 1981a,b, Wabakken 1985, Brainerd et al. 1994, Eide 1995, Gundersen 1995). It is likely that pine martens select for certain habitats in order to avoid predators, seek shelter, and maximise foraging and reproductive success (e.g. Thompson & Harestad 1994). Thus, habitats that increase fitness by increasing the chances of survival and reproduction should be

Table 2. Significant differences between estimated selection ratios computed by the Bonferroni inequality when testing H_o: $X_a = X_b$ at the $\alpha = 0.10$ level for radio-locations (N = 1,495) of 19 Eurasian pine martens. The categories are listed in ascending order of preference. An asterisk indicates a significant difference between the row habitat and the column habitat, and ns indicates no significant difference.

Habitat type	CC 0-1 m	DECID	OPEN	P 1-10 m	P 10-20 m	S 1-10 m	P ≥ 20 m	S 10-20 m
DECID	ns							
OPEN	ns	ns						
P 1-10 m	ns	ns	ns					
P 10-20 m	*	ns	*	ns				
S 1-10 m	*	ns	ns	ns	ns			
P ≥ 20 m	*	*	*	ns	ns	ns		
S 10-20 m	*	*	*	ns	ns	ns	ns	
S ≥ 20 m	*	*	*	*	*	ns	ns	ns

preferred to those that do not, regardless of their management history.

In this paper we examined tree height instead of forest age based on the results of Brainerd et al. (1994), who suggested that forest structure rather than age may be a more precise determinant of habitat selection for this species. Most of the forest stands in this study were even-aged, and lacked a developed understorey. Rocky glacial till, however, provided abundant underground access points for foraging and resting (Brainerd et al. 1995). Ground layer varied with soil type, and in general pine-dominated forest occurred on xeric, low productivity sites while spruce-dominated forest occurred on mesic sites of higher site productivity. Stand height and age were highly correlated, yet many stands ≤70 years old had attained heights of ≥20 m due to high site productivity. By using tree height, rather than age, we found that pine martens consistently preferred taller spruce-dominated forest and avoided open habitats throughout the year. These results generally agree with snow-tracking studies in Scandinavia and northwestern Russia (Grakov 1972, Bjärvall et al. 1977, Degn & Jensen 1977, Pulliainen 1981a,b, Wabakken 1985, Eide 1995, Gundersen 1995).

Pine martens have many enemies, most notably the red fox (Lindström et al. 1995). Habitats such as clearcuts and openings were probably dangerous because of the lack of escape cover. The red fox is a habitat generalist and frequently uses open habitats (Christensen 1985, Eide 1995, Gundersen 1995) shunned by pine martens. Storch et al. (1990) found that pine martens continued avoiding open habitats when an epizootic of sarcoptic mange reduced fox densities at Grimsö (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994).

The pine marten feeds upon a wide variety of food items, and its diet varies seasonally and annually (Storch et al. 1990, Helldin 1999). The bank vole *Clethrionomys glareolus* is an important prey species during winter (Storch et al. 1990), occurring in forest interiors as well as clearcuts with associated boulders (Hansson 1994). The field vole *Microtus agrestis* is a denizen of grassy, open habitats such as clearcuts and rarely penetrates forest interiors (Ims 1991, Hansson 1994). Pine martens utilise this species during summer, but not during winter (Storch et al. 1990) when snow cover may prevent subnivean access in open areas (*cf.* Pulliainen 1981b, Buskirk 1984, Buskirk, Forrest, Raphael & Harlow 1989). Helldin (1999) showed that consumption of microtine rodents was correlated with microtine density, and that alternate species, including mountain hares *Lepus timidus*, Eurasian red squirrels *Sciurus vulgaris*, and forest grouse (Tetraonidae) were utilised more during microtine lows. Red squirrel, capercaillie *Tetrao urogallus*, and hazel grouse *Bonasa bonasia* are associated to varying degrees with medium-aged or older seral stages, with red squirrel particularly affiliated with spruce-dominated stands (Wabakken 1985, Rolstad & Wegge 1987, Wegge, Rolstad & Gjerde 1992, Swenson & Angelstam 1993, Andrén & Delin 1994, Eide 1995, Gundersen 1995). The use of habitats by pine martens in our study areas is consistent with the habitat preferences of important prey.

When our study animals were active, they were less reluctant to use clearcuts and open habitats than when they were resting. This might be explained by the fact that they relied heavily on nests of Eurasian red squirrels in spruce trees as resting sites (Brainerd et al. 1995), which were not available in clearcuts and open habitat. As a parallel to this pattern, Buskirk (1983) found that American martens in Alaska preferred stands dominated by black spruce *Picea mariana* when active and stands dominated by white spruce *P. glauca* when inactive. The American martens often rested in red squirrel *Tamiasciurus hudsonicus* middens, which were concentrated in white spruce stands (Buskirk 1984).

We expected differential use of habitats between sexes based on studies of American martens, showing that females were more selective in choosing habitats than males (e.g. Buskirk & Powell 1994). Such selection may indicate a strategy to simultaneously maximise survival and reproduction while decreasing energetic costs. Our results did not support this hypothesis, as there was no indication of differential habitat selection between the two sexes. Elsewhere we have also shown that both sexes selected resting sites similarly throughout the year (Brainerd et al. 1995).

Although pine martens in our study areas preferred taller spruce forests and avoided open habitats, the general impression was that they displayed flexibility in habitat selection. This allowed individuals to exploit a wide range of habitats within a relatively fine-grained landscape mosaic. We hypothesise that pine marten fitness is maximised through preferential use of habitats affording the greatest opportunity for foraging, predator avoidance and shelter, i.e. spruce-dominated forest with large, mature trees, and by avoiding the habitats associated with the greatest risks and costs, i.e. clearcuts and open areas.

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