

# Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests

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We examined selection of resting and denning sites by the Eurasian pine marten (*Martes martes*) in southern boreal Scandinavia. We radio-instrumented and monitored 25 pine martens during 1987 and 1989–1991 in two managed forest areas at Grimsö, Sweden, and Varaldskogen, Norway. Pine martens were radio-located at 299 resting sites 358 times, and at 49 denning sites 109 times. Cavities in trees and rotten snags were preferred by adult females as dens for birthing and early rearing of juveniles. Such cavities were rarely used as resting sites. Use of underground resting sites was negatively correlated with mean 24-hour ambient air temperature ( $T_a$ ). During winter, marten rested underground at  $T_a$  significantly lower than when they rested in trees. Selection of resting and denning sites may be influenced by predation risks and energetic constraints. Arboreal cavities for denning and underground sites as thermal cover appear to be important for Scandinavian pine marten. We hypothesize that in areas with cold winter temperatures and/or an abundance of enemies such as the red fox (*Vulpes vulpes*), the lack of such sites may limit pine marten distribution and abundance.

## 1. Introduction

Relatively few studies have dealt with the ecology of the pine marten (*Martes martes*) in the boreal forest region of Fennoscandia. In this region, this species has long been considered an

old forest specialist (e.g. Brainerd 1990, Selås 1990a). However, recent research suggests that stand age may be secondary to forest structural characteristics in determining habitat selection (Brainerd et al. 1994). Elements of old forest structure, such as trees or snags with large, hol-

low cavities may nonetheless be critical as denning sites for pine marten (Selås 1990b, Sonerud 1985a, Johnsson et al. 1993). In Finland, a snow-tracking study revealed that subnivean sites were particularly important for resting in winter, although squirrel (*Sciurus vulgaris*) nests and other arboreal structures were also used (Pulliainen 1981).

Predation may be an important element influencing pine marten selection of resting and denning sites. Red fox (*Vulpes vulpes*: Pulliainen 1981, Lindström et al. 1995), lynx (*Lynx lynx*: Jonsson 1986), eagle owls (*Bubo bubo*: Pulliainen 1981, Nyholm 1970) and golden eagles (*Aquila chrysaetos*: Nyholm 1970, Pulliainen 1981, Korpimäki & Norrdahl 1989) have preyed on pine martens in Fennoscandia. Lindström et al. (1995) concluded that red fox predation may directly and negatively effect pine marten densities in our study areas and in much of Scandinavia. Although adult pine martens are occasionally preyed upon by red foxes, kits may be particularly vulnerable to predation early in their development. The need for safe, spacious havens where red foxes and other enemies cannot reach neonates is probably critical for their successful rearing and later recruitment.

In addition, both Eurasian and American martens (*Martes americana*) have highly conductive fur and elongated bodies, features which raise the energetic costs of thermoregulation (Iversen 1972, Worthen & Kilgore 1981, Buskirk et al. 1988, Harlow 1994). American martens apparently compensate for this by seeking underground shelter during cold periods (Buskirk 1984, Buskirk et al. 1989), a phenomenon also suggested for Eurasian pine martens (Pulliainen 1981, Storch 1988).

In this paper we present data on resting and denning site selection by radio-instrumented pine martens in southern boreal Scandinavia. We examine the use of arboreal cavities as resting and natal denning sites by both sexes throughout the year. We also analyze pine marten use of underground and above-ground resting sites as adaptive strategies for minimizing energy costs and reducing predation risks. We discuss the possible implications for pine marten population ecology relative to red fox predation and modern forestry practices.

## 2. Study areas

Our research was conducted in two forested areas near the southern limit of the boreal zone (Ahti et al. 1968) of Sweden and Norway. Grimsö Wildlife Research Station (59°40'N, 15°25'E) is situated in southcentral Sweden, and our efforts were restricted to the southern portion (50 km<sup>2</sup>) of the study area. Varaldskogen Wildlife Research Area (60°10'N, 12°30'E) is located on the Norwegian-Swedish border 175 km northwest of Grimsö, and covers 100 km<sup>2</sup>. Grimsö is relatively flat (75–125 m A.S.L.), whereas the topography at Varaldskogen is more hilly, varying between 200–400 m A.S.L. Both areas are dominated by managed stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Stands dominated by deciduous trees are rare, but birch (*Betula pubescens* and *B. pendula*), alder (*Alnus incana* and *A. glutinosa*) and aspen (*Populus tremula*) are sometimes present as an admixture in coniferous stands. Bogs and agricultural fields are rare at Varaldskogen, but comprise 21% of the Grimsö study area. Lakes and rivers comprise between 5–15% of both study areas. The substrate in both areas is a rocky glacial till, with fields of large boulders in many places. Detailed descriptions of Grimsö and Varaldskogen are given by Cederlund (1981) and Rolstad et al. (1988), respectively.

Mean 24-hour ambient air temperature ( $T_a$ ) was recorded daily at weather stations within 50 km of each study area throughout the year, and ranged from –18°C to 27.2°C for the study period. Seasons for this analysis included winter (16 November–15 April), spring/summer (16 April – 15 September) and fall (16 September–15 November). Average  $T_a$  during winter were –7.7°C, –0.8°C, –0.5°C, and –1.6°C for 1986–87, 1988–89, 1989–90, and 1990–91 at Grimsö; at Varaldskogen,  $T_a$  averaged –0.5°C and –1.6°C for 1989–90 and 1990–91 for the winter period. During spring/summer, the combined seasonal temperatures averaged 10.4°C, 12.1°C, 12.5°C, and 11.3°C at Grimsö for the summers of 1987 and 1989–91. Average spring/summer temperatures at Varaldskogen were somewhat higher (1990: 14.1°C; 1991: 14.6°C). During the fall, temperatures averaged 4.8°C (1987), 6.7°C (1989), 4.5°C (1990), 5.4°C (1991) at Grimsö and 6.5°C (1990) and 7.2°C (1991) at Varaldskogen.

Snow coverage varied greatly between years. At Grimsö, the mean winter snow depths were 40.6, 6.2, 3.9 and 13.1 cm for 1986–87, 1988–89, 1989–90, and 1990–91, respectively. At Varaldskogen, snow depths averaged 10.0 cm in 1989–90 and 30.2 cm in 1990–91. The winters of 1988–89, 1989–1990 and 1990–91 were virtually snow-free, since periods of snowfall were immediately followed by warm, wet periods which melted snow in both study areas.

## 3. Materials and methods

Pine martens were captured primarily during winter during 1986–87 and 1989–1991 at Grimsö ( $n = 16$ ) and 1989–1991

at Varaldskogen ( $n = 9$ ). These include 3 kits (2–3 months old) captured, radio-instrumented and monitored in July of 1990 and 1991 at the natal dens of 3 radio-instrumented females. Data on kits were used to supplement the material for females during the denning season. Three of the pine martens included in the Grimsö material were also used in Storch (1988). Material for adult-sized pine martens (i.e. >0.5 yr; 8 females and 14 males) were used for describing selection of resting sites.

We used radio-telemetry equipment to locate pine martens at resting sites ( $n = 299$  sites, 358 relocations) and natal denning sites ( $n = 49$  sites, 109 relocations). These were generally visited during daylight hours, which corresponded with their general period of inactivity throughout the year (this study, unpubl.). At the onset of the denning period (15 April–8 August), females shifted from an apparently random use of sites to a highly site-specific mode. Presence of kits was inferred in the early part of the season, and confirmed later by observations (including vocalizations of kits). All females denned in this study. However, one female monitored during the spring and summer of 1987 and 1991 denned only during the latter period.

Sampling intervals for all sites varied between males ( $11.29 \pm 20.60$  days,  $x \pm SD$ ,  $n = 218$ ) and females ( $6.29 \pm 10.03$  days,  $x \pm SD$ ,  $n = 224$ ) (Mann-Whitney  $U = 20622.50$ ,  $P = 0.005$ ). Sampling intervals were similar between resting sites ( $n = 125$ ) and denning sites ( $n = 101$ ) for adult-sized females (Mann-Whitney  $U = 6177.00$ ,  $P = 0.72$ ).

We compared the use of resting sites below ground with arboreal structures between sexes and seasons. We tested for differences between sexes in use of resting site categories for the combined sample. We further examined the relative use of arboreal cavities, other arboreal structures and underground sites as resting and natal den sites

by both sexes during the spring/summer season. In addition, we compared use of resting sites underground and in arboreal structures with  $T_a$  seasonally and throughout the year. Chi-square tests are corrected for continuity where applicable, and included only categories with  $n > 5$ . The basic methods apply to both study areas (see Brainerd et al. 1994). Tests are two-tailed unless otherwise specified. Throughout the text, means are presented with their standard deviations.

## 4. Results

### 4.1. Differential use of resting and denning sites

Seasonal use of different resting site types (Table 1) did not vary for males ( $\chi^2 = 0.58$ ,  $df = 1$ ,  $P = 0.45$ ) or females ( $\chi^2 = 0.97$ ,  $df = 1$ ,  $P = 0.68$ ). Selection of resting site types did not vary between sexes during winter ( $\chi^2 = 0.46$ ,  $df = 1$ ,  $P = 0.50$ ) or during the spring/summer period ( $\chi^2 = 0.07$ ,  $df = 1$ ,  $P = 0.78$ ). Females used arboreal cavities more than males when all seasons were combined (Bonferonni-Z test,  $k = 3$ ,  $P = 0.05$ ); use of other categories was similar between sexes for the combined sample.

Seven of eight primary natal dens were in cavities in aspen ( $n = 6$ ) or pine ( $n = 1$ ) trees or snags. Cavities varied in age, and most appeared to have been excavated by black woodpeckers

Table 1. Seasonal resting site use by sex for adult-sized pine martens at Grimsö, Sweden ( $n = 15$  martens,  $n = 121$  relocations), and Varaldskogen, Norway ( $n = 7$  martens,  $n = 237$  relocations), 1987–1991.

Sex	Season <sup>1</sup>	Arboreal cavity <sup>2</sup>		Arboreal structure <sup>3</sup>		Underground structure <sup>4</sup>		Ground structure <sup>5</sup>		Total <i>n</i>
		<i>n</i>	(%)	<i>n</i>	(%)	<i>n</i>	(%)	<i>n</i>	(%)	
Female	Winter ( $n = 8$ )	3	(4)	39	(51)	34	(45)	0	(0)	76
	Spring/Summer ( $n = 8$ )	6	(14)	22	(50)	16	(36)	0	(0)	44
	Fall ( $n = 2$ )	4	(36)	3	(27)	4	(36)	0	(0)	11
	Total ( $n = 8$ )	13	(10)	64	(49)	54	(41)	0	(0)	131
Male	Winter ( $n = 14$ )	2	(2)	54	(46)	62	(53)	0	(0)	118
	Spring/Summer ( $n = 10$ )	4	(5)	40	(48)	37	(45)	2	(2)	83
	Fall ( $n = 2$ )	0	(0)	12	(46)	14	(54)	0	(0)	26
	Total ( $n = 14$ )	6	(3)	106	(47)	113	(50)	2	(1)	227
Total		19	(5)	170	(47)	167	(47)	2	(1)	358

<sup>1</sup> Number of martens in parentheses, <sup>2</sup> Cavities in live aspens or pine trees, or rotten snags of either species,

<sup>3</sup> Arboreal structures included nests ( $n = 155$ ), witch's broom ( $n = 1$ ), and branches ( $n = 2$ ), or were unidentified ( $n = 12$ ). Nests were of squirrels ( $n = 90$ ), birds (columbids or corvids,  $n = 27$ ), or were unidentified ( $n = 38$ ),

<sup>4</sup> Usually located in rocky substrate ( $n = 163$ ), but also in the root system of a pine tree ( $n = 3$ ) and a stump ( $n = 1$ ),

<sup>5</sup> Stacks of cut logs.

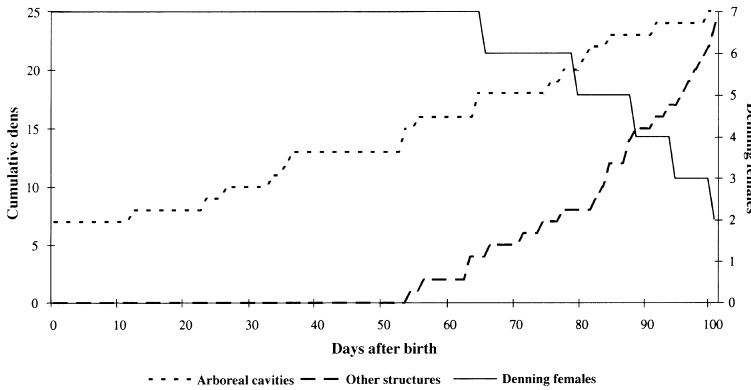


Fig. 1. Cumulative use of arboreal cavities and other structures relative to the number of denning female pine martens at Grimsö, Sweden ( $n = 4$  martens,  $n = 65$  relocations) and Varaldskogen, Norway ( $n = 3$  martens,  $n = 44$  relocations) during 1987–1991.

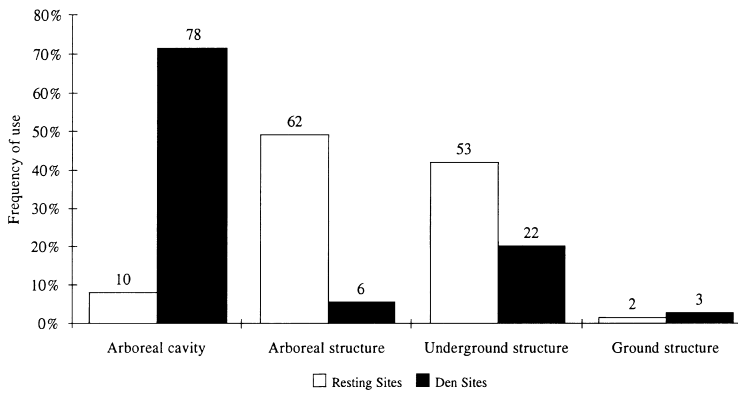


Fig. 2. Relative use of different structures as resting and denning sites by pine martens at Grimsö, Sweden and Varaldskogen, Norway during the spring/summer season (1987–1991).

(*Dryocopus martius*). The remaining birth den was located in a squirrel nest in a mature spruce tree; radio-contact was lost with this family shortly after its discovery.

Denning sites in cavities were used exclusively the first 53–98 ( $66.4 \pm 15.3$ ) days after birth ( $n = 7$  adult females, Fig. 1), with switching between such sites in some instances. Pine marten families became increasingly mobile and used a greater variety of temporary denning sites above and below ground as the denning season progressed. These temporary sites were in arboreal structures (primarily in squirrel or bird nests), underground (rocky substrate) and ground structures (ant hills or stacked logs), as well as arboreal cavities.

Den site use differed from resting site use for both sexes during the spring/summer season ( $\chi^2 = 110.66$ ,  $df = 2$ ,  $P < 0.0001$ , Fig. 2). We found a strong selection for arboreal cavities as denning sites compared to their use as resting sites during this season (one-tailed  $\chi^2 = 97.56$ ,  $df = 1$ ,  $P < 0.0001$ ).

#### 4.2. Selection of resting sites relative to $T_a$

Selection of resting sites relative to  $T_a$  varied seasonally (Table 2). During winter, pine martens rested underground at significantly lower  $T_a$  than when they rested in trees.  $T_a$  did not appear to dictate pine marten choice of resting sites in trees or underground during the rest of the year. Relative use of underground sites was negatively correlated with  $T_a$   $Y = 61.28 - 1.48 \chi$ ,  $R^2 = 0.41$ ,  $P < 0.0001$ , (Fig. 3). This relationship was, however, better explained with a binomial regression model ( $Y = 48.38 - 2.00 \chi + 0.10 \chi^2$ ,  $R^2 = 0.61$ ,  $P < 0.0001$ ); this suggested that martens also sought underground shelter during warmer summer periods.

### 5. Discussion

For pine martens and other *Martes* species, selection of resting and denning sites may be influenced by predation risks (e.g. Buskirk 1984, Lindström

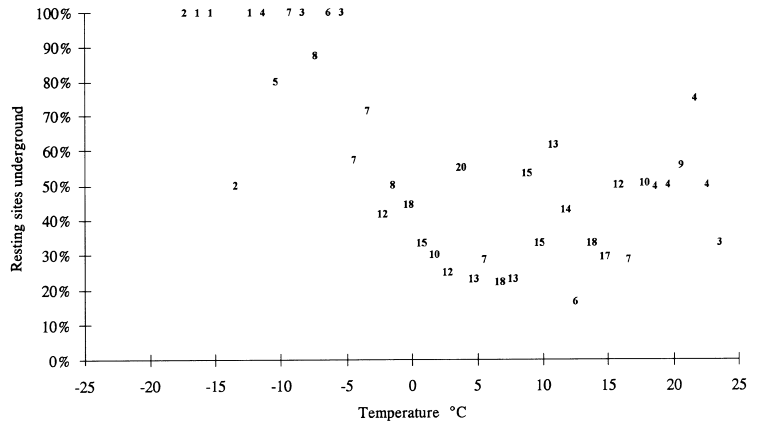


Fig. 3. Frequency of use of underground sites by pine martens at Grimsö, Sweden and Varaldskogen, Norway (1987–1991) relative to  $T_a$ .  $T_a$  is expressed in whole increments, and sample points are represented by their respective sizes..

et al. 1995) and energetic constraints (e.g. Buskirk 1984, Buskirk et al. 1988, Buskirk et al. 1989, Buskirk & Harlow 1989). In addition, other factors such as space limitations at sites, habitat preferences and proximity to foraging areas may play a role in determining selection of these sites (Buskirk 1984, Buskirk & Powell 1994). The pine marten appears to have a well-developed memory (e.g. Sonerud 1985a, 1985b, 1989, Nilsson et al. 1991), which may facilitate repeated use of resting and denning sites within their territories.

In our study areas, pine martens preferred arboreal cavities as secure shelter for birth and rearing of neonates. Pine martens have been observed denning in such sites elsewhere (Pelikán & Vackar 1978, Selås 1990b), as well as in nesting boxes and other man-made structures (Aholá & Terhivuo 1982, Baudvin et al. 1985, Sonerud 1985a, Selås 1990b). In this study, arboreal cavities were primarily excavated by black woodpeckers, suggesting that pine martens may depend on this species for providing den sites (see Johnsson 1993). Such cavities were roomy, relatively dry and virtually inaccessible to potential

enemies such as red foxes. The slow development of young after birth (Brassard & Bernard 1939, Tumanov 1972, Nyholm 1980, Selås 1990c) and their general helplessness the first few months of life probably influences selection for these sites as natal dens (Selås 1990b). Pine marten families abandoned arboreal cavities when kits were between two and three months old; increased size and mobility of juveniles at this age probably allowed for movement to other sites in our study areas.

Arboreal cavities were rarely used by pine martens as resting sites in Finland and Northern Russia (Pulliainen 1981). American martens rarely rested in arboreal cavities during winter (Spencer 1987). In this study, female pine martens displayed a greater affinity than males for arboreal cavities as resting sites. This seems natural, given the importance of these sites during the denning period and the fact that a female and kit were observed resting together as late as October at such a site (this study, unpubl.).

Clearcutting practices may favor populations of red fox through increased small mammal

Table 2. Use of pine marten resting sites underground and in trees relative to ambient temperature at Grimsö, Sweden, and Varaldskogen, Norway.

Season	Arboreal			Underground			Mann-Whitney Test	
	Mean $T_a$	SD	<i>n</i>	Mean $T_a$	SD	<i>n</i>	<i>U</i>	<i>P</i> <sup>1</sup>
Winter	2.95	5.02	98	-2.65	7.41	96	2520.50	<0.0001
Spring/summer	13.68	5.22	72	14.87	4.99	53	1677.50	0.25
Fall	8.12	4.29	19	5.49	5.46	18	123.50	0.15

<sup>1</sup> Corrected for ties.

abundance (Christiansen 1979, Christensen 1985). Two of our three instrumented marten kits were killed by red foxes after they had moved from arboreal natal dens to more temporary dens on or under the ground (see Lindström et al. 1995).

Modern forestry practices have generally reduced the structural diversity of Scandinavian forests, and foresters have only recently begun to recognize the value of arboreal cavities as nesting sites for many species. In our study areas, forest managers took measures to preserve living and dead trees with cavities, to the benefit of pine martens and other hole-nesting species. Arboreal cavities may protect pine marten neonates from predation by red foxes and other species during their early development.

Energetic constraints forced pine martens to seek warm microenvironments during periods of cold winter weather. Pulliainen (1981) noted that pine martens in his study area and in neighboring Russia tended to use subnivean resting sites more at more northerly latitudes than in more southerly areas, which suggested a relationship between cold temperatures and their use. American martens possess limited energy reserves in winter (Buskirk & Harlow 1989), and thus must reduce energetic costs in winter by seeking insulated underground resting sites (Buskirk 1984, Buskirk et al. 1989). Subnivean resting sites associated with coarse woody debris were the most insulated sites used by American martens (Buskirk et al. 1989). Such sites are generally absent in our study areas as a result of "forest cleaning" practices. In Norway, pine martens have been observed resting in sites associated with coarse woody debris in mountainous forest in the Valdres region (D. Bakka, pers. comm.), an area with lower winter temperatures and greater snow depths compared to our study areas.

Future research should experimentally assess the importance of arboreal cavities and underground shelter for pine martens at the landscape scale. We hypothesize that in areas with cold winter temperatures, deep snow and presence of red foxes or other potential predators, the lack of such sites may indeed limit pine marten distribution and abundance.

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