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Agricultural University of Norway

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GRIMSO WILDLIFE RESEARCH STATION

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Abstract

The objective of this thesis was to examine factors that influence habitat selection and space use of the Eurasian pine marten (*Martes martes*) within the southern boreal forest region of Norway and Sweden. In order to document pine marten habitat use and spacing patterns 25 (16 males, 9 females) pine martens were captured, radio-instrumented and relocated 4641 times in two study areas in Norway and Sweden during 1987-1991.

I present a general hypothesis on the effects of modern clearcutting practices on pine martens, where clearcut size and intensity of cutting were considered to have differential effects on pine marten densities. When cut size is relatively fine-grained with respect to pine marten mobility, and of relatively moderate intensity, increased prey density and accessibility may favor pine marten populations. As scale and intensity of clearcutting increases, however, the net gain in productivity probably cannot compensate for net habitat loss, negatively impacting pine marten densities at the landscape level.

Resting sites were selected by both sexes in a similar manner throughout the year. However, females strongly selected cavities in trees and snags as denning sites relative to their use of resting sites by either sex. Average ambient temperature (T_a) associated with resting sites underground (-2.65°C) was significantly lower than for arboreal resting sites (2.95°C) during winter. In general, resting sites were consistently located underground at $T_a <$ -5°C.

The hypothesis that old forest should be strongly preferred if this species is an old-growth forest specialist was tested. Data from this study indicated no strong selection for old coniferous forests > 70 years, although some selection during winter was observed in one of the study areas. Our data indicate that pine martens do not appear to be reliant on old forest stands in our study areas, probably since such stands have been modified by forestry practices and do not resemble primeval old-growth stands.

However, stands dominated by mature ($\geq$20 m in height) Norway spruce (*Picea abies*) trees were preferred by pine martens, and clearcuts (barren or with trees <1 m in height) and open areas such as bogs and fields were strongly avoided throughout the year by both sexes when resting or active. Between habitats, pairwise comparisons of selection ratios indicated mature spruce-dominated stands were preferentially selected over other habitats.

Pine martens exhibited intrasexual territoriality, and spatial use patterns did not differ between seasons or sexes. Home ranges (95% minimum convex polygon (MCP)) averaged 7.17 km^2, core areas (adaptive kernel method) averaged 3.22 km^2 and mean distance between movements $\geq$24 hours averaged 1.47 km. These average movements were not related to the seasonal indices of vole abundance. Core areas contained a greater proportion of preferred spruce-dominated forest than 95% MCP ranges, and 95% MCP ranges contained a higher proportion of this habitat than local 9.00 km^2 landscapes. The best predictors of 95% MCP range size were sampling duration, and proportion and mean shape index of patches of preferred habitat in the surrounding landscape. Neither the effects of body mass or sex or interaction between these could account for the observed 15-fold variation in 95% MCP range size.

Pine marten populations may be negatively influenced by aspects of modern forestry practices. Within stands, foresters should strive to retain dead and living trees with cavities for denning, and logs and woody debris for thermal shelter and subnivean access where broken, rocky substrates are lacking. Fragmentation of mature (trees $\geq$20 m tall) spruce-dominated forests habitat has a negative effect on pine marten space use, with direct implications for population densities in this territorial species. Further research is needed to elucidate the effects of patch size and isolation of preferred habitat on pine marten densities at the landscape level.

Key words: Scandinavia, forest management, pine marten, *Martes martes*, resting sites, denning sites, habitat use, home range size, forest fragmentation.

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The Eurasian pine marten is elusive and difficult to capture, and radio-collars have limited range due to their small size. This means that skilled and dedicated technicians are required if research on such a species is going to succeed. This project would not have succeeded without the valiant efforts of Dagh Bakka, Erlend Rolstad, and Kent Sköld, who displayed matchless skill, dedication, interest and enthusiasm for capturing and monitoring these difficult critters under sometimes arduous conditions. It was indeed a privilege to work with you, and I extend my deepest gratitude for a job "well done"! In addition to these efforts, I appreciate the help of others participated that in field work, including Per Ahlquist, Mikael Gustavsson, J.-O. Helldin, Erik Lindström, Jørund Rolstad, Ilse Storch and Lisa Van Allen, as as well as numerous students from NLH and SLU.

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taught me a great deal about Swedish nature, and his friendship, insight and support have been of inestimable value. The hospitality and friendship of Przemyslaw Majewski, a fellow veteran of Varaldskogen and Grimsö, also eased the difficult periods of this study. Göran "Georgie" Hartman and Johan Danielsen also provided much needed friendship, humor and support.

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I dedicate this thesis to the loving memory of my father, Byron Lee Brainerd, who instilled in me a deep and abiding respect and love for nature, and encouraged me to pursue a career in wildlife biology. My greatest regret is that he did not live to see this final goal fulfilled.

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List of papers

This thesis consists of the following papers and an extended synopsis, referred to in the text by their Roman numerals.

I. **Brainerd, S. M. 1990**. The pine marten and forest fragmentation: a review and general hypothesis. *In* Transactions of the 19th IUGB Congress. *Edited by* Myrberget, S. Trondheim, pp. 421-434. [1]

II. **Brainerd, S. M., Helldin, J-. O., Lindström, E. R., Rolstad, E., Rolstad, J. and Storch, I. 1995.** Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. Ann. Zool. Fennici 32:151-157.[2]

III. **Brainerd, S. M., Helldin, J-. O., Lindström, E., and Rolstad, J. 1994.** Eurasian pine martens and old industrial forest in southern boreal Scandinavia. *In* Martens, sables and fishers: biology and conservation. *Edited by* Buskirk, S. W., Harestad, A., Powell, R., and Raphael, M. Cornell University Press, Ithaca, pp. 343-354.[3]

IV. **Brainerd, S. M., and Rolstad, J. 1997.** Habitat selection by the Eurasian pine marten (*Martes martes*) in managed forests of southern boreal Scandinavia. Manuscript.

V. **Brainerd, S. M., and Rolstad, J. 1997.** Space use by the Eurasian pine marten (*Martes martes*) in relation to habitat quality in southern boreal Scandinavia. Manuscript.

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SYNOPSIS

Introduction

Throughout its range, the Eurasian pine marten (*Martes martes*) has long been considered a species that is vulnerable to human activities (e.g. Langley and Yalden 1977). Its low reproductive potential (Selås 1990a, Mead 1994) has made it particularly susceptible to overharvest in much the same manner as its congeners, the American marten (*Martes americana:* Strickland 1994) and the sable *(Martes zibellina:* Bakeyev and Sinitzin 1994). In boreal Scandinavia, economic demand for its valuable fur and predator control campaigns lead to periodic overharvest (Dass ca. 1670 in Selås 1990b and Lindström 1997, Modin 1915, Selås 1990b, Helldin and Lindström 1992, Lindström 1997). By the early 20th century, the pine marten was nearly exterminated in Norway and Sweden as the result of intensive fur trapping and predator control efforts (Modin 1915, Eliasson 1943, Selås 1990b, Helldin and Lindström 1992, Lindström 1997), and as a result protective measures were enacted, with this species receiving full protection in both countries by 1930 (Selås 1990b, Helldin and Lindström 1992, Lindström 1997). Pine marten numbers slowly recovered, and hunting seasons were eventually reinstated between 1939-1971 (Selås 1990b, Helldin and Lindström 1992, Lindström 1997). Marten harvests slowly increased, probably as a result of increasing populations and interest in trapping of this species, through the late 1970´s. An epizootic of sarcoptic mange lead to a severe decline in populations of the red fox (*Vulpes vulpes*) in Scandinavia from the late 1970´s through to the early 1990´s (Lindström and Mörner 1985, Lindström 1991, Lindström et al. 1994). Pine marten numbers increased dramatically during this period, and data show that this increase was chronologically and spatially linked with the red fox decline throughout Sweden (Paper I, Storch et al. 1990, Helldin and Lindström 1992, Lindström et al. 1995), which suggests that the red fox had a direct impact on pine marten populations in fashion similar to its influence on populations of roe deer (*Capreolus capreolus*), mountain hares (*Lepus timidus*), capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and hazel grouse (*Bonasa bonasia*) (Lindström et al. 1994, Lindström et al. 1995).

In Scandinavia, the Eurasian marten has been traditionally considered to be a species reliant upon old-growth forests (e.g. Bjärvall et al. 1977, Selås 1990a). The influence of clearcutting practices on pine marten populations is not well understood, although data from boreal Russia indicates that large-scale clearcutting had a negative impact on densities (Aspisov 1959, Grakov 1972). Data from northern Sweden indicated that pine marten densities were 2-3 times higher within an old-growth forest reserve when compared to the surrounding landscape of commercially-managed, fragmented forest (Bjärvall et al. 1977). At the same time, authors noted the increase in pine marten populations and the role of this species as a predator on small game, including hares (*Lepus* sp.) and forest grouse (subfamily Tetraoninae) (e.g. Semenov-Tian-Shanskii 1959, Angelstam 1984, Wegge et al. 1987, Lindström et al. 1987, 1989, Marcström et al. 1988, 1989, Swenson 1991, Kurki et al. 1997). Researchers (Henttonen 1989, Rolstad et al. 1991, Wegge et al. 1992) hypothesized that forestry practices that convert old-growth forest into clearcut may have had a positive influence on medium-sized predators (including pine martens) by increasing the biomass of microtine rodents that thrive in such habitats (see review and hypothesis by Ims 1991). In relatively fine-grained mosaics (relative to species mobility, cf. Levins 1968, Pielou 1974, Wegge and Rolstad 1986, Rolstad and Wegge 1989a, Rolstad 1991, Andrén 1994) of clearcuts and older forest, increased edge benefit pine martens by creating increased access to microtines in clearcuts and along boundaries between these habitats (Larin 1955, Krasovskii 1970, Grakov 1972). Romanov (1956, 1961, cited in Grakov 1972) was, perhaps, the first to address these dual effects of modern forestry practices in the Russian taiga, based on scale and intensity of clearcutting.

Unlike the Eurasian pine marten, its close relative the American marten has been the subject of intense research during the past two decades. Overharvest has been a chronic problem, particularly in the eastern part of its range, where unregulated fur-trapping is held responsible for its disappearance or decline in many states and provinces (e.g. Clark et al. 1987, Strickland and Douglas 1987, Strickland 1994, Berg and Kuehn 1994). In addition, habitat destruction has been suggested to be a primary cause of population decline in areas where American martens have become extinct or are currently threatened (Yeager 1950, Bergerud 1969, Dodds and Martell 1971, Davis 1983, Thompson 1991, Gibilsco 1994, Thompson and Harestad 1994). American martens generally avoid large clearcuts (see reviews by Clark et al. 1987, Strickland and Douglas 1987, Buskirk and Powell 1994, Thompson and

Harestad 1994) and can experience higher mortality in such areas (Thompson 1994). American martens specifically need physically complex structure at ground level to meet foraging, resting, energetic and survival needs (review in Buskirk and Powell 1994). Cavities in snags are important structures for resting and denning (Martin and Barrett 1983, Wynne and Sherburne 1984, Snyder and Bissonette 1987, Flynn and Schumacher 1995), and removal of such structures may have negative consequences. Human exploitation of old-growth forests has had a negative effect in eastern North America (e.g. Soutiere 1979, Steventon and Major 1982, Snyder and Bissonette 1987, Bissonette et al. 1989, Thompson 1991, 1994, Thompson and Colgan 1991, 1994, Thompson and Harestad 1994), where its plight has been compared to that of the northern spotted owl (*Strix occidentalis caurina*, Dawson et al. 1987, Thomas et al. 1990). Indeed, evidence indicated that intensive logging activity has resulted in a serious population decline of the Newfoundland subspecies (*A. m. atrata*), which is now listed as threatened by the Canadian government (Bissonette et al. 1989, Thompson 1991). However, some studies suggest that the American marten is also rather flexible in its choice of habitats, particularly in boreal regions (Koehler and Hornocker 1977, Magoun and Vernam 1986, Paragi et al. 1996), and that lesser disturbances, such as small-scale clearcutting or burns, may augment prey abundance and diversity, while affording adequate shelter for foraging and resting (Koehler et al. 1975, Hargis and McCullough 1984).

Our knowledge of the ecology of the Eurasian pine marten in Scandinavian forests is very limited, particularly with regard to the influences of modern forestry practices. This is primarily due to the difficulties involved in studying this elusive animal. Unlike the American marten, this species is relatively difficult to live-trap. Although some researchers have employed radio-telemetry to examine various facets of pine marten ecology in Scandinavia (Storch 1988, Storch et al. 1990, Overskaug et al. 1994), no detailed study on habitat use and spacing patterns relative to modern forestry practices has been conducted. Detailed studies on habitat use and movements have been primarily limited to snow-tracking studies (Pulliainen 1981a, 1984, Wabakken 1985, Eie 1992, Eide 1995, Gundersen 1995). Storch (1988) and Storch et al. (1990) presented data on spacing patterns and habitat use on a limited number ($n = 3$) of radio-collared pine martens which were later incorporated into the material used in this thesis.

This thesis examines the influence of modern forestry practices on pine marten habitat and range use in southern boreal Scandinavian forests. The objectives of Paper I were: 1) to review the current knowledge of pine marten ecology relative to modern forestry practices, and 2) to hypothesize the influence of such activity on pine martens at different levels of scale. Paper II examines the importance of different structures as resting and denning sites. Paper III examines the importance of old (> 70 years) stands of semi-natural coniferous forests to pine martens. This preliminary analysis paves the way for the more detailed analyses presented in Paper IV, which quantifies pine marten habitat selection relative to indices of forest structure. Paper V focuses on home range size and movements of pine martens and explores alternative hypotheses for explaining variation in measures of space use relative to body size, vole density and habitat quality and fragmentation.

Study Areas

This study was conducted in two localities near the southern limit of the boreal zone of Scandinavia (Ahti et al. 1968): the 140 km^2 Grimsö Wildlife Research Area (GWRA: 59° 40'N, 15° 25'E) in southcentral Sweden and the 100 km^2 Varaldskogen Wildlife Research Area (VWRA: 60° 10'N, 12° 30'E) in southeastern Norway on the Swedish border (Fig. 1). The GWRA is relatively flat (75-125 m a. s. l.) whereas the topography in the VWRA is more hilly, with elevations varying between 200-400 m a. s. l. Both areas are dominated by commercial stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Stands dominated by deciduous trees are rare, but birch (primarily *Betula pubescens*), alder (*Alnus incana*) and aspen (*Populus tremula*) are sometimes present as an admixture in coniferous stands. Bogs and agricultural land comprised roughly 25% of the GWRA and <10% of the VWRA, while clearcuts with trees removed or < 1m in height comprised roughly 5% of both study areas. Lakes and rivers comprise 5-15% of the study areas. Both areas are dominated by a substrate of rocky glacial till, interspersed with fields of large boulders.

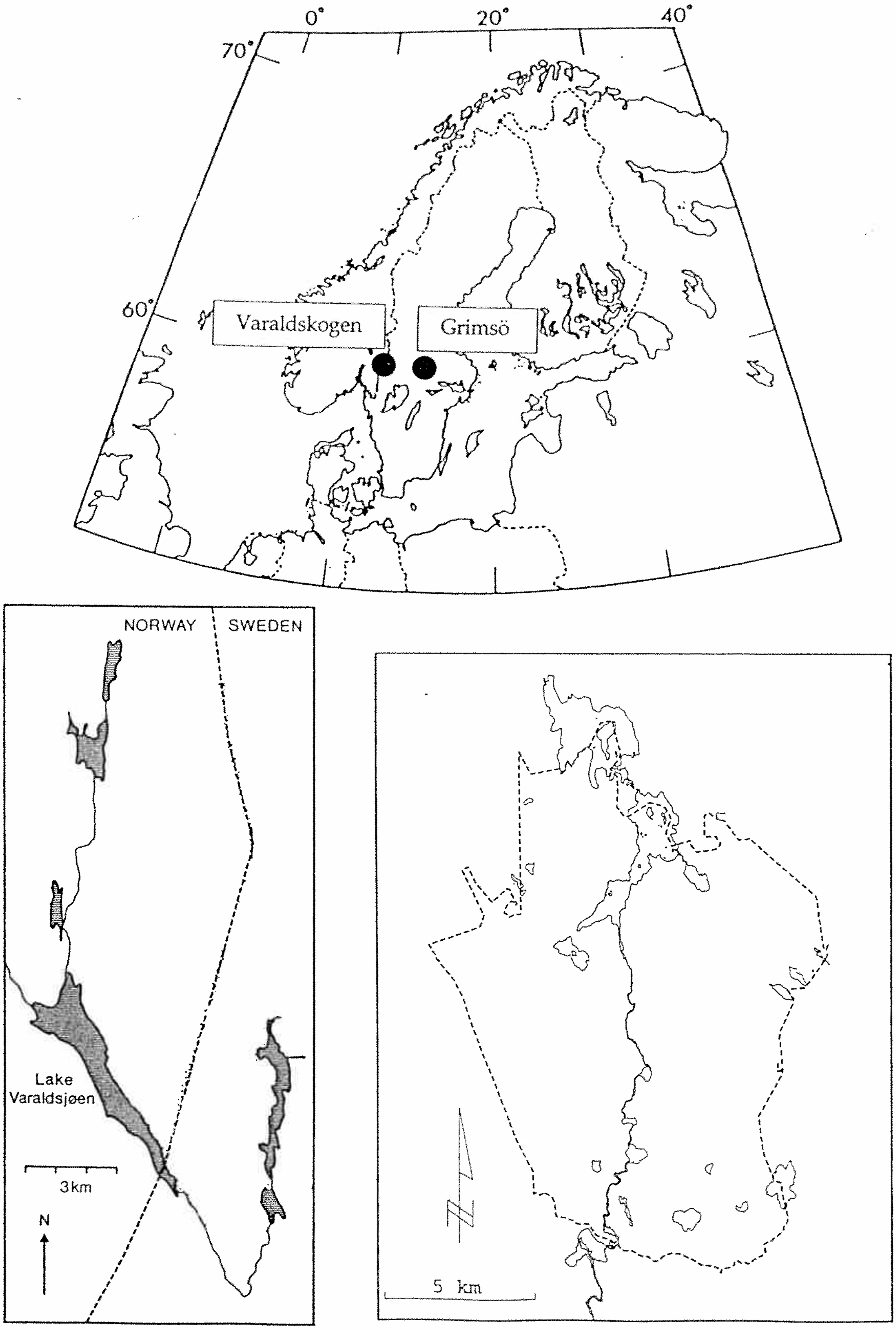

Fig. 1. Locations of the Varaldskogen and Grimsö Wildlife Research Areas in southern boreal Scandinavia.

Within this region, primeval forest was regenerated by fire, which has been successfully suppressed the last 100 years (e.g. Esseen et al. 1992). From the mid-17th century, forests in this region were intensively utilized for fuel, sawmills and the iron industry. This exploitation culminated in the late 19th century, when most of the available large-timbered tracts had been exploited. During 1870-1950 these forests were moderately utilized by selective cutting methods. A few smaller clearcuts (<1 ha) were made in the 1910´s to 1940´s, and from about 1950 clearcutting and replanting 5-50 ha units has been the dominant forestry method in both areas.This history of utilization has created a mosaic landscape of even-aged, single-layered stands up to about 80 years of age. In the VWRA, about 20% of the productive forest is covered by older, multi-layered stands, naturally rejuvenated after intensive logging in the late 19th century (see Rolstad et al. 1988, Rolstad and Wegge 1989b,c). In the GWRA, a 5.22 km^2 forest reserve was centered in our study area. This reserve regenerated naturally after a fire in 1914 (Angelstam 1992), and very little forest management has occurred in the area since 1972, and thus portions of this forest are in a semi-natural, uneven-aged state. Almost all old forest stands have been managed by selective cutting or thinning. Less than 0.1% of the VWRA (<10 ha) resembles old-growth forest structure, and true old-growth conditions are lacking in both study areas. Clearcutting practices intensified in both study areas through the 1950´s and 1960´s, and by the time of the study large portions of both areas were in early successional seres. Most of the old, natural forest has now been cut, and clearcutting has created a mosaic of clearcuts, plantations, and older forest stands in both areas. The majority (> 80%) of clearcuts are < 10 ha, and rarely exceed 50 ha. In both areas, clearcuts and plantations often adjoin, creating contiguous regenerating stands of several hundred ha.

The climate in both study areas is moderately continental, and mean daily temperatures ranged from -18°C to 27°C with mean temperatures of 16.2°C and -7.3°C in the warmest (July) and coldest (January) months, respectively. Snow depths of 30-100 cm are normal in both study areas from mid-Novemeber through the end of April. With the exception of the winter of 1986-87, winter temperatures were unusualy mild during the study period. During 1986-87, snow depths averaged 40.6 cm in the GWRA and in the VWRA snow depths averaged 10 cm in 1989-90 and 30 cm in 1990-91. During the winters of 1988-89, 1989-90 and 1990-91, little snow accumulated in the GWRA with mean snow depths averaging 6.2, 3.9, and 13.1 cm, respectively. The VWRA was virtually snow-free during the winter of 1989-1990. During these mild winters periods of snowfall were generally followed by warm, wet periods which melted the snow.

Trapping was allowed in the VWRA from November to March each year. In the GWRA, however, martens were protected throughout the year, although trapping was allowed from November to March in areas surrounding the GWRA.

General Methodology

Data were collected on pine martens captured and radio-instrumented during the winters of 1986-87, 1988-89, 1989-90 and 1990-91 in the GWRA (n = 11 males, 5 females) and the winters of 1989-90 and 1990-1991 in the VWRA (n = 5 males, 4 females), with a total of n = 4641 locations recorded (Papers II-V). Sample sizes of monitored animals and number of locations varied with the study objectives and error criteria for each paper in the thesis. Although the age of some individuals was determined through dental X-ray or cementum annuli counts (Helldin 1997), this was not possible for all individuals.

Pine martens were live-trapped with wooden box-traps (40 x 40 x 60 cm) baited primarily with honey or visceral organs of cervids (moose, *Alces alces*, and roe deer) (Papers II-V). Animals were immobilized with a combination of ketamine hydrochloride and xylazine hydrochloride. The dosages for ketamine and xylazine were 10 and 2 mg/kg body weight (drug concentrations 100 mg/ml), respectively. Small plastic rototag and a metal ear-clip were affixed in each ear, and martens were instrumented with 2-stage neckband transmitters (Televilt AB, Sweden) equipped with either metal loop or whip antennas. Size of radio-packages reflected the general 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 9 and 6 months for males and females, respectively. Pine martens were released at their trapsites after they had recovered from sedation.

Radio-locations included triangulations, cross bearings, close-tracking locations (≤ 100 m from the animal) (Papers III-V) and visual observations (Papers II-V). Error polygons were considered acceptable at the distances tracked in our study areas (see Cederlund and Lemnell 1979, Cederlund et al. 1979). We included only triangulations with the longest side ≤ 250 m, or cross-bearings with the longest distance ≤ 200 m from the pine marten for habitat selection analysis. For analysis of home ranges and movements, we accepted triangulations with the longest side ≤ 500 m , or cross-bearings with a maximum distance of ≤ 500 m between the tracking station and pine marten. Angle between respective bearings was ≥ 45° for triangulations, and the angle between cross-bearings was 45°-135°. Since we often continuously radio-tracked pine martens over 3-12 hour periods, we used only independent locations (Swihart and Slade 1985) to minimize autocorrelation and to standardize data across individuals and between study areas.

The use of underground sites was compared with that of arboreal structures between seasons and sexes for resting and denning (Paper II). In addition, the effects of temperature on the use of resting sites underground and in arboreal structures was examined. Nonparametric statistics were used to test for differences between categories. Regression analysis was used to examine the use of underground sites relative to ambient temperature throughout the year.

We used two methods for habitat analyses. In Paper III, we examined selection of four forest age classes, and in Paper IV we examined use of nonforested habitat and forest habitats classified by dominant tree height and tree species. In Paper III, we tested for deviation from expected values with a chi-square goodness-of-fit test and thence the Bonferonni-Z confidence interval test (Neu et al. 1974), with observed and expected values pooled across individuals. In Paper IV, we replaced the goodness-of-fit test with a log-likelihood test, and employed an advanced method that used selection ratios for individuals as a test statistic (Thomas and Taylor 1990, McDonald et al. 1991, Aebischer et al. 1993, Manly et al. 1993) to test the null hypothesis that martens selected habitat in proportion to availability. Differences between categories were tested with nonparametric statistics.

We estimated home ranges by the 95% minimum convex polygon (MCP) method (Mohr 1947; Papers III-V) and core areas (Paper V) by the adaptive kernel method (Worton 1989).

95% MCP ranges and core areas were estimated by the Tracker Wildlife Tracking and Analysis Software (version 1.1, Camponotus AB, Sweden). We used the Ranges IV program (Kenward 1990) to plot utilization distributions (Ford and Krumme 1979, Kenward 1987) of 95% MCP ranges, and included data for those pine martens with clear asymptotes (between 25 and 35 locations) in these analyses. We inspected utilization distributions to identify the point of discontinuity (generally 65-75% of the total area) for each pine marten. This continuity provided a method for defining each pine marten's core area (Kenward 1987).

We calculated mean distances between consecutive locations separated by $\geq$ 24 hours by season. Vole indices in both study areas were based on the sum of the number of bank voles (*Clethrionomys glareolus*) and field voles *(Microtus agrestis*) captured per 100 trap-nights (see Wegge and Storaas 1990, Lindström et al. 1994). Spring indices correspond roughly with the late winter and early summer seasons, and fall indices coincided with the late-summer and early-winter seasons.

In Paper V, habitat content (using categories similar to Paper IV) within core areas, 95% MCP ranges and 9.00 km^2 local landscapes centered on arithmetic centers of 95% MCP ranges were compared (Paper V). An analysis of covariance was used to test the effects of ln-transformed body mass (kg) and sex and interaction of these variables on ln-transformed 95% MCP range size (km^2) in order to test the hypothesis that range area and body mass were positively correlated (McNab 1963, Harestad and Bunnell 1979). Sizes of 95% MCP ranges (km^2) were regressed against measures of proportion and fragmentation (FRAGSTATS: McGarigal and Marks 1995) of preferred, spruce-dominated forest with trees $\geq$ 20 m tall within local landscapes in order to test the hypothesis that range size was inversely correlated with habitat quality.

Results and Discussion

Review and hypothesis: the influence of forest fragmentation on pine marten densities (Paper I)

I review earlier studies regarding the life requirements of the Eurasian pine marten with regard to the possible effects of forest fragmentation, as well as pertinent literature on its congener, the American marten. Although pine martens are adapted to a wide variety of forest types throughout their range, they generally avoid open areas such as bogs and clearcuts (Grakov 1972, Pulliainen 1981a,c, Fedyk et al. 1984, Wabakken 1985, Krüger 1990, Marchesi 1989, Storch et al. 1990, Hansson 1994) and prefer mesic, mature spruce-dominated stands (Grakov 1972, Bjärvall et al. 1977, Degn and Jensen 1977, Pulliainen 1981a, Nesvadbova and Zedja 1984, Wabakken 1985, Marchesi 1989, Storch et al. 1990).

This species is considered to be an opportunistic, omnivorous generalist, and consumes a variety of food items, primarily small mammals and birds, although insects and vegetable matter are also occasionally consumed (Nasimovic 1948, Höglund 1960, Lockie 1961, Nyholm 1970, Morozov 1976, Pulliainen 1981b, Warner and O´Sullivan 1982, Wabakken 1985, Reig and Jedrzejewski 1988, Marchesi and Mermod 1989, Storch et al. 1990, Clevenger 1993a,b, 1994, Jedrzejewski et al. 1993, Pulliainen and Ollinmäki 1996, Helldin in manus). In many studies small rodents are favored, particularly *Clethrionomys* sp. (Nasimovic 1948, Morozov 1976, Reig and Jedrzejewski 1988, Marchesi and Mermod 1989, Storch et al. 1990, Jedrzejewski et al. 1993, Pulliainen and Ollinmäki 1996), although *Microtus* sp. can also be important prey (Lockie 1961, Pulliainen 1981b, Storch et al. 1990, Helldin in manus). In the GWRA, consumption of *Microtus* sp. by pine martens varies seasonally, and may be linked to snow conditions rather than to abundance (Storch et al. 1990).

Russian and Scandinavian studies indicate that large-scale and intensive clearcutting practices are probably detrimental to pine marten populations (Aspisov 1959, Grakov 1972, Bjärvall et al. 1977). It has been hypothesized that clearcutting practices favor microtine rodents (see review and hypothesis by Ims 1991) and data show that the field is abundant in such habitat (Sonerud 1986, Henttonen 1989, Ims 1991, Hansson 1994), although a rigorous test of this hypothesis has yet to be tested (H. Andreassen, pers. comm. 1997). Researchers (Henttonen 1989, Rolstad et al. 1991, Wegge et al. 1992) have hypothesized that forest cutting practices promoted increased densities of pine martens and other medium-sized carnivores as a result of greater abundance of prey in such habitat. Other authors have speculated that increased edge in heterogeneous mosaics of clearcut and forest may benefit pine martens (Larin 1955, Krasovskii 1970, Grakov 1972).

Scale and intensity of forest cutting practices may differentially influence pine marten populations. By relating grain size forest fragmentation to species mobility (cf. Levins 1968, Pielou 1974, Rolstad 1991, Ims et al. 1993, Andrén 1994) I hypothesize that, in fine-grained mosaics of clearcuts and older forests pine martens may benefit from increased edge and access to abundant microtine prey. In larger-grained mosaics, patches of remnant forest become increasingly isolated, and I expected pine marten densities to decrease as a result of habitat loss and decreased accessibility of microtine rodents within large clearcuts. Rolstad (1991) and Ims et al. (1993) develop and expand a related hypothesis on the effects of different scales of habitat fragmentation on the root vole (*Microtus oeconomus*) and the capercaillie based on empirical evidence, and a similar model was presented by Thompson and Harestad (1994) for American martens. Although no vigorous test has yet been published, data on Eurasian pine martens (Kurki et al. in manus) and American martens (Bissonette and Hargis 1995) lend some support to this general hypothesis.

Choice of resting and denning sites (Paper II)

We examined selection of resting sites ($n = 299$) and natal dens ($n = 109$) by pine martens ($n = 25$). Resting sites situated underground ($n = 167$) or in trees ($n = 170$) were used in a similar manner by both sexes throughout the year. Resting sites in trees were primarily in nests of Eurasian red squirrels (*Sciurus vulgaris*) or birds (Columbidae, Corvidae). Cavities in trees or snags were rarely used as resting sites by either sex, although females used such sites more than males when seasons were combined. In general, we found a strong selection for arboreal cavities as denning sites compared to their use as resting sites by either sex during the spring/summer season. Such selection has been observed elsewhere in Norway for this species (Selås 1990c). Seven of eight primary natal dens were located in cavities in aspen or pine trees or snags. Such primary denning sites were used exclusively the first 53-98 days after birth. As the denning season progressed, family groups became more mobile, switching between sites above and below the ground surface.

When choosing resting and denning sites, pine martens were probably influenced by predation risks (e. g. Buskirk 1984, Lindström et al. 1995) and energetic constraints (e. g. Buskirk 1984, Buskirk et al. 1988, 1989, Buskirk and Harlow 1989). In addition, other factors including space limitations, habitat preferences and proximity to foraging areas may also determine selection of these sites. Preference of arboreal cavities as denning sites was probably due to their inherent security from mammalian and avian predators, as well as their sheltering effect from inclement weather during this critical period. Pine marten neonates are generally helpless during the first few months of life (Brassard and Bernard 1939, Selås 1990a), and as kits became more mobile, these sites were abandoned in favor of temporary sites both above and below ground. This study highlights the importance of such arboreal cavities, which should be preserved by forest managers to accomodate pine martens and other cavity nesters.

Ambient temperature influenced pine marten selection of resting sites. In winter pine martens rested underground at significantly lower ambient temperatures (T_a) than when they rested in trees. Throughout the year, relative use of underground sites was negatively correlated with ambient temperature, and results suggested that pine martens also sought underground shelter during warmer summer periods. Pine martens have short fur and a high surface-to-volume ratio with associated high thermal costs resulting from a lower critical temperature (T_c) that is higher than predicted for its body size (Harlow 1994). High thermal conductance raises the energetic costs of thermoregulation in *Martes* sp. (Iversen 1972, Worthen and Kilgore 1981, Buskirk et al. 1988, Harlow 1994), and T_c = 16°C has been reported for the closely-related and morphologically similar American marten (Buskirk et al. 1988). We found that average T_a associated with resting sites underground (-2.65°C) was significantly lower than that associated with arboreal resting sites (2.95°C) during winter. Furthermore, resting sites were consistently located underground at $T_a < -5°C$, which was consistent with earlier observations (Storch 1988). Although the availability of resting sites was not measured, we did not consider this to be limiting within our study areas. In North America, insulative coarse woody debris associated with old-growth forests is considered a critical, limiting factor for American marten populations (Buskirk et al. 1989). Pine martens in our study areas benefited from the general availability of underground shelter in the rocky glacial till that dominated the substrate in both study areas. We hypothesize that in areas with cold winter temperatures, deep snow and presence of red foxes or other potential predators, the lack of underground shelter and arboreal cavities may limit pine marten distribution and abundance.

Is the pine marten an old forest specialist? (Paper III)

We tested the hypothesis that the pine marten is an old-forest specialist. In general, we found a broad use of forest age classes, which indicated that age of forests did not appear to be an overriding factor in pine marten habitat selection. When we examined use of old forest (> 70 years) by individuals, we found that pine martens used old forest more than available during winter in the VWRA, but not in the GWRA. When these samples were pooled, we found that pine martens consistently used old forest more than available within 95% MCP ranges. During the spring and summer seasons, pine martens did not use old forest more than its availability within individual 95% MCP ranges in either study area, or when study areas were combined. We then pooled observations and expected values for individual martens to further examine use of forest age categories.

In the GWRA, pine martens did not select for old forest relative to younger age classes during either season for active, inactive or pooled locations. In the VWRA, however, pine martens preferred old forest for resting in winter, but otherwise used old forest and younger forest age classes in a similar manner. When seasons were combined, however, we found that pine martens in this study area preferred old forest for resting. A similar result was observed for the pooled sample, which was dominated by inactive locations in this study area.

Further investigation of use of 4 categories of forest age classes showed a similar result with regard to selection of old forest. However, this analysis highlighted the general avoidance of clearcuts, which were avoided during resting bouts and when locations were combined during winter, and generally during spring and summer in both study areas. In the GWRA, pine martens avoided regenerating stands (9-30 years old) while resting and when active and inactive locations were pooled. No such avoidance was observed in the VWRA, where forest age classes were generally used as available, except where otherwise noted. In the GWRA, pine martens selected for middle-aged forest (31-70 years old) during the spring and summer, but no such selection was observed during winter, where stands ≥ 9 years were used as available.

The use of forest age as a habitat variable for analyzing habitat selection by martens may be misleading (Chapin et al. 1997), since elements of forest structure are probably of overriding importance. In our study, the structure of most stands was modified by forest cultivation practices. This was particularly so in the GWRA, where thinning practices had created generally even-aged stands throughout the study area, with the exception of a small 5 km^2 old forest reserve. In the VWRA, many stands > 50 years were in a semi-natural, uneven-aged state, although regenerating stands were generally monocultures, and were often spruce-dominated. Although this paper was intended as a preliminary analysis of marten habitat selection relative to forest age classes, it showed that pine martens in commercial Scandinavian forests were quite capable of using early seres of coniferous-dominated forest. Although some selection of old forest was found, these results refute the general notion that this species is an old-forest species, at least within the context of commercial stands modified by silvicultural practices. We hypothesized that structural elements of forests, rather than forest age as such, probably exert a stronger influence on habitat selection in this species.

Habitat selection by pine martens (Paper IV)

In Paper III, we examined the importance of forest age to pine martens, and concluded that elements of forest structure probably influenced habitat selection. In Paper IV we used dominant tree species and height as indices of forest macrostructure within our study areas in order to further explore habitat selection in this species. Forest age, height, site productivity and dominant tree species were the only common variables between data bases for different forest ownerships in our two study areas. We chose to use dominant tree species height, since it was a function of site index and forest age (cf. Hamilton 1986). Stand height and age were highly correlated, yet many stands $\leq$ 70 years old had attained heights $\geq$ 20 m because of high site productivity indices (cf. Hamilton 1986). Field layer varied with soil type, and in general pine-dominated forest occurred on drier, less productive sites than those of spruce-dominated stands. A rocky glacial till provided an abundance of underground access points for foraging, resting and denning (see Paper II).

We found that pine martens (n = 19) preferred spruce-dominated forest with trees $\geq$ 20 m tall, while avoiding clearcuts (treeless or with trees <1 m tall) and open habitats such as bogs, fields and other treeless habitat. Habitat use did not vary between seasons (winter and summer half-years), sexes, activity modes, or years. Between habitats, pairwise comparisons of selection ratios indicated that spruce-dominated stands $\geq$ 20 m tall were preferentially selected over the lowest ranking habitats (i. e. pine-dominated stands < 20 m in height, clearcuts, open areas and deciduous stands), but were selected in a similar manner to earlier spruce-dominated seres < 20 m tall and pine-dominated stands $\geq$ 20 m tall.

By using tree height, rather than age, we were able to document that our pine martens consistently preferred stands dominated by large spruce trees and avoided open habitats throughout the year. Winter studies in Scandinavia and northwestern Russia (Grakov 1972, Bjärvall et al. 1977, Degn and Jensen 1977, Pulliainen 1981a,c, Wabakken 1985, Eide 1995, Gundersen 1995) also highlight preference for spruce-dominated forest stands which are mature for cutting. American martens also generally select late-successional, mesic coniferous stands with high cover coefficients and avoid areas devoid of tree cover (see reviews in Buskirk and Powell 1994, Buskirk and Ruggerio 1994, Thompson and Harestad 1994).

Pine martens have many enemies, most notably the red fox (Lindström et al. 1995), and habitats such as clearcuts and openings were probably dangerous because of the scarcity of escape cover. The red fox is a habitat generalist, and frequently uses open habitats (Christensen 1985, Hansson 1994, Eide 1995, Gundersen 1995) shunned by pine martens. Storch et al. (1990) found that pine martens did not relax this avoidance of open habitats when an epizootic of sarcoptic mange reduced fox densities in the GWRA (Lindström 1991, Lindström et al. 1994). In a snow-tracking study, Gundersen (1995) found a significant correlation between the ratio of pine marten to red fox track indices relative to the proportion of spruce-dominated forest > 30 years, which may suggest that pine martens are adapted to forests with greater cover and fewer enemies.

Although pine martens occur in regions where spruce trees are absent (Selås 1990b) it appears the proportion and degree of fragmentation of such habitat strongly influenced 95% MCP range size in this study. Mature spruce forests have relatively high cover coefficients, and snow depth, density and hardness are less compared to other habitat types in Scandinavia (Wabakken 1985). In addition, mature spruce-dominated stands are habitat for a number of important prey species (Hansson 1978, 1983, Wabakken 1985, Storch et al. 1990, Swenson 1991, Wegge et al. 1992, Swenson and Anglestam 1993, Andrén and Dehlin 1993, Eide 1995, Gundersen 1995, Rolstad et al. in press). In addition, squirrels nests were important resting sites in our study, and thus the relative abundance of these in mature spruce forest must also make such habitat attractive to pine martens.

Pine martens in our study displayed a flexibility in habitat selection which allowed individuals to exploit the range of relatively fine-grained habitat mosaics relative to their range of movement (see Paper V). Reproduction and survival were probably maximized through preferential utilization of habitats affording the greatest opportunity for foraging, predator avoidance, and shelter (i. e. stands with large, mature spruce trees), and avoidance of those habitats associated with the greatest risks and costs (i. e. clearcuts and open areas).

The influence of habitat quality on pine marten spacing patterns (Paper V)

In order to investigate patterns of spatial use of pine martens relative to habitat and landscape characteristics, we radio-tracked 19 radio-collared individuals captured in our two study areas. We found that these exhibited intrasexual territoriality, similar to other studies on Eurasian martens (Marchesi 1989, Schröpfer et al. 1989, Krüger 1990, Balharry 1991, Clevenger 1993) and American martens (reviews in Buskirk and McDonald 1989, Katnik et al. 1994, Powell 1994). We compared 95% MCP range and core area size between sexes and seasons and found no differences between sexes during either season or when these were combined. Nor did we detect differences between seasons for either sex or for the pooled sample. Overall 95% MCP range size averaged 7.17 ± 4.93 km^2. Core area size did not differ between sexes during summer, although these tended to do so in winter. When seasons were combined, this tendency was strengthened. We detected no differences for core area size between seasons for either sex or the pooled sample, and overall size of core areas averaged 3.22 ± 1.79 km^2. Size of 95% MCP ranges and core areas for both sexes were generally similar in magnitude to those reported in the literature for Eurasian pine martens (Marchesi 1989, Krüger 1990, Balharry 1991, Clevenger 1993c, Zalewski et al. 1995), although home ranges of greater magnitude (up to 82 km^2) have been reported from northern Finland (Pulliainen 1981a, 1984). It should be noted, however, that data on non-resident pine martens were not included in Paper V, and that our unpublished data indicate that wandering pine martens can range from 15-322 km^2 over periods ranging from 2-9 months, and that some individuals (including adults) can shift or abandon home ranges. Our pine martens had a daily movement radius similar to findings from continental Europe (Marchesi 1989, Zalewski et al. 1995) but less than those reported for pine martens in northern Finland (Pulliainen and Heikkinen 1980, Pulliainen 1981a).

Mean distance between consecutive movements ≥ 24 h was 1.47 km, and was not related to the seasonal abundance of bank voles or field voles. Although microtines were the single most important prey category in the winter diet of pine martens in the vicinity of the

GWRA, condition and reproductive potential did not track microtine density (Helldin in manus). Helldin and Lindström (1993) concluded that pine martens do not experience food shortages during microtine lows, since they frequently feed on prey that fluctuate asynchronously with microtines. Our results support this notion, since no clear relationship between microtine abundance and movement patterns was observed in our study areas.

In general, pine martens had lower proportions of open habitats and water within their core areas relative to their 95% MCP ranges and associated local landscapes. The proportion of matrix habitats were similar between core areas and 95% MCP ranges. However, core areas and 95% MCP ranges had significantly lower proportions of pine-dominated forest and regenerating spruce forest compared to local landscapes, which suggests that although pine martens are indifferent to these habitats within 95% MCP ranges, they select against them at the landscape level. In contrast, core areas contained higher proportions of spruce-dominated forest with trees $\geq$ 10 m tall. 95% MCP ranges contained less matrix habitat than local landscapes, and a higher proportion of spruce-dominated forest $\geq$ 20 m in height compared to local landscapes. The amount of mature spruce habitat averaged 39.7 ha within core areas, 73.3 ha within 95% MCP ranges, and 71.2 ha within local landscapes. These observations are consistent with selection displayed by our pine martens for such stands (Paper IV). Although no comparative data are available for Eurasian or American martens, similar relationships with regard to habitat content between home ranges and local landscapes have been reported for the capercaillie (Gjerde and Wegge 1989) and northern spotted owls (Carey et al. 1990).

Our results indicated that total 95% MCP range sizes for individuals varied a magnitude of nearly 15, and that this variation could not be explained by sexual differences or energetic requirements based on body mass (cf. McNab 1963, Harestad and Bunnell 1979). For American martens, Katnik et al. (1994) found no relationship between home range size and body mass for either sex in Maine, and a review by Buskirk and McDonald (1989) found no relationship between male body mass and corresponding home range, although a significant relationship was found for females.

In this study, preferred habitat comprised <30% of the landscape, which suggests that the effects of patch size and isolation may have had an influence on pine marten space use (see

Andrén 1994). Although we found no effect of patch size or isolation on home range size, we found that home range size increased with the degree of elongation and convolution of patches of preferred habitat. Since habitats were relatively fine-grained relative to the mobility of this species the relative proportion of preferred habitat and its configuration appeared to have a strong influence on pine marten home range sizes. We found that sampling duration and landscape variables quantifying the availability and degree of fragmentation of mature ($\geq$20 m in height) spruce-dominated forest explained 70% of the variation in 95% MCP range size. In other studies, home range size was found to be inversely correlated with the size of forest patches for tawny owls (*S. aluco*) in Great Britain (Redpath 1995) and positively correlated with proportion and amount of old forests within home ranges for Mexican spotted owls (*S. o. lucida*) in northern Arizona (Ganey and Balda 1989). Capercaillie cocks compensated for a reduction in the amount of preferred habitat by having larger territories (Wegge and Rolstad 1986). Since territorial spacing may have the effect of regulating population density in *Martes* sp. (Buskirk and McDonald 1989), hypothesized relationships between habitat quality and population density (Van Horne 1983) may apply to the Eurasian pine marten.

Although forest fragmentation may have a detrimental effect on pine marten populations by removing preferred habitat and increasing predation risk, pine martens in our study areas were able to survive and reproduce. Indeed, during our study pine marten numbers were at or near a historical peak as a result of relaxed predation from red foxes (Lindström et al. 1995) and relatively low trapping levels (martens were protected in the GWRA). We suggest that, with the return of red fox numbers to pre-mange levels, as well as the increased interest in trapping this species, the negative impacts of forest fragmentation on pine marten populations may be enhanced.

Conclusions and management implications

This study provides data which indicate that Eurasian pine martens may be susceptible to modern forestry practices. Cavities within mature pine or aspen trees (both living and dead) provided spacious shelter for birthing and rearing neonates and were used nearly exclusively the first two months after birth. Such structures may be critical to pine marten reproduction in areas with relatively dense populations of red foxes. We hypothesize that when rock substrate is lacking, coarse woody debris may fulfill the dual roles of providing subnivean access to prey as well as thermoshelter in Scandinavian boreal forests. Although we do not have empirical evidence to support this hypothesis, data on the ecologically similar American marten (Buskirk et al. 1988, 1989, Corn and Raphael 1992) indicate that these may also be important for *Martes martes*. We therefore suggest that foresters leave dead, fallen trees and large hollow logs on the forest floor after cutting in order to further facilitate prey access and maintenance of energy balance during cold winter periods, particularly in areas where glacial till is lacking.

Removal and fragmentation of mature spruce-dominated forest may expose pine martens to greater predation risk in more open habitats, while simultaneously reducing foraging success and access to secure resting sites. The degree and scale of such fragmentation will undoubtedly have differential effects on this species, in much the same manner as reported for other species (e.g. Ims et al. 1993). Forest fragmentation probably favors prime enemies, including red fox (Christiansen 1979, Christensen 1985, Lindström et al. 1995) and trappers (Hodgman et al. 1994), while simultaneously removing and isolating patches of important habitat. Although further research is needed in order to provide a recipé for forest management planning for this species, our data indicate that maintenance of larger, well-interspersed patches of mature spruce-dominated forests with elements of old-growth forest structure (such as trees and snags with cavities) will likely be beneficial for this and other species exhibiting similar habitat preferences in this region.

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Paper I

The pine marten and forest fragmentation: a review and general hypothesis

Scott M. Brainerd

Brainerd, S.M. 1990. The pine marten and forest fragmentation: A review and general hypothesis. - Trans. 19th IUGB Congress, Trondheim 1989.

Studies show that the Eurasian pine marten (*Martes martes*) is both a food generalist and a habitat specialist, with an affinity for old forest habitats. Martens avoid open areas, such as clearcuts, meadows, and bogs, but may hunt along edges. Both sexes have rigid, intrasexual territories which may vary in size seasonally or annually, or shift completely over time, perhaps as a result of varying food abundance and habitat quality. Several studies indicate that large scale timber harvesting negatively affects the American pine marten (*Martes americana*), where abundance of most preferred food species generally declined within cuts, but the situation in Scandinavia is still unclear, where *Microtus* voles, a seasonally important food source, are abundant in clearcuts. Fine-grained mosaics of clearcuts and old forest may increase food availability to this habitat specialist by increasing edge. In larger-grained mosaics, patches of remnant become increasingly isolated, and pine marten numbers are expected to decrease as a result of habitat loss and decreased accessibility of potential prey within large clearcuts.

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Introduction

The importance of habitat heterogeneity to wildlife species has long been emphasized (Leopold 1933), and is central to the developing discipline of landscape ecology (e.g. Hansson 1979, Harris 1984, Andrén and Angelstam 1988, Rolstad and Wegge 1987, 1989). Until recently, most studies on forest fragmentation effects have focused on the presence and abundance of passerine bird species (e.g. Järvinen et al. 1977, Whitcomb et al. 1981 Helle 1984). Research on the capercaillie (*Tetrao urogallus*), however, highlights the importance of studying forest fragmentation effects on old-forest species with spatial use patterns within the scale of current clearcutting practices (Lindén and Pasanen 1987, Rolstad and Wegge 1987, 1989). As a medium-sized mammal, the Eurasian pine marten (*Martes martes*) is ideal for studying the effects of modern clearcutting practices because the scale of clearcutting falls within the range of daily movement and home range size for this species.

The pine marten is distributed throughout the boreal and boreo-nemoral forests of Eurasia (Nowak and Paradiso 1983). It is preyed upon by golden eagles (*Aquila chrysaetos*, Nyholm 1970, Pulliainen 1981a, Korpimäki and Norrdahl 1989), eagle owls (*Bubo bubo*, Nyholm 1970, Pulliainen 1981a), red fox (*Vulpes vulpes*, Pulliainen 1981a), and lynx (*Lynx lynx*, Jonsson 1983: in Wabakken 1985). The American pine marten (*Martes americana*) occupies a similar niche in North America, and has been more intensively studied, particularly with reference to modern forestry practices (see reviews by Clark et al. 1987, Strickland and Douglas 1988). In Fennoscandia, pine marten numbers have apparently increased in recent years (Lindlöf and Ellström 1980, Swedish Hunting Association Harvest Statistics 1981-88, Järvinen, pers. comm.), perhaps due to decreased competition with red fox (Storch et al. in manus). This increase has occurred despite a concurrent reduction of habitat through clearcutting practices during the same period. In Fennoscandia, clearcutting promotes increased densities of small mammals, particularly the field vole (*Microtus agrestis*: Sonerud 1986, Henttonen 1989) and is hypothesized to have promoted population increases of medium-sized predators, including pine marten (Henttonen 1989). Soviet authors (Larin 1955, Krasovskii 1970, Grakov 1972) have speculated that increased edge in heterogeneous mosaics of clearcut and forest may benefit pine marten, although Grakov (1972) cautions that extensive, large-scale clearcutting may have the opposite effect.

The boreal forests of Fennoscandia have a long history of landscape change, and have been subjected to natural disturbances such as fire and storms for thousands of years (e.g. Zackrisson 1977). Man has also altered the boreal forest landscape through forest cutting, burning, and land-clearing over a period of at least 5000 years (Hämet-Ahti 1983, Tolonen 1987). Perhaps the most dramatic man-induced change, however, has resulted from fragmentation by large-scale modern forestry practices during the past 30 years (e.g. Punkari 1984, Helle 1985, Gamlin 1988). Today, much of the forest land in Sweden, Norway, and Finland is presently in commercial use, and refugia for old-forest dependent species is rapidly diminishing.

This paper reviews current knowledge on Eurasian pine marten ecology and synthesizes effects of timber harvesting on both species. I follow the logic of Pielou (1974) in relating grain-size of fragmented forest mosaics to marten home range sizes, and introduce the idea of "medium grained" mosaics. I conclude with a general hypothesis on the effects of grain-size on pine marten densities in Fennoscandia, suggesting that fine-grained mosaics may be beneficial (edge effects) while larger-grained patterns may have a negative effect (habitat loss).

Martes martes in the forested landscape: a review

A food generalist.- The Eurasian pine marten is an opportunistic, omnivorous predator (Höglund 1960, Lockie 1961, Nyholm 1970, Morozov 1976, Pulliainen 1981b, Warner and O'Sullivan 1982, Wabakken 1985, Debieve et al. 1987, Reig and Wlodzimierz 1988, Marchesi and Mermod 1989, Storch et al. in manus), concentrating primarily on small mammals and birds. Food choice is apparently determined by what is abundant and accessible (Storch et al. in manus) as is the case for the American pine marten (Weckwerth and Hawley 1962). Most food habit studies are based on analyses of scats collected during snow-tracking in winter and early spring, although some include data from summer and/or autumn (Lockie 1961, Nyholm 1970, Warner and O'Sullivan 1982, Marchesi and Mermod 1989, Marchesi 1989b, Storch et al. in manus).

Small mammals are generally the most common prey (Nyholm 1970, Pulliainen 1981b, Reig and Wlodzimierz 1988, Marchesi and Mermod 1989, Storch et al. in manus), and pine marten numbers appear to fluctuate with their densities (Pulliainen 1981c), although not drastically as in smaller mustelids. The relative importance of bank voles (*Clethrionomys glareolus*), field voles, and wood mice (*Apodemus sylvaticus*) varies regionally, annually, and seasonally. Bank voles are an important food source, particularly during winter (Pulliainen 1981b, Wabakken 1985, Reig and Wlodzimierz 1988, Marchesi 1989b, Storch et al. in manus). Field voles may be seasonally important (Pulliainen 1981b, Storch et al. in manus) and are the primary prey in Scotland (Lockie 1961), and wood mice are occasionally taken where they occur (Lockie 1961). Squirrels (*Sciurus vulgaris*) are an important food when abundant (Höglund 1960, Nyholm 1970, de Jounge 1981, Pulliainen 1981b, 1984a, Wabakken 1985). Shrews (Sorcidae) are often eaten, though the relative importance varies from study to study (Höglund 1960, Wabakken 1985, Debieve et al. 1987, Marchesi 1989b, Storch et al. in manus) and from year to year within study areas (Storch et al. in manus). In Soviet Karelia, Morozov (1976) found that female marten stomachs contained twice the amount of squirrel remains as those of their male counterparts. Norwegian lemmings (*Lemmus lemmus*) are taken in northern Finland (Pulliainen 1981b). Hares and rabbits (Leporidae) are occasionally eaten (Nyholm 1970, Pulliainen 1981b, Warner and O'Sullivan 1982, Marchesi and Mermod 1989, Storch et al. in manus), and are an energetically important food during winter in some North American studies (Bateman 1986, Thompson and Colgan 1987a).

Birds are eaten by pine martens, but rank lower than small mammals in most food studies. Tetraonids are preyed upon (Morozov 1976, Pulliainen 1981b), such as capercaillie (Wegge et al. 1987), hazel grouse (*Tetrastes bonasia*, Wabakken 1985), ptarmigan (*Lagopus lagopus*, Wabakken 1985), and in some cases marten take significant numbers (Wegge et al. 1987, Swenson pers. comm.). Nesting owls and their young are eaten in nesting cavities, including Tengmalm's owls (*Aegolius funereus*, Baudvin et al. 1980, Sonerud 1985a,b), tawny owls (*Strix aluco*, Baudvin et al. 1980), and hawk owls (*Surnia ulula*, Sonerud 1985b) are sometimes eaten, although none of these species are apparently primary sources of nourishment. The same holds true for woodpeckers, including black woodpeckers (*Dryocopus martius*, Wabakken 1985). Forest passerines (Passeriformes) are utilized (Lockie 1961, Nyholm 1970, Balat 1971a,b, Pulliainen 1981b, Warner and O'Sullivan 1982, Wabakken 1985, Mermod and Marchesi 1989, Mermod 1989b, Storch et al. in manus), particularly during summer, although in Ireland the highest proportion of avian prey, including passerines, occurred in winter (Warner and O'Sullivan 1982). Pine martens eat eggs throughout the year (Höglund 1960, Lockie 1961, Nyholm 1970, Morozov 1976, Pulliainen 1981b, Wabakken 1985, Warner and O'Sullivan 1982, Debieve et al. 1987, Marchesi and Mermod 1989, Marchesi 1989b, Storch et al. in manus), suggesting that these are cached for winter consumption (Höglund 1960).

Insects, amphibians, fish, vegetable matter, and carrion supplement the pine marten diet, sometimes to a large extent (Höglund 1960, Lockie 1961, Nyholm 1970, Morozov 1976, Pulliainen 1981b, Warner and O'Sullivan 1982, Marchesi and Mermod 1989, Marchesi 1989b, Storch et al. in manus). In northern Finland, berries (*Vaccinium* spp.) and mushrooms (e.g. *Rhizopogon rubescens*) were an important early winter food, and cervid carcasses were utilized throughout the snow season (Pulliainen 1981b). In Switzerland, fruits (such as *Sorbus* and *Rosa*) were ranked second only to small mammals in proportions consumed (Marchesi 1989b). Frogs (*Salentia*) and lizards (*Squamata*) are consumed during summer (Nyholm 1970, Morozov 1976).

A habitat specialist.– The common name "pine marten" implies a preference for pine (*Pinus* spp.) forests not born out in most studies. In Fennoscandia and the Soviet Union pine marten prefer mesic spruce (*Picea* spp.)-dominated coniferous or mixed coniferous-deciduous forests (Grakov 1972, Bjärvall et al. 1977, Degn and Jensen 1977, Pulliainen 1981a, Nesvadbova and Zedja 1984, Wabakken 1985, Storch et al. in manus, Marchesi 1989a,b). Such spruce forests are often characterized by high overstory canopy coverage (Wabakken 1985). Lowland deciduous forests are important in Switzerland, however (Marchesi 1989b), and supported higher pine marten densities than coniferous forests at higher elevations. In Fennoscandia and the northern Soviet Union, pine forests of all age classes are avoided (Grakov 1972, Pulliainen 1981a, Wabakken 1985). In northeastern Poland, however, pine marten tracks were mainly located in mesic pine forests (Fedyk et al. 1984), and it appears that mesic sites with lush undergrowth may influence use of habitat. Open areas, such as naturally occuring bogs and meadows, as well as clearcuts, are avoided during winter (Grakov 1972, Pulliainen 1981a, Fedyk et al. 1984, Wabakken 1985, Storch et al. in manus, Krüger 1989, Marchesi 1989a,b,), and openings wider than 200 m are rarely crossed (Pulliainen 1981a, 1986). Preliminary results from telemetry research indicate that openings are also avoided during early summer (Storch et al. in manus). Marchesi (1989a,b) and Grakov (1972) indicate that forest edges are often used. These results are in general agreement with findings for American pine marten (see reviews by Allen 1982, Clark et al. 1987, Strickland and Douglas 1988, Buskirk 1989), although it should be noted that increased use of clearcuts is observed during late summer (Soutiere 1979).

The role of food resources.– In Fennoscandia, use of spruce-dominated coniferous and mixed forests may partly be explained by presence of common food items, such as bank voles, squirrels, and forest grouse (Wabakken 1985). However, many prey species display much wider habitat preferences, or are more associated with open areas (Wabakken 1985). Old forests, particularly spruce forests, have lush canopy coverage which influences the character and depth of snow. In Norway, decreased snow hardness and depth in older spruce forests may have facilitated excavation of small mammals (Wabakken 1985). Grakov (1972) found a link between microhabitat structure and spruce forests, stating that access to small mammals, berries, and insects was increased by deadfall trees and branches, which were generally lacking in adjacent pine forests. Subnivean access points created from woody debris or broken, rocky substrates, allow pine martens access to food in clearcuts (Grakov 1972), and cavities in trees allow access to nesting bird species (e.g. Sonerud 1985a,b). Pine marten may hunt along edges between forest and openings (Grakov 1972, Marchesi 1989a,b) which may explain consumption of species usually found in open areas, such as field voles. In North America, heterogeneous mosaics, such as those created by fire, may increase food abundance, habitat diversity, and edges which may benefit pine martens (Koehler et al. 1975, Koehler and Hornocker 1977, Stephenson 1984).

The distribution of food items probably influences pine marten habitat selection. Wabakken (1985) found that bank voles, which were highly preferred, were most abundant in old spruce forests frequented by pine martens. Consumption of certain rodent species common in open areas, such as field voles (Lockie 1961, 1964, Pulliainen 1981b), lemmings (Pulliainen 1981b), or others (e.g. *Pitymys* spp., *Arvicola terristris*: Mermod and Marchesi 1989) suggests that pine marten either venture into these open areas, or conversely, that these species invade forest interiors during population highs. Lockie (1961) discovered that pockets of this species were scattered equally in woodlands and open meadows, which may partially explain their high occurrence in his study. In a similar situation in Alaska, Buskirk and MacDonald (1984) hypothesize that American marten concentrate on *Microtus* species associated with meadows over forest-dwelling *Clethrionomys* voles due to the clumped distribution of the former, which would thereby maximize foraging efficiency. Storch et al. (in manus) found that although field voles were entirely absent from the winter diet of Swedish pine martens, both field and bank voles occurred in equal proportions in most early summer scats, implying perhaps increased availability during snow-free seasons. The occurrence of cavity-nesting birds in the diet (including their eggs and nestlings) suggests that marten may actively search tree cavities for these species. Similarly, seasonally abundant vegetable or invertebrate foods may also influence habitat selection.

The role of cover.– Microhabitat features are important for denning, thermoregulation, foraging, resting, and escaping enemies. Denning sites are typically in tree-cavities, rock cavities, or squirrel's nests (Selås 1990, and unpubl. data, Grimsö Wildlife Research Station). Thermal cover provided by underground dens seems to be especially important in winter (Storch 1988), probably due to the low insulative properties of pine marten fur (Buskirk et al. 1988). Hollow snags are of such overriding importance as natal dens that they may be used in open areas without canopy coverage (unpubl. data, Grimsö Wildlife Research Station). Rocky substrates allow pine marten escape cover throughout the year, and allow access to prey (unpubl. data, Grimsö Wildlife Research Station). Boreal pine forests do not appear to have the same level of complex understory structure needed for shelter and subnivean access (Grakov 1972), although cavities in large pines may occasionally be used for denning and resting (Selås 1990, and unpubl. data: Grimsö Wildlife Research Station). Similarly, the American pine marten prefers lush coniferous forests on mesic sites, with high canopy coverage and a diverse microhabitat structure for food access, resting and denning (e.g. Allen 1982, Clark et al. 1987, Strickland and Douglas 1988, Buskirk 1989).

The pine marten may be susceptible from attack by avian predators during winter because its dark coloration (Pulliainen 1981a), unlike other closely related mustelid species (e.g. *Mustela nivalis*, *M. erminea*). Pine marten may also be exposed to attack by mammalian predators, such as fox and lynx, in areas without tree cover normally used by pine marten as escape cover (e.g. Storch et al. in manus, Jonsson 1983: in Wabakken 1985). Increased use of clearcuttings in late summer by American pine marten (Soutiere 1979, Steventon and Major 1982) may be related to increased vegetative cover, which perhaps serves as cover from both avian and mammalian predators. A variety of mammalian and avian predators also prey irregularly on the American pine marten (e.g. Clark et al. 1987, Strickland and Douglas 1988), which may explain similar behaviors of open area avoidance in this species (Thompson, pers. comm.).

Spacing patterns and movements.- Adult, resident pine marten (Weckwerth and Hawley 1962) display a typical mustelid spacing pattern with a high degree of intrasexual intolerance (Storch 1988, Krüger 1989, Schröpfer et al. 1989, Marchesi 1989b) and utilize scent marking to a large extent (Pulliainen 1982, 1984b). Male territories are often larger than those of females (Storch 1988, Schröpfer et al. 1989, Krüger 1989) and more than one female territory may be included within a male territory (Krüger 1989, Marchesi 1989b). Pulliainen (1982, 1984b) suggests that pine marten are not truly territorial because they tended to scent-mark throughout their ranges, not just at the edges as would be expected with a truly territorial species (e.g. Thompson and Colgan 1987b). I disagree with this premise because the fox, which is also regarded as territorial, likewise scent-marks throughout its territory (Macdonald 1987, Lindström, pers. comm.).

Home range estimates from snow-tracking vary from 3-82 km² (Nasimovic 1948: in Pulliainen 1981a, Pulliainen 1981a, 1984b), and it seems probable that the larger ranges were actually those of dispersing juveniles, since these animals achieve full body size by the age of 6 months (Marchesi 1989b). Few telemetry studies on Eurasian pine marten are available, but published results show that home ranges in heterogeneous environments are approximately 9-20 km² for males and 2-10 km² for females (Storch 1988, Krüger 1989, Marchesi 1989a,b, Schröpfer et al. 1989). Daily movements cover an average of 4-7 km (Pulliainen 1981a, Marchesi 1989b), and the longest recorded daily movement was 29.2 km (Pulliainen 1981a). Long-distance movements range from 28-65 km (Nyholm 1970, Pulliainen 1981a).

Topography and habitat heterogeneity appear to exert strong influences on movements and home range size (North America: Clark et al. 1987, Thompson and Colgan 1987a,b, Strickland and Douglas 1988; Eurasian pine marten: Lockie 1964, Marchesi 1989a,b). Buskirk and MacDonald (1989) discuss the ecological significance of home range size in American pine marten, and hypothesize a strong relationship between site conditions and home-range size in such habitat specialists with low reproductive capacity. Home range size may fluctuate seasonally (Storch 1988, Krüger 1989, Marchesi 1989b, Schröpfer et al. 1989), and is probably related to food limitation in winter (Schröpfer et al. 1989) and breeding and denning activity in summer (Storch 1988, Krüger 1989). Male marten sometimes change home ranges over time (Schröpfer et al. 1989, Marchesi 1989b). Annual changes in home range size in Ontario were attributed to fluctuating numbers of important prey species (Thompson and Colgan 1987a,b). Reafforestation has apparently aided the recent invasion of pine marten into new areas in Ireland (O'Sullivan 1983) and Scotland (Lockie 1964), and habitat corridors, such as wooded strips and hedges were essential links between habitat islands in a patchwork of forest islands and agricultural fields in Switzerland (Marchesi 1989a,b).

Foraging behavior seems to have a set pattern within a given home range (Marchesi 1989b). Swiss pine marten use a combination of exploratory, randomized searching coupled with a tendency to concentrate in "core areas", similar to that found by Thompson and Colgan (1987b). In North America, male and female marten partition joint territories by foraging in different, exclusive core areas within them during periods of food scarcity (Thompson 1986). Marten usually hunt at night during the winter (Pulliainen 1981a, Marchesi 1989b), but shift to a more diurnal schedule during summer months.

Population trends.- Population trends in Eurasian pine marten populations are difficult to assess, and the only long-term data available are from harvest reports, which do not include measures of relative trapping effort. In Scotland, pine marten numbers gradually increased in the early twentieth century after near extermination by gamekeepers during the previous one hundred years (Lockie 1964), and in fact, Langley and Yalden (1977) noted that extinction of the pine marten from most of its range in Great Britain was related to intensive eradication efforts by gamekeepers, rather than deforestation. American pine marten populations are sensitive to harvest pressure and can easily be exterminated from areas if trapping is unregulated (see reviews by Clark et al. 1987, Strickland and Douglas 1988). Apart from human influences, pine marten populations in Eurasia also fluctuate naturally, probably in response to environmental factors (Lockie 1964), such as food supply (Pulliainen 1981c), similar to findings in North America (Thompson and Colgan 1987a, Hawley and Newby 1957).

In Sweden, marten were protected during from the mid-1930's to the mid-1950's after overtrapping had nearly exterminated the species from many areas. When harvests resumed, records show a slow, steady increase in fur take of this species until decimation of the fox population by sarcoptic mange in the late 1970's (Lindström and Mörner 1985), when take increased dramatically (Fig. 1). Storch et al. (in manus) hypothesize that this rapid increase in the pine marten harvest was a result of released predation and competitive pressure from the red fox. The increase in observations of free-ranging pine marten by field biologists working at Grimsö Wildlife Research Station, Sweden, during the period 1974-1989 corroborate these harvest statistics, suggesting that there actually was a population increase and not just intensified trapping pressure on marten (Lindström, pers. comm.). A similar increase in pine marten abundance has occurred in Finland (Järvinen, pers. comm.).

In the northwestern Soviet Union, an increase in pine marten harvests occurred during the post-war period (Larin 1955), and peaked in the early 1960's (Grakov 1972), concurrent with a major intensification of large-scale timber harvesting. Krasovskii (1970) found a positive correlation between pine marten fur purchase and wood export figures from the northern European Soviet republics, and hypothesized that pine marten populations were increasing as a result of increased small mammal abundance in clear-cuts. However, Grakov (1972) points out that this correlation was artificial, noting that wood exports and number of pine marten pelts sold were both declining as remaining forest area declined. Grakov (1978) discusses long-term changes in the abundance of pine marten in the Soviet Union, noting that populations decreased during periods of heavy harvest, and increased during periods of partial or total protection from trapping.

The effects of timber harvesting

North American studies.- The only published, empirical accounts of timber harvesting effects on pine marten are from North America. Canadian research has focused on the effects of coarse-grained, sequential cutting practices where extensive tracts of forest have been removed in Newfoundland (cuts up to 1600 ha, Snyder and Bissonette 1987) and Ontario (cut sizes 200-600 ha, with contiguous cuts up to 5000 ha, Thompson and Colgan 1987a,b). In the United States, studies in Maine (Soutiere 1979, Steventon and Major 1982) compared an extensively fragmented site (2570 ha, with 50% clearcut, 25% selectively-cut) with a study site comprised of undisturbed and selectively-cut forests (1760 ha). During a three year period, selective-cutting reduced

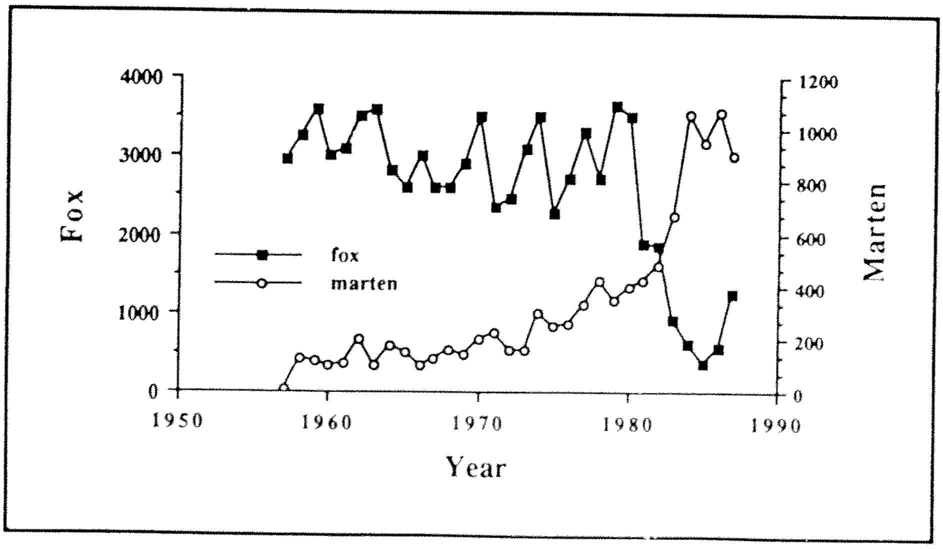

Fig. 1. Harvest of pine marten and fox from Gävleborgs län. Sweden, 1957-1988 (Lindlöf and Ellström 1980, Swedish Hunting Association Harvest Statistics 1981-88).

the proportion of undisturbed forest from 79% to 31%. In Wyoming, an experimental study was conducted comparing a lightly fragmented study area (one 9.6 ha clearcut and 5 selective-cuts ranging from 8.1-75.0 ha) with relatively undisturbed coniferous forest within Grand Teton National Park (Campbell 1979, Clark and Campbell 1979, Clark 1984).

American pine marten generally avoid foraging in clearcuts throughout the year (Campbell 1979, Clark and Campbell 1979, Soutiere 1979, Steventon and Major 1982, Clark 1984, Snyder and Bissonette 1987), although increased use of these areas has been observed in late-summer when higher vegetative cover, availability of raspberries (*Rubus idaeus*), and greater seasonal availability of vertebrate prey such as ground-nesting birds and small mammals, were probably important factors. (Soutiere 1979, Steventon and Major 1982).

This general avoidance of clearcuts is apparently linked to lowered abundances of southern red-backed voles (*Clethrionomys gapperi*), an important prey species, up to 15 years after cutting (Soutiere 1979, Steventon and Major 1982, Martell 1983). This avoidance is most pronounced in winter, when snow depths generally limit prey availability (Steventon and Major 1982). In general, the pattern of replacement of *Clethrionomys* species with *Microtus* species in young, regenerating cuts is similar to that of Fennoscandia, although densities of *Microtus* in North America may not be as high as those of related species in Europe (see Martell 1983, Thompson 1986, Sonerud 1986, Henttonen 1989). In north-central Ontario, the diet of pine martens in fragmented landscapes is dominated by grouse and *Microtus* rodents, whereas martens in uncut landscapes concentrate on *Clethrionomys* (Thompson 1986). In this same region deer mice (*Peromyscus maniculatus*), a species seldom used by martens, invade clearcuts as these become more xeric (Martell 1983).

Foraging activity in areas fragmented forests is concentrated in remnant patches of mature coniferous stands (Soutiere 1979, Steventon and Major 1982, Thompson and Colgan 1987b, Snyder and Bissonette 1987). In Newfoundland, pine marten selected larger patches of residual coniferous stands and avoided patches less than 15 ha (Snyder and Bissonette 1987). In Maine, pine marten were captured within the entire size range (0.3-13.5 ha) of coniferous forest islands within clearcut forests (Soutiere 1979); males were captured in the most isolated stands, whereas females were captured almost exclusively in and adjacent to larger blocks of uncut and selectively-cut forest. In Ontario, Thompson and Colgan (1987b) found that preferred foraging sites, or core areas, are significantly further apart in cutover landscapes than in adjacent, uncut stands. Travel speeds between core areas were likewise higher in these cut areas, and hunting success was diminished.

Clearcuts may act as sinks (e.g. Pulliam 1988) for dispersing juvenile pine marten. In Ontario, average ages of live-captured and trapper-killed pine marten in cut areas were significantly lower (1-2 years old) than those caught in unfragmented forest (3 years old: Thompson and Colgan 1987b). The fact that Thompson (pers. comm.) found that some young pine marten had their entire home ranges within large cuts suggests that dispersing pine marten are forced into marginal habitat. Transient pine marten, usually juveniles, do not appear to actively select habitats to the same extent as resident, adult pine marten (Soutiere 1979). This suggests that juveniles spend more time in clearcuts because 1) they are displaced by adults in optimal, forested habitats, or 2) they have not developed an efficient foraging pattern, or 3) they explore all possibilities for available space for territory establishment, or 4) some combination of these factors. One would expect the average dispersal distance to be greater, and more variable, in fragmented forests with lower available space than in more homogeneous, undisturbed forests.

Coarse-grained clearcutting lowers pine marten densities (Soutiere 1979, Thompson and Colgan 1987a), but small clearcuts do not appear to alter home range sizes (Campbell 1979, Clark and Campbell 1979, Clark 1984). Home range lengths were similar in undisturbed and selectively-cut stands, but longer in clearcut stands in Maine (Soutiere 1979). In Ontario, home ranges were significantly larger for both sexes in mosaics of coarse-grained clearcuts and mature coniferous forest (Thompson and Colgan 1987b). In Newfoundland, pine marten numbers remained low in an extensively clearcut region despite the fact that trapping had been banned for over 50 years (Snyder and Bissonette 1987).

The above studies have generated some recommendations to managers responsible for maintaining pine marten and other forest species in commercial forests. Snyder (1984: in Strickland and Douglas 1988) recommended to foresters that distances between isolated blocks should not exceed 250 m, with uncut strips 0.1 km wide along waterways to allow communication between patches. In Maine, Soutiere (1979) proposed that clearcutting should be done in small blocks or patches, and that at least 25% of the remaining area be retained in forest cover of at least 25 m^2/ha of pole stage and larger trees. In their review, Clark et al. (1987) state that contiguous optimum habitats of 150 km^2 should be connected to smaller habitat patches by corridors of at least mariginal habitat. They further state that clearcutting should be minimized, and be replaced with selective-cutting to maintain canopy coverage and mesic conditions. Dead standing and leaning trees and snags, and woody debris associated with logging should also be preserved for foraging, resting, and denning (Clark et al. 1987).

The overall suggestion from these studies is that widespread, coarse-grained clearcutting is detrimental to pine marten populations in North America. However, Koehler et al. (1975) remind us that not all disturbances are necessarily bad for American pine marten, noting that interspersion of younger seral stages within an old forest mosaic may be beneficial. They state that small disturbed areas may require less time to reestablish cover and food, and that small clearings would be less restrictive to pine marten movements in winter. They argue that a diversity of communities provides a variety of food throughout the year and a continuing replacement of habitat over time.

Eurasian studies.– At present, evidence indicates that Eurasian pine marten generally avoid clearcuts and open areas, even during snow free periods. In Switzerland, pine marten avoided open areas, including agricultural areas and all but the smallest forest clearings (Marchesi 1989a,b), but isolated, remnant forest patches were utilized if connecting corridors were present. Grakov (1972) reviewed Soviet literature on effects of clearcutting on pine marten in the USSR, noting that pine marten tracks are least frequent in clearcuts < 10 years old. In general, pine marten tracks were most common in spruce forests, less common in clearcuts, and the least common in deciduous stands.

Clearcutting increases small mammal densities in Fennoscandia, by replacing territorial bank voles, which dominate old mesic forests, with high densities of non-territorial field voles (Sonerud 1986, Henttonen 1989). Both species are important to pine marten, and the suggestion made by Henttonen is that the food base for small and medium-sized predators has greatly increased as a result of modern forestry practices. Where open areas are juxtaposed with old forest patches, pine marten numbers may be maximized due to their tendency to forage near edges. In the Soviet Union, it has long been suspected that smaller clearcuts create a heterogeneous mosaic beneficial to pine marten, primarily by increasing edge and thus improving foraging (Larin 1955, and Romanov 1956, 1961: in Grakov 1972). Synchronous denudation of extensive tracts of taiga lead to substantial reductions in both pine marten and squirrel densities (Grakov 1972).

A few investigations have compared pine marten densities in different landscape types. In Scandinavia, Bjärvall et al. (1977) found that densities were 2–3 times higher within a national park dominated by uncut, old forest than in a surrounding area, where forests were harvested, although relative grain-size or proportions of cut and uncut forest in the experimental study area were not described. Grakov (1972) likewise demonstrated that pine marten densities and capture rates decreased when 25–35% of the virgin forest area was removed. Aspisov (1959: in Grakov 1972) found that pine marten densities increased with plantation age (0.6/1000 ha in young plantations, 2.8/1000 ha intermediate woods, 3.7/1000 ha in mature plantations), although what forest types were involved is unclear. Larin (1955) found that marten tracks along transects were less abundant in areas of recent forest cutting (0.3/km) than in uncut areas with edge created through natural interspersion of forest and bogs (0.6/km). On two islands in the Baltic Sea, pine marten densities during periods without control averaged about 1.1-1.7/1000 ha on Bergön (1800 ha) and between 1.2-1.7/1000 ha on Rånön (2350 ha) during an experimental study involving periods of total removal of this species; the maximum number caught on the latter island was six (2.5/1000 ha: Marcström et al. 1989). Both islands are forest covered, and clearcuts (<20 years) cover 10-15% of Rånon and 30-35% of Bergön. A questionnaire survey in Czechoslovakia gave a rough estimate of about 6 pine marten/1000 ha (Nesvaboda and Zejda 1984) in managed forests.

There is little direct evidence for displacement of juveniles into marginal habitat. A subadult female pine marten was found to be crossing relatively large distances over open areas to access adjacent forest blocks within its territory, unlike older animals, in an ongoing telemetry study in West Germany (Krüger 1989, and pers. comm.).

The effects of clearcutting on pine marten in northern Eurasia are still unclear, but the following points may be made: 1) relative abundance of potential prey (*Microtus*) increases greatly in regenerating clearcuts, 2) pine marten avoid openings during winter, but use forest edges, 3) marten densities generally appear lower in clearcut areas, although we have no information on relative grain-size of cuts. This information, coupled with the observed increase in pine marten numbers in Fennoscandia, can be used in formulating a general hypothesis on the effects of modern forestry practices on *Martes martes*.

A general hypothesis: Fragmentation, grain-size, and pine marten densities in Fennoscandia

As a habitat specialist, Eurasian pine marten are apparently linked to stands of older, coniferous forests on mesic sites. Food resources within such forests are lower than in regenerating clearcuts, although they may be relatively more available during winter snow periods. In some studies, field voles are an important element in the diet, which increase dramatically within clearcuts. Pine marten are generally opportunistic foragers, and feed on a wide variety of food items. Presumably, edge and interspersion of habitats are therefore beneficial to pine marten. Edges are important for foraging pine marten in Switzerland, and this implies a certain optimal balance between open areas and old, coniferous forest stands. On the other hand, synchronous denudation of large tracts of coniferous forest should, in general, be highly unfavorable, due to removal of cover required for escape from predators, foraging, denning, and resting (thermal regulation in winter).

I propose that pine marten populations respond differentially to varying grain size of cutting patterns (Fig. 2). As an example, I assume that a large, homogeneous, spruce-dominated coniferous forest containing a viable population of pine marten is evenly fragmented, with cuts of equal size and an even interspersion of forest blocks. Then 55% of the forest area is arbitrarily removed in an instantaneous fashion, such that the landscape is dominated by open area without regenerating trees (although it is doubtful that such extreme cases exist in Fennoscandia, the relatively high rate of clearcutting in northern Sweden in recent years approaches 30% (Angelstam, pers. comm.)). At small, fine-grained cut sizes, habitat may be more favorable to pine marten, and thus support higher densities than in the original, lesser productive old forest. In such situations, close

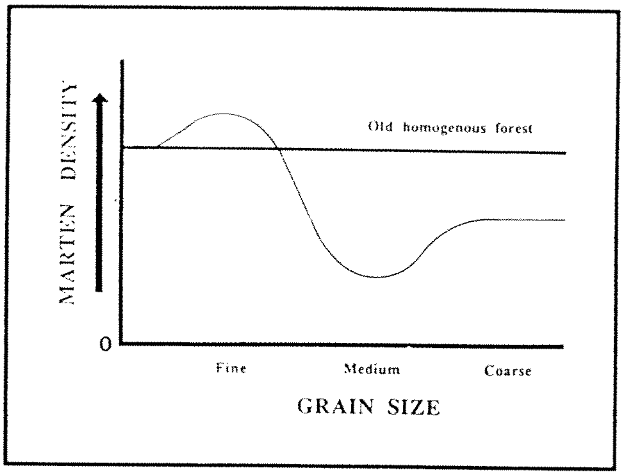

Fig. 2. A generalized model predicting differing pine marten densities relative to varying grain sizes of an evenly dispersed system of recent cuts and old forest, with 55% of the old forest area removed by clearcutting (see text for full explanation).

interspersion of small clearcuts and forest blocks increase forest edge, and allow easy travel between forest patches. Thus pine marten can at once enjoy an increased food supply of small rodents and seasonally abundant insects, passerine birds, and berries along forest edges while retaining important habitat for the reasons already discussed. As cut size increases, patches of remaining forest become increasingly dispersed within a pattern dominated by large clearcuts, and travel between these forest patches, which are important for foraging and shelter, becomes more restricted. If remnant forest stands are too small to support individual, territorial pine marten, and distances between them are relatively large (> 500 m, for example), such a "medium-grained" situation may support few animals. If on the other hand, remnant forest blocks are large enough to support several pine marten, a linear relationship between remnant forest area and pine marten densities may exist. In other words, adult pine marten living in such large forest blocks surrounded by extensive clearcuts should have territory sizes similar to those in large homogeneous tracts of coniferous forest.

I seek to illustrate the possible effect increased prey biomass may have on a generalist predator with specialized habitat requirements. The fine-grained mosaic represents a situation where edge effect is important, and food, rather than habitat, dictates abundance. The medium- and coarse-grained patterns represent situations where habitat becomes limiting, due to the specialized needs of pine marten, despite increased biomass of important prey species, such as *Microtus*. Such a model may help to explain increases in pine marten densities in northern Europe prior to the fox decline. It also fits well with the premise of many researchers that large clearcuts have a detrimental effect on pine marten densities.

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Paper II

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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, hollow 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^2) 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^2. 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 ± 20.60 days, $x \pm SD$, $n = 218$) and females (6.29 ± 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[1]	Arboreal cavity[2]		Arboreal structure[3]		Underground structure[4]		Ground structure[5]		Total
		n	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*
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

[1] Number of martens in parentheses, [2] Cavities in live aspens or pine trees, or rotten snags of either species, [3] 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 ($n = 38$), [4] Usually located in rocky substrate ($n = 163$), but also in the root system of a pine tree ($n = 3$) and a stump ($n = 1$), [5] Stacks of cut logs.

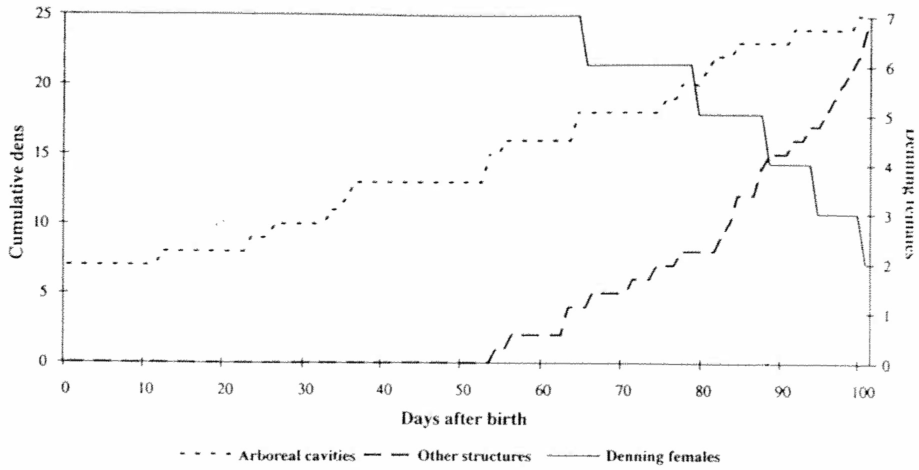

Fig. 1. Cumulative use of arboreal cavities and other structures relative to the number of denning female pine martens at Grimsö, Sweden (n = 4 martens, n = 65 relocations) and Varaldskogen, Norway (n = 3 martens, n = 44 relocations)during 1987–1991.

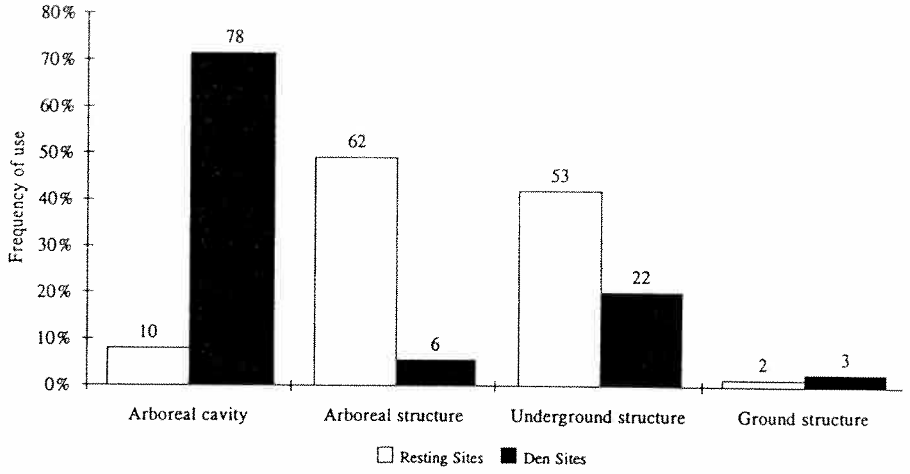

Fig. 2. Relative use of different structures as resting and denning sites by pine martens at Grimsö, Sweden and Varaldskogen, Norway during the spring/summer season (1987–1991).

(*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 ± 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

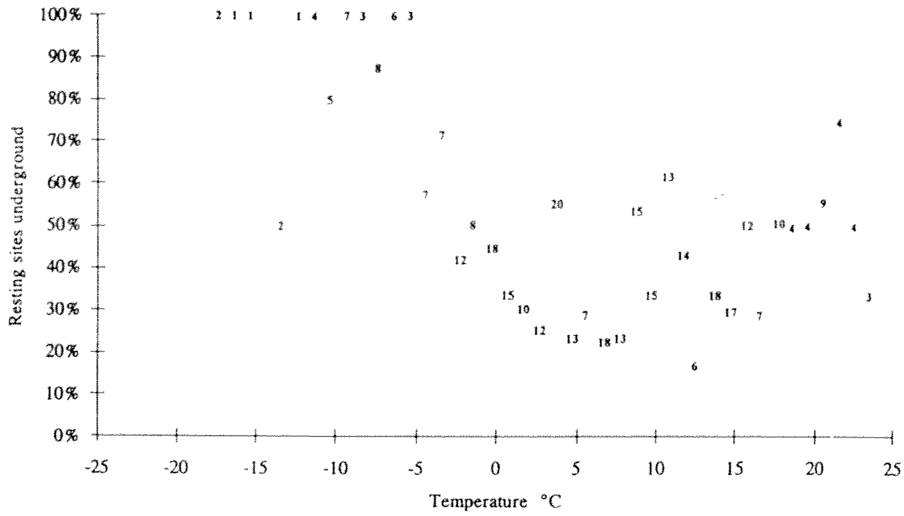

Fig. 3. Frequency of use of underground sites by pine martens at Grimsö, Sweden and Varaldskogen, Norway (1987–1991) relative to T_a T_a is expressed in whole iincrements, and sample points are represented by their respective sizes..

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 (Ahola & 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 syudy, 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*	*n*	Mean T_a	*SD*	*n*	*U*	*P*[1]
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

[1] 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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Paper III

25 Eurasian Pine Martens and Old Industrial Forest in Southern Boreal Scandinavia

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Erik Lindström, and Jørund Rolstad

The rapid conversion of Fennoscandian boreal forests from relatively natural forests to a mosaic of uniform monocultures of coniferous trees has awakened concern over the fate of a variety of forest-adapted species (Punkari 1984, Helle 1985, Gamlin 1988, Baskin 1990). In boreal Eurasia, pine martens (*Martes martes*) are often associated with old stands of coniferous forest (Aspisov 1959, Grakov 1972, Bjärvall et al. 1977, Wabakken 1985, Storch et al. 1990). In Sweden and Russia, snow-tracking censuses indicated that densities of marten tracks were higher in tracts of undisturbed, old virgin forests than in surrounding areas fragmented by large-scale clear-cutting (Aspisov 1959, Grakov 1972, Bjärvall et al. 1977, Jonsson 1992). These studies support the notion that old coniferous forests are important habitat for pine martens. In Scandinavia, popular accounts (e.g., Selås 1990*a*) imply that this species is an old-forest specialist, on the basis of these studies and research on the closely related American marten (*M. americana*: see reviews by Clark et al. 1987; Strickland and Douglas 1987; Bissonette et al. 1989; Thompson 1991; Buskirk and Powell, this volume; Thompson and Harested, this volume) and sable (*M. zibellina*: review in Baskin 1990). Since the 1960s, however, Eurasian pine marten numbers have increased markedly in Russia (Grakov 1972, Baskin 1990) and Fennoscandia (Krott and Lampio 1983, Storch et al. 1990, Helldin and Lindström 1991) despite continued clear-cutting and intensified forest management. Indeed, increased prey biomass in clear-cut areas (Hansson 1978, Sonerud 1986, Henttonen 1989) may have benefited martens and other medium-sized predators, thus offsetting the negative effects of forest removal to some extent (Romanov 1956, Krasovsky 1970, Henttonen 1989, Baskin 1990, Brainerd 1990).

The structural characteristics associated with old virgin forests (snags, woody debris, large trees with cavities, abundant shrub layer, diverse vertical structure) may be less abundant in managed forests. In southern boreal Scandinavia, however, forestry practices often create an abundance of dead and rotting stems, branches, and stumps in younger forests (Hansson 1978; Majewski and Rolstad, in preparation). Such structural components may be analogs of the physical structure of virgin forest.

As part of a broader ecological study on Eurasian pine martens in the industrial forests of southern boreal Scandinavia, we investigated the use of different age classes of coniferous forests during 1987–1991. In this chapter we address the widely held notion that the Eurasian pine marten is an old-forest specialist by testing for its preference for old seminatural stands of industrial coniferous forest.

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 south-central Sweden, and our efforts were restricted to the southern portion (50 km^2) of the study area. Varaldskogen Wildlife Research Area (60°10′N, 12°30′E) is located on the Norwegian-Swedish border 175 km west of Grimsö and covers 100 km^2. Grimsö is relatively flat (75–125 m elevation), whereas the topography at Varaldskogen is more hilly, varying between 200 and 400 m elevation. Both areas are dominated by commercial stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Stands dominated by deciduous trees are rare, but birch (*Betula pubescens*), alder (*Alnus incana*), and aspen (*Populus tremula*) are sometimes present in coniferous stands. Bogs and agricultural fields are rare at Varaldskogen but compose 21% of the Grimsö study area. Lakes and rivers compose between 5 and 15% of both study areas. The substrate in both areas is glacial till, dominated in many places by fields of large boulders.

Modern forestry practices have created a fine-grained mosaic (Pielou 1974, Rolstad 1991) of clear-cuts, plantations, and older-forest stands for martens in both areas. The majority (>80%) of clear-cuts are 10 ha or less, and rarely exceed 50 ha. At Grimsö these cuts are generally interspersed in a mosiac of older forest; in Varaldskogen, clear-cuts and plantations often adjoin, creating contiguous cutover areas of several hundred hectares. Two-thirds of the Grimsö study area is in spruce-dominated (>50%) stands, whereas about half of the Varaldskogen forests are dominated by spruce.

Average January temperatures are −4.4°C for Grimsö and −7.3°C at

Varaldskogen, with average snowfalls about 40–50 cm. The winters of 1988–1989, 1989–1990, and 1990–1991, however, were unusually mild and virtually snow-free. Average July temperatures are 16.2°C in both study areas. Detailed descriptions of Grimsö and Varaldskogen are given by Cederlund (1981) and Rolstad et al. (1988), respectively.

Materials and Methods

For this analysis, we used data collected on Eurasian pine martens captured during the winters of 1986–1987, 1988–1989, 1989–1990 and 1990–1991 at Grimsö (n = 12: 7 males and 5 females) and the winters of 1989–1990 and 1990–1991 at Varaldskogen (n = 6: 3 males and 3 females). Two females at Grimsö and two males at Varaldskogen were monitored for more than a year. Data on three of the martens included in the Grimsö data were also used in Storch et al. 1990. The basic methods apply to both study areas.

Wooden box traps (40 × 40 × 60 cm) were baited with either honey or the viscera of cervids from the area. Martens were drugged with a combination of ketamine hydrochloride (Ketalar, 10 mg/kg body weight) and xylazine (Rompun, 2 mg/kg body weight). Each animal was marked with a small plastic rototag and a metal earclip, and with a radio collar (Televilt AB, Ramsberg, Sweden) equipped with either a metal loop or whip antenna. Radio collars weighed 40 g for males and 25 g for females, about 2.5% of body weight. Martens were released at their trap sites after recovery and monitored from forest roads in each area. They were also visually located with hand-held receiving equipment, primarily at resting sites or more rarely while they were moving.

A subsample of marten radiolocations at Grimsö (n = 887) and Varaldskogen (n = 394) were selected for this analysis. Active locations composed 52% and 22% of the Grimsö and Varaldskogen samples, respectively. Radiolocations included triangulations, biangulations, close-tracking locations (100 m or less from the animal), and visual observations. In this analysis, we included only triangulations with the longest side 250 m or less and 1000 m or less from the furthest tracking station and cross bearings with the longest bearing 200 m or less from the marten. Each triangulation was also evaluated in terms of the angle between respective bearings, which was greater than 45°. The angle between cross bearings was 45–135°. Since martens often were continuously radio-tracked over 3- to 12-hour periods, only independent locations (Swihart and Slade 1985) were used in this analysis to avoid autocorrelation and to standardize data across individuals and study areas. This method was applied to locations less than 12 hours apart. For some martens the independence criterion could not be satisfied. In such instances, locations more than 12 hours apart were considered independent. Home range centers for independence analyses were computed on the RANGES IV program (Kenward 1987). Martens were not sampled evenly, and possible influences associated with varying sample sizes were compensated for by weighting expected values for each individual with its number of locations.

Habitat use was determined by plotting locations on detailed forest habitat maps provided by the Swedish and Norwegian Forest Services. Habitat availability was measured within the home range (95% minimum area convex polygon, Mohr 1947) for each individual. This analysis was split into two seasons: winter (16 Nov–15 Apr), and spring-summer (16 Apr–15 Sep) for all years. Most transmitters failed before autumn, and this season was excluded from the analysis because of low sample sizes.

Four forest age classes were considered: 0–8 years, 9–30 years, 31–70 years, and more than 70 years. These categories roughly corresponded to clear-cuts, young plantations, middle-aged plantations or seminatural forests, and old seminatural forests, respectively. Only locations in forest habitats (including clear-cuts), which compose more than 95% of the Grimsö data and 100% of those at Varaldskogen, were used in this analysis; nonforest habitat types such as bogs and agricultural fields were not included.

We tested for preference for old forest in three ways. First, we compared the proportion of each marten's locations in old forest against the proportion of this forest class within the marten's home range. Within each season, only martens with 20 or more locations were included in this analysis. Active selection, indicated by plots above the 45° median line, was tested with a 1-tailed, 1-group Wilcoxon's signed-rank test within each season and study area. (Points exactly on the median line were excluded.) Possible differences among study areas and seasons were tested with a 1-way, 2-group Wilcoxon signed-rank test. Next, we compared the total number of marten locations with their weighted expected values between old and younger forest age classes (1-tailed chi-square goodness-of-fit test). Active, inactive, and total locations were analyzed within seasons and study areas, and all martens were included. Finally, chi-square tests were used to further compare use and availability among the four forest age classes for this sample. If use varied from that expected, the Bonferonni-Z simultaneous confidence interval test (Neu et al. 1974) identified forest classes which were preferred or avoided within each season and study area. Statistical significance was inferred if $P < 0.05$.

Results

Use of Old Forest by Individual Martens

Habitat use nearly differed between seasons ($Z = -1.92$, $P = 0.054$) but not between study areas ($Z = -0.80$, $P = 0.43$ (Fig. 25.1). During winter, martens selected old forest at Varaldskogen ($T^+ = 0$, $n = 4$, $P < 0.05$) but not at Grimsö ($T^+ = 11$, $n = 9$, $P = 0.10$). When the winter samples from both areas were combined, martens preferred old forest over habitat available within their home ranges ($T^+ = 15$, $P < 0.02$, $n = 13$). During spring and summer, martens did not use old forest more than expected at Grimsö ($T^+ = 21$, $n = 9$, $P > 0.40$) or Varaldskogen ($T^+ = 2$, $n = 4$, $P > 0.15$), or when these area samples were combined ($T^+ = 31$, $n = 13$, $P > 0.10$).

Use of Old Forest by the Sample Population

Eurasian pine martens did not use old forest more than forests 70 years old or younger at Grimsö during the winter or spring-summer seasons, or when these seasons were combined (Table 25.1). At Varaldskogen, martens preferred resting sites in old forest during winter, but active locations during both seasons and resting sites during the spring-summer season were distributed randomly between old and younger forests. When study areas were combined, martens used old forests more than expected in general and for resting. During spring and summer, martens tended to select old forests while moving but not while resting. When seasons and study areas were combined, active locations occurred in old forest more than expected: the same was true when active and inactive locations were pooled.

Use of Forest Age Classes by the Sample Population

During winter, martens preferred old forest for resting at Varaldskogen, but not at Grimsö (Fig. 25.2). In both study areas, martens avoided forests 0–8 years old while resting, and when active and inactive locations were pooled within study areas ($P < 0.001$). Otherwise, their use of forest age classes did not differ from that expected in either study area.

During the spring and summer months, martens did not show a preference for old forests (Fig. 25.3). In both study areas, martens avoided forests 0–8 years old for resting and moving, a trend that continued when active and inactive locations were combined ($P < 0.001$). At Grimsö, martens strongly avoided forests 9–30 years old for resting but not for movement. This avoidance remained when active and inactive locations were pooled ($P < 0.01$).

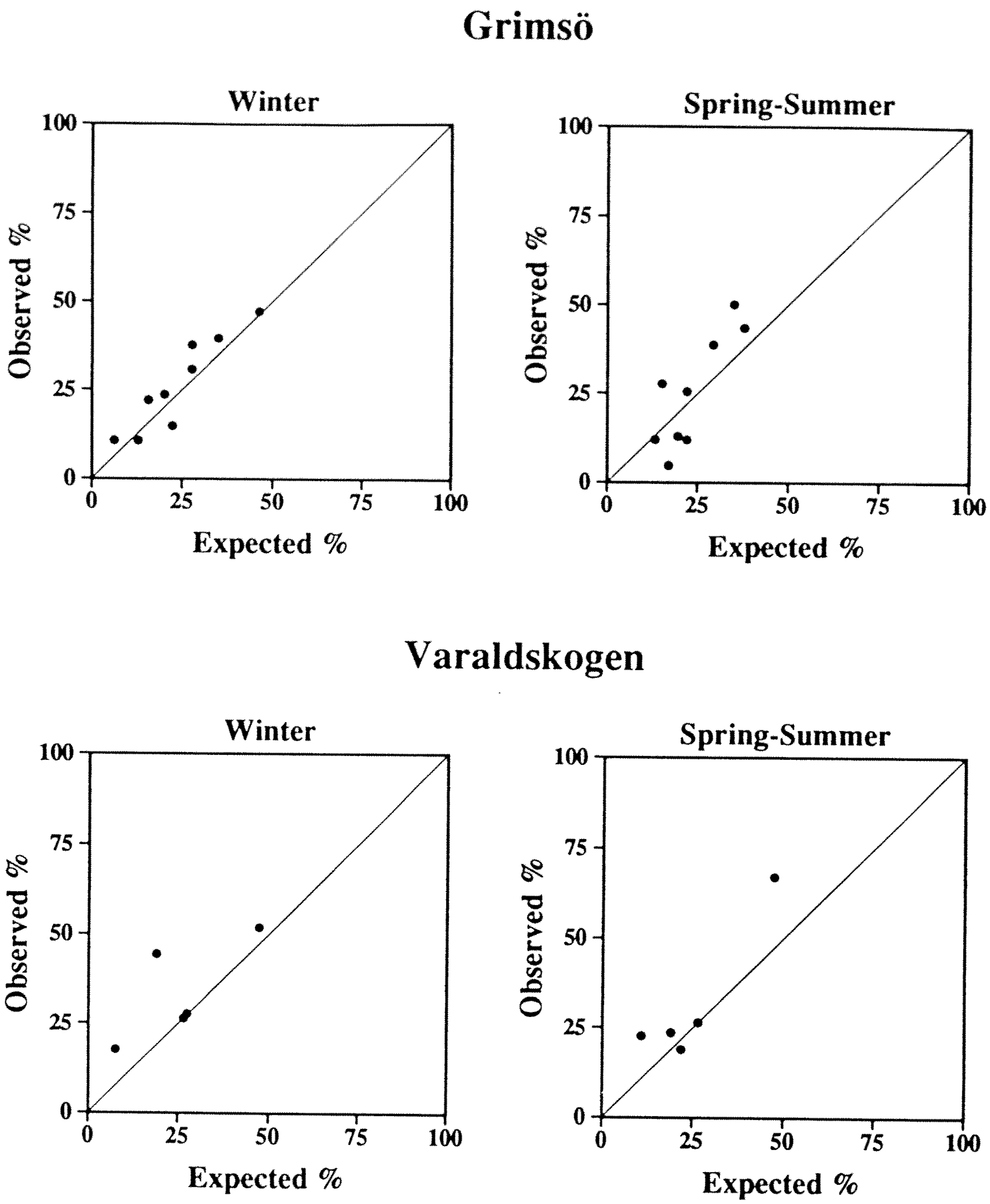

Figure 25.1. Observed/expected ratios of use of forests more than 70 years old by Eurasian pine martens (*Martes martes*) at Grimsö Wildlife Research Station, Sweden, and Varaldskogen Wildlife Research Area, Norway, during winter and spring-summer seasons, 1986–1991. Each point represents proportionate use of this forest class by each individual within its home range.

Table 25.1. Comparison of observed and expected Eurasian pine marten (*Martes martes*) radiolocations in forests ≤70 years old and >70 years old at Grimsö Wildlife Research Station, Sweden, and Varaldskogen Wildlife Research Area, Norway by season, 1986–1991

Study area and season[a]	Activity	≤70 yr		>70 yr			
		Obs.	Exp.	Obs.	Exp.	*n*	*P*
Grimsö							
winter (11)	Active	148	152	53	49	201	0.26
	Inactive	167	170	59	56	226	0.32
	All	315	322	112	105	427	0.22
spr-sum (8)	Active	175	185	72	62	247	0.07
	Inactive	166	159	47	54	213	0.14
	All	341	344	119	116	460	0.37
TOTAL (12)	Active	323	337	125	111	448	0.06
	Inactive	333	329	106	110	439	0.33
	All	656	666	231	221	887	0.22
Varaldskogen							
winter (6)	Active	36	39	15	12	51	0.16
	Inactive	98	114	50	34	148	0.001
	All	134	153	65	56	199	0.03
spr-sum (6)	Active	26	28	11	9	37	0.22
	Inactive	112	118	46	40	158	0.14
	All	138	146	57	49	195	0.09
TOTAL (6)	Active	62	67	26	21	88	0.11
	Inactive	210	232	96	74	306	0.002
	All	272	299	122	95	394	<0.001
Combined							
winter (17)	Active	184	191	68	61	252	0.15
	Inactive	265	284	109	90	374	0.01
	All	449	475	177	151	626	0.008
spr-sum (14)	Active	201	213	83	71	284	0.05
	Inactive	278	277	93	94	371	0.45
	All	479	490	176	165	655	0.16
TOTAL (18)	Active	385	404	151	132	536	0.03
	Inactive	543	561	202	184	745	0.06
	All	928	965	353	316	1281	0.008

Note: *P* values are for a 1-tailed chi-square goodness of fit test with 1 df.

[a] Numbers in parentheses are the number of martens studied for that season.

Martens at Grimsö preferred forests 31–70 years old for resting and movement, and this preference increased when these locations were pooled ($P < 0.001$). At Varaldskogen, forests 9–70 years old were used as expected, even when seasons were combined for active, inactive, and pooled locations in this study area.

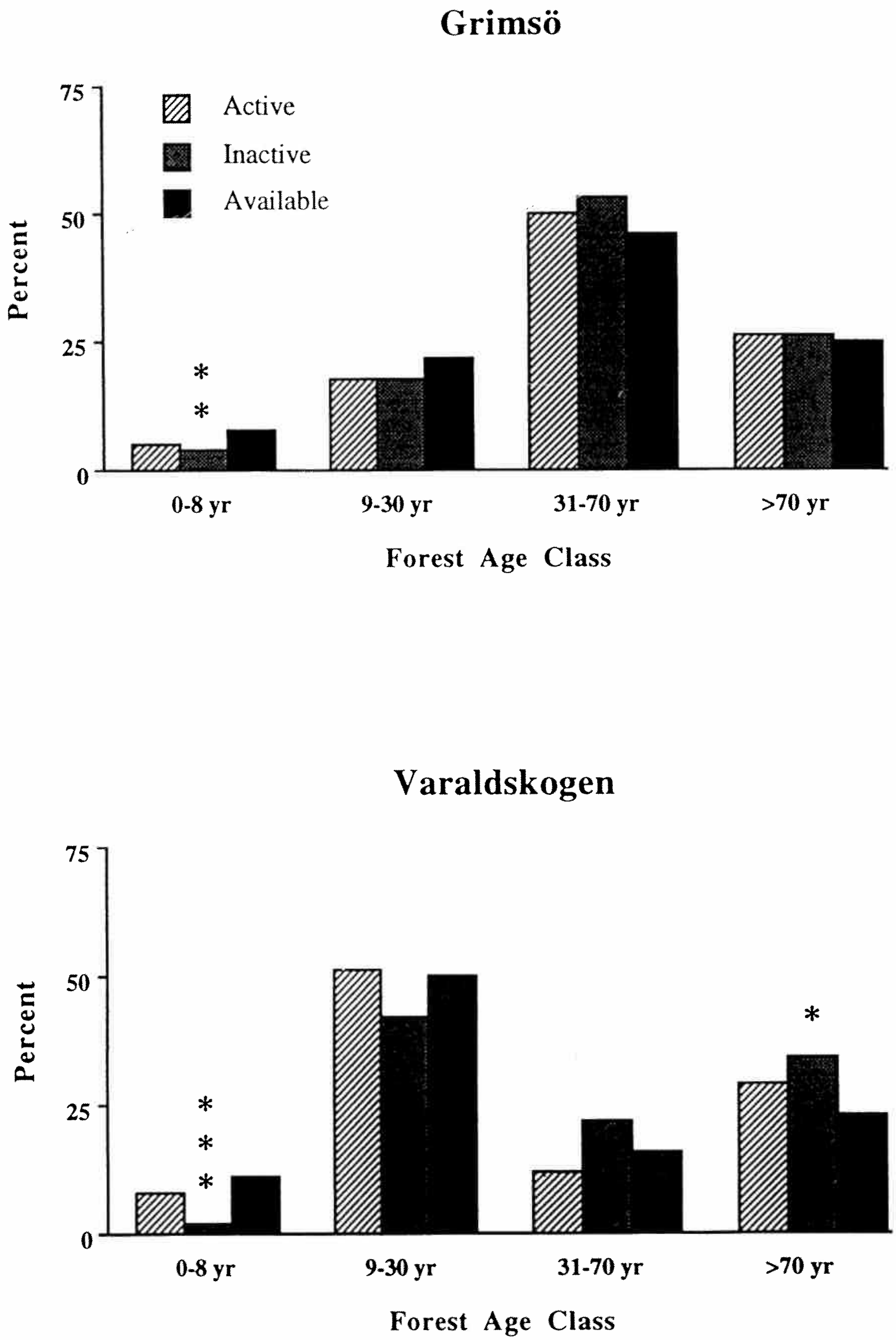

Figure 25.2. Eurasian pine marten (*Martes martes*) use of forest age classes during winter at Grimsö Wildlife Research Station, Sweden, and Varaldskogen Wildlife Research Area, Norway, 1986–1991. Sample sizes are given in Table 25.1. *P*-values for Bonferonni-Z tests: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

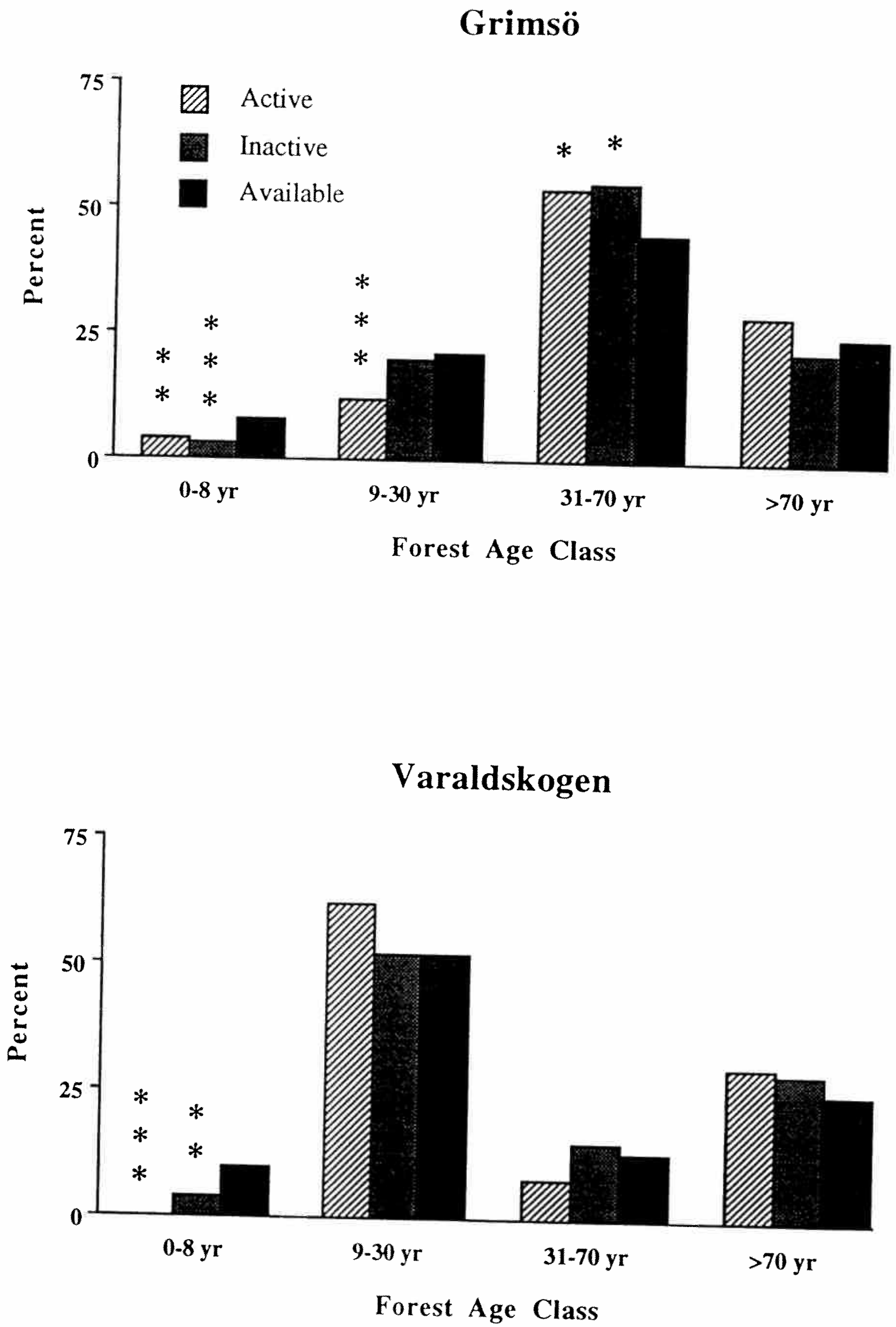

Figure 25.3. Eurasian pine marten (*Martes martes*) use of forest age classes during spring-summer at Grimsö Wildlife Research Station, Sweden, and Varaldskogen Wildlife Research Area, Norway, 1986–1991. Sample sizes are given in Table 25.1. *P*-values for Bonferonni-Z tests: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Discussion

Snow-tracking studies in Eurasia (Aspisov 1959, Grakov 1972, Wabakken 1985), including Grimsö (Storch et al. 1990) have indicated that martens prefer old-forest stands in winter. We found this preference held for that season but could not confirm it for spring-summer (Storch et al. 1990). The rather broad use of forest age classes in our study suggests that Eurasian pine martens were able to meet their life requirements in forests altered by modern forestry practices. What can explain this broad use of younger forests?

Eurasian pine martens probably select forests where foraging efficiency is maximized (Thompson 1986; Thompson and Harested, this volume) and predation threats are reduced (Brainerd 1990, Storch et al. 1990). They are diet generalists (Höglund 1960, Lockie 1961, Nyholm 1970, Morozov 1976, Pulliainen 1981*b*, Wabakken 1985, Storch et al. 1990) and thus can find food in a wide variety of habitats. Foraging may be concentrated where martens can obtain the most prey (Thompson 1986), which may be in early seres (e.g., voles: Hansson 1978, Sonerud 1986, Henttonen 1989). Martens have many enemies (Nyholm 1970, Pulliainen 1981*a*, Jonsson 1983, Korpimäki and Norrdahl 1989, Storch et al. 1990) including the fox (*Vulpes vulpes*), and overhead escape cover probably influences habitat selection (Pulliainen 1981*a*, Wabakken 1985, Storch et al. 1990). Many young forest stands should provide adequate escape cover for martens.

Structure near the ground may facilitate foraging, resting, and escaping predators. In our study areas, the abundance of dead stems from thinning and cutting practices in younger forests may provide cover for a variety of prey species, including microtines (Hansson 1978). The broken, rocky substrate randomly distributed in both areas may also facilitate access to prey, as well as providing cover for resting, thermoregulation, and escaping enemies.

In our study areas, many younger forests were spruce-dominated. Spruce forests, with their dense crowns, higher site productivity, lighter and softer snow cover, and diversity of prey species (Wabakken 1985) were favored by Eurasian pine martens in other studies (Grakov 1972, Pulliainen 1981*a*, Wabakken 1985). Squirrels (*Sciurus vulgaris*) prefer old spruce-dominated forests (Andrén and Lemnell 1992), and martens often rest in squirrel nests in spruce trees (Pulliainen 1981*a*, Storch 1988). Squirrels are important to martens as food (Höglund 1960; Nyholm 1970; Pulliainen 1981*a*, 1984; Wabakken 1985; Storch et al. 1990), and martens hunt them heavily when they are abundant and other prey species are relatively scarce (Nyholm 1970), preferring old spruce forests during these periods.

Large trees and snags with cavities excavated by black woodpeckers (*Dryocopus martius*), important to martens as natal dens (Selås 1990*b*), are found in a variety of forest types and ages in commercial forests (Majewski and Rolstad, in preparation). In our study, female martens used such structures in all forest classes more than nine years old (Brainerd et al., in preparation). Snow cover, which restricts access to prey and impedes martens' movements (Grakov 1972, Wabakken 1985), was generally lacking during most of our study and may have allowed martens to use a wider variety of forest types than in winters of normal snowfall (Storch et al. 1990).

Eurasian pine martens were consistently located in old-forest stands within their home ranges during winter, but this did not indicate a strong preference for such stands (Fig. 25.1). If martens depend on old forests, they should exhibit a strong preference for such forests when they are scarce within home ranges and prefer them less as their availability increases. During spring-summer, the effect was very nearly the opposite of what we might expect for an old-forest specialist. The literature implies, however, that old forests are important to pine martens in Eurasia. How should we interpret our results in the light of such studies?

Clear-cutting practices may adversely affect Eurasian pine marten populations (Grakov 1972, Brainerd 1990). Martens generally avoided clear-cuts and young plantations 0–8 years old in our study, as in other studies (Grakov 1972, Pulliainen 1981*a*, Wabakken 1985, Storch et al. 1990). At Grimsö and Varaldskogen, cutting mosaics were fine-grained (from the perspective of pine martens), unlike the coarse-grained, contiguous clear-cutting (>1000 ha) of northern Sweden and Russia. The lower marten densities observed in the fragmented forests of these regions (Aspisov 1959, Bjärvall et al. 1977, Jonsson 1992) may be related to the intensity and scale of cutting. Large-scale clear-cutting may adversely affect marten populations (Grakov 1972; Thompson and Colgan 1987*b*; Thompson 1991; Thompson and Harested, this volume), whereas small (<10 ha) cuts may benefit marten populations through increasing their food supplies (Brainerd 1990).

Martens in cutover areas may experience higher predation by foxes, which prefer clear-cuts (Christensen 1985) for hunting field voles (*Microtus agrestis*), a favored prey (Lindström 1982). Increased fox densities in cutover areas may reduce marten densities through direct predation, particularly on juveniles, although published data supporting this hypothesis are lacking (see Jonsson 1992). In regenerating forests lacking snags and cavity trees, natal dens may be located on the ground (D. H. Bakka, pers. commun.), perhaps exposing newborn martens to higher predation risks.

Old virgin forests may have higher structural diversity than commercial forests of similar age. Complex physical structure may increase martens' foraging success (Thompson 1986; Thompson and Harested, this volume), with woody debris providing access to small mammals, overwintering insects, and other food in winters of high snowfall (Grakov 1972). Such debris might also provide shelter for resting and denning (Buskirk et al. 1988, 1989; Buskirk and Powell, this volume) or for escaping from enemies.

Old stands of industrial coniferous forest had some importance to Eurasian pine martens, particularly during winter months. Such stands varied in structure from monocultures devoid of understory and vertical structure to semi-natural stands with diverse structure. Younger forests, including many monocultures of spruce and pine, were generally used in proportion to their availability, and forests 31–70 years old were even favored. This implies that Eurasian pine martens are capable of using a wide variety of forest types in commercial forests and are therefore not old-forest specialists. Structural elements such as site productivity, tree species composition, canopy coverage, vertical structure, and rockiness and the presence of dead wood and tree cavities probably influence marten habitat selection, and we plan to examine their importance (Brainerd et al., in preparation). As Buskirk and Powell emphasized in this volume, habitat selection patterns may be best explained in terms of fitness (Fretwell 1972). At the individual level, martens can exploit a wide variety of forest ages and types. At the population level, however, densities should be highest where reproduction and survival are maximized. The ideal habitat for martens is probably in landscapes dominated by expanses of mature, natural forests, where foraging opportunity, cover, and choice of denning sites may be increased and predation risks reduced.

Acknowledgments

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Paper IV

Habitat selection by the Eurasian pine marten (*Martes martes*) in managed forests of southern boreal Scandinavia

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Habitat selection by the Eurasian pine marten (*Martes martes*) in managed forests of southern boreal Scandinavia

S. M. Brainerd, J. Rolstad

Abstract

We examined habitat selection in the Eurasian pine marten (*Martes martes*) in managed forest in two study areas located in the Varaldskogen Wildlife Research Area, Norway and the Grimsö Wildlife Research Area, Sweden, near the southern limit of the boreal forest zone. We live-trapped and radio-instrumented 19 pine martens and relocated these by radio-telemetry (n = 1495 locations). Pine martens generally preferred spruce-dominated forest with large (≥ 20 m tall) trees and avoided clearcuts and open habitats. Males and females used habitats in a similar manner. In general, the utilization pattern of habitats was little influenced by year, seasons and activity modes. Between habitats, pairwise comparisons of selection ratios indicated that stands dominated by large spruce trees were preferentially selected over the lowest ranking habitats (i.e. pine-dominated stands with trees <20 m tall, clearcuts, open areas and deciduous stands), but were selected in a similar manner to other spruce-dominated categories and pine-dominated stands ≥20 m tall. Although pine martens exhibited clear selection and avoidance of certain habitat types, they were able to exploit a wide range of seres in forests with a long history of exploitation.

Introduction

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 et al. 1977, Wabakken 1985, Brainerd 1990, Storch et al. 1990). Pine marten densities have been found to be higher in unfragmented, mature forests relative to areas fragmented by modern forestry practices (Bjärvall et al. 1977, Bjärvall and Lindström 1991, Gundersen 1995). In Brainerd et al. (1994), we found that pine martens displayed a generalized use of forest habitat types relative to age, and concluded that forest structure, rather than age, probably influences pine marten selection of habitat. We hypothesized that habitats that provide elements of cover and access to food should be preferred, and those that increase predation risk and energy expenditure should be avoided.

Boreal forest in Scandinavia has had a long history of exploitation (Tenow 1974), and during the past 300 years this utilization has intensified in conjunction with the development of the forest industry (Esseen et al. 1992). Old-growth forests, which are regarded as important, if not critical for the closely-related American marten (*Martes americana*, e.g. Thompson 1991), have virtually been eliminated in south boreal Scandinavia. The disturbance regime in primeval boreal forest was fire-driven (Zackrisson 1977), and created a natural mosaic of different seres within the forest (Heinselman 1981). Fire suppression over the past 100 years has effectively eliminated early post-fire seres (Zackrisson 1977), but commercial forest cutting has created a patchy pattern of different successional stages (Gamlin 1988). Forestry practices in this region are among the most mechanized and efficient in the world, with almost all forest land now used for timber and pulp production (Esseen et al. 1992). Although primeval forests and those intensively managed are composed of mosaics of different seral classes, the vertical structure of stands is much more complex in uneven-aged primeval stands when compared to their managed, even-aged counterparts (cf. Swenson and Angelstam 1993).

In this paper our working hypotheses are that 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 these hypotheses is that 1) spruce-dominated habitats harbor a greater variety of prey species due to their inherently higher site productivity and cover coefficient compared to pine-dominated stands (cf. 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 such species as red fox (*Vulpes vulpes*; Lindström et al. 1995), lynx (*Felis lynx*; Jonsson 1983), golden eagles (*Aquila chrysaetos*, Nyholm 1970, Pulliainen 1981a, Korpimäki and Norrdahl 1989) and eagle owls (*Bubo bubo*, Nyholm 1970, Pulliainen 1981a). Our objective was to examine and assess habitat selection by the Eurasian pine marten relative to season, year, activity mode and sex in managed boreal forest.

Methods

Study areas

Our research was conducted in 2 managed forests near the southern limit of the boreal zone (Ahti et al. 1968) of Sweden and Norway. Grimsö Wildlife Research Area (GWRA: 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. Varaldskogen Wildlife Research Area (VWRA: 60° 10'N, 12° 30'E) is located on the Norwegian-Swedish border 175 km west of the GWRA, and covers approximately 100 km^2. The GWRA is relatively flat (75-125 m A.S.L.), whereas the topography in the VWRA is more hilly, varying between 200-400 m A.S.L. Both areas are dominated by commercial stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Fig. 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. Open areas, such as bogs and agricultural fields, comprise <10% of the VWRA and roughly 25% of the GWRA (Fig. 1). Both clearcuts and bodies of water comprise approximately 5% of both study areas. A rocky glacial till, dominated by fields of large boulders in many places, dominates the substrate in both study areas.

Within this region, primeval forest was regenerated by fire, which has been successfully suppressed the last 100 years (e.g. Esseen et al. 1992). From the mid-17th century, forests in this region were intensively utilized for fuel, sawmills and the iron industry. This exploitation culminated in the late 19th century, when most of the available large-timbered tracts had been exploited. During 1870-1950 these forests were moderately utilized by selective cutting methods. A few smaller clearcuts (<1 ha) were made in the 1910´s to 1940´s, and from about 1950 clearcutting and replanting 5-50 ha units has been the dominant forestry method in both areas.This history of utilization has created a mosaic landscape of even-aged, one-layered stands up to about 80 years of age. In the VWRA, about 20% of the productive forest is covered by older, multi-layered stands, naturally rejuvenated after intensive logging in the late 19th century (see Rolstad et al. 1988, Rolstad and Wegge 1989*a*, *b*). In the GWRA, a 5.22 km^2 forest reserve was centered in our study area. This reserve regenerated naturally after a fire in 1914 (Angelstam 1992), and very little forest management has occurred in the area since 1972. Almost all old forest stands have been managed by selective cutting or thinning. Less than 0.1% of the area (<10 ha) resemble old-growth forest structure, and true old-growth conditions are lacking. Clearcutting practices intensified in both study areas through the 1950´s and 1960´s, and by the time of the study large portions of both areas were in early successional seres. Most of the old, natural forest has now been cut., and clearcutting has created a mosaic of clearcuts, plantations, and older forest stands in both areas. The majority (> 80%) of clearcuts are < 10 ha, and rarely exceed 50 ha. In both areas, clearcuts and plantations often adjoin, creating contiguous regenerating stands of several hundred ha.

Mean-24-hour-temperatures were recorded daily at weather stations within 50 km of each study area throughout the year, and ranged from -18°C to 27°C for the study period. Winter seasonal averages in the GWRA were -8°C, -1°C, 0°C, and -2°C for the winters of 1986-87, 1988-89, 1989-90, and 1990-91, respectively; in the VWRA, winter seasonal averages were 1°C and -3°C for 1989-90 and 1990-91. During summer, temperatures averaged 10°C, 12°C, 12°C, and 11°C in the GWRA for the summers of 1987 and 1989-91. Average summer temperatures in the VWRA were somewhat higher (1990: 15°C; 1991: 14°C). Snow coverage varied greatly between years. In the GWRA, the winter averages were 40, 6, 4 and 13 cm, respectively. In the VWRA, snow depths averaged 10 cm in 1989-90 and 30 cm in 1990-91. The winters of 1988-89, 1989-1990 and 1990-91 in the GWRA and 1989-90 in the VWRA were virtually snow-free, since periods of snowfall were immediately followed by warm, wet periods which melted the snow. In the VWRA, the winter of 1990-91 was characterized by continuous snow coverage in open areas from December-February.

Data collection and sampling

We used data collected on pine martens captured during the winters of 1986-87, 1988-89, 1989-90 and 1990-91 in the GWRA (*n* = 13 pine martens; 8 males and 5 females) and the winters of 1989-90 and 1990-1991 in the VWRA (*n* = 6 pine martens; 3 males and 3 females). Two females in the GWRA and 2 males in the VWRA were monitored during more than 1 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 et al. 1990, Brainerd et al. 1994, Brainerd et al. 1995). A subsample of *n* = 1495 independent radio-locations from the GWRA (*n* = 1045) and the VWRA (*n* = 450) were used in this paper. Locations were nearly equally distributed between winter (*n* = 724) and summer (*n* = 772). Active locations comprised 41% of winter locations and 44% of summer locations. Although we estimated ages of some of our animals in the GWRA (Helldin 1997), this was not possible with all individuals and thus we do not differentiate between pine marten age categories in this paper. The basic methods apply to both study areas.

We live-trapped pine martens with wooden box-traps (40 x 40 x 60 cm) baited primarily with honey or visceral organs of cervids (moose, *Alces alces*; roe deer, *Capreolus capreolus*). We then immobilized these pine martens with a combination of ketamine hydrochloride and xylazine hydrochloride. The dosages for ketamine and xylazine were 10 and 2 mg/kg body weight (drug concentrations 100 mg/ml), respectively. We then affixed a small plastic rototag and a metal ear-clip in each ear, and instrumented them with 2-stage neckband transmitters (Televilt AB, Sweden) equipped with either metal loop or whip antennas. Size of radio-packages reflected the general 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 9 and 6 months for males and females, respectively. We released pine martens at their trapsites after they had recovered from sedation.

Radio-locations included triangulations, cross bearings, close-tracking locations ($\leq$ 100 m from the animal) and visual observations. We included only triangulations with the longest side $\leq$ 250 m and $\leq$ 2500 m from the furthest tracking station, or cross bearings with the longest distance $\leq$ 200 m from the pine marten for habitat selection analysis. Angle between respective bearings was $\geq$ 45° for triangulations, and the angle between cross-bearings was 45°-135°. Since we often continuously radio-tracked pine martens over 3-12 hour periods, we used only independent locations (Swihart and Slade 1985) to minimize autocorrelation and to standardize 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 $\geq$ 12 hours apart as independent. Home range centers for independence analyses were computed by the RANGES IV program (Kenward 1990).

We determined habitat use from 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), $n \geq 30$ locations (Kenward 1992) for each individual. This analysis was split into 2 seasons: winter (16 October-15 April), and summer (16 April-15 October).

We classified habitat types according to the following categories: clearcut with dominant tree height ≥ 0-1 m (CC 0-1 m), deciduous stands (DECID), open areas including bogs, meadows, or agricultural fields (OPEN), stands dominated by either pine (P) or spruce (S) in the following size categories based on dominate tree height: small (1-10 m), medium (10-20 m), or large (≥ 20 m). Lakes, rivers and other bodies of water were excluded from habitat analysis, since these were not used by our pine martens (*sensu* Manly et al. 1993).

Analysis of habitat selection

We employed the log-likelihood test statistic (Sokal and Rohlf 1981, Manly et al. 1993) to test the null hypothesis that martens selected habitat in proportion to availability. We then analyzed pine marten habitat utilization by using the Design III category as defined by Thomas and Taylor (1990) and as elaborated upon by McDonald et al. (1991) and Manly et al. (1993). Since pine martens were territorial, we took a conservative approach and analyzed habitat utilization within total 95% MCP ranges using the Design III method, where habitat use of individuals was compared to the availability of habitat types within each individual's home range.

We followed the procedures of Manly et al. (1993) in our habitat analysis, and computed selection coefficients as the ratios of means across all animals which incorporated individual variation into the standard errors. A resource selection coefficient for the sample population, X_i, was estimated for each habitat type (i = habitat 1-9) proportional to the probability of a particular habitat being utilized. Selection coefficients and their associated standard errors were *ln*-transformed in order to obtain more robust confidence intervals. These data were then used to compute Bonferroni joint confidence intervals to test the hypothesis that the i^{th} habitat was used in proportion to its availability, where values that do not intersect zero indicate rejection of the null hypothesis.

The breakdown of the Design III analysis was based on compositional analysis (Aebischer et al. 1993) of habitat selection coefficients between seasons, years, sexes and activity modes. This entailed statistical comparison of *ln*-transformed selection coefficients ($ln\ X_{ij}$) for the i^{th} habitat type within the j^{th} pine marten home range. Logarithmic transformations in this compositional analysis required that each animal used all habitat types, which was not always the case for our pine martens. In cases where the proportional habitat use was estimated at zero, we substituted the value for *ln* (0.01) = -4.61, since this value represented a value smaller than the lowest recorded nonzero value of -2.97 (Aebischer et al. 1993). The data were tested for normality by running a Kolmogorov-Smirnov test on the multivariate residuals for each habitat category. The null hypothesis that data were normally distributed was rejected for some habitat categories, and therefore we chose to employ two-tailed ($\alpha = 0.05$) nonparametric tests to test the general hypothesis that habitat types were not used as available within or between different data groupings. We subjectively chose to include only pine martens with $n \geq 10$ locations for each comparison.

In order to gain an overall perspective on pine marten habitat selection, we compared selection ratios for the total sample between habitat types in a pairwise fashion by calculating the selection ratio

$$R_{ab} = X_a/X_b$$

for all possible pairs of habitat types (a) and (b). Each of these pooled ratios was then *ln*-transformed in order to obtain more robust confidence intervals for use in construction of Bonferonni intervals (*sensu* Manly et al. 1993).

Results

We found that the pattern of habitat utilization was similar between study areas for most habitat categories (Mann-Whitney U-tests, $P > 0.10$). The exception was for OPEN habitat, which was used less in the VWRA ($ln\ X_i = -2.10 \pm 0.05$ SE) compared to the GWRA ($ln\ X_i = -0.96 \pm 0.12$ SE) (Mann-Whitney $U = 3.00$, $n_G = 13$, $n_V = 3$, $P = 0.009$). However, OPEN habitat was strongly avoided in both study areas (Design III tests, $P < 0.001$). We therefore chose to combine study areas for further analysis. We found no differences between sexes within years, seasons or activity modes (Mann-Whitney U tests, $P > 0.05$).

Log-likelihood tests showed significant departure from a random selection of habitats for observations in winter (active: $X_L^2 = 66.45$, d.f. = 8, $P < 0.001$; inactive: $X_L^2 = 181.02$, d.f. = 8, $P < 0.001$) and summer (active: $X_L^2 = 84.40$, d.f. = 8, $P < 0.001$; inactive: $X_L^2 = 164.30$, d.f. = 8, $P < 0.001$). 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 (Sokal and Rohlf 1981, Manly et al. 1993), we decided to conduct Design III habitat selection analyses on these data since the statistics indicated a strong departure from random.

During winter, pine martens avoided CC 0-1 m when inactive and OPEN in both activity modes, and preferred S 10-20 m when inactive and S $\geq$ 20 m in both activity modes (Fig. 2). However, comparison of winter individual selection ratios ($ln\ Xij$) revealed no differences between activity modes (Mann-Whitney U-tests, $P > 0.08$). During summer, pine martens avoided CC 0-1 m habitat while inactive and OPEN when both inactive and active, and preferred S $\geq$ 20 m in both activity modes (Fig. 3). Individual pine martens differentially utilized CC 0-1 m (Mann-Whitney $U = 42.00$, $n_a = 10$, $n_i = 12$, $P = 0.046$) and OPEN (Mann-Whitney $U = 29.50$, $n_a = 11$, $n_i = 11$, $P = 0.04$) between activity modes during summer. Seasonally, active pine martens differentially utilized OPEN (Mann-Whitney $U = 33.50$, $n_a = 11$, $n_i = 12$, $P = 0.04$) and CC 0-1 m (Mann-Whitney $U = 42.00$, $n_a = 10$, $n_i = 12$, $P = 0.047$).

Pine martens generally utilized habitats similarly between years (Kruskal-Wallis tests, $P > 0.05$). With one exception, we found no differences between years for either activity mode during either season. During winter, however, pine martens varied in use of P ≥ 20 m from year to year for active locations (Kruskal-Wallis $H = 9.19$, d.f. = 3, $P = 0.03$), although this variation was not correlated with snow depth (Spearman´s rank correlation, $P = 0.86$).

We compared pairs of estimated selection ratios for all possible pairs of habitats for the pooled sample. There were $k' = 36$ possible comparisons between pairs of these ratios, and we set α at 0.1/36 = 0.003, which gave individual confidence limits of 99.7%. Table 1 indicates which selection ratios were significantly different on this basis, when habitats were listed in order of their estimated ratios. We found that S ≥ 20 m was selected with significantly higher probability than most lower ranking habitats. However, we noted that probability of selection for this habitat was not significantly greater than for those for S 1-10 m, S 10-20 m, or P ≥ 20 m. S 10-20 m and P ≥ 20 m were selected with a significantly higher probability when compared to CC 0-1 m, DECID and OPEN habitats, but were selected similarly to lower-ranking coniferous-dominated seres. S-1-10 m and P 10-20 m were selected with a significantly higher probability than CC 0-1 m, and we found a similar relationship between P 10-20 m and OPEN habitats.

Discussion

Within their home ranges, pine martens exploited a wide variety of habitat types in forest landscapes that have a history of exploitation and manipulation. We know that pine martens are capable of exploiting a variety of habitat types from Mediterranean shrubland (Clevenger 1993, 1995), lowland deciduous forests in Switzerland (Marchesi 1989), mesic pine forests in Poland (Fedyk et al. 1984, Jedrzejewski et al. 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). Pine martens probably select habitat in order to maximize fitness (Fretwell 1972, Buskirk and Powell 1994, Brainerd et al. 1994). It is likely that pine martens choose habitats in order to avoid predators, seek shelter, and maximize foraging and reproductive success (e.g. Thompson and Harestad 1994). Thus, habitats that increase fitness by increasing chances for survival and reproduction should be preferred over those that do not, regardless of their history.

We chose to examine tree height instead of forest age based on the results of an earlier study (Brainerd et al. 1994), where we concluded that forest structure, rather than age, was probably of overriding importance for habitat selection for pine martens. Most of the forest stands in this study were even-aged, and lacked a developed understory layer. A rocky glacial till, however, provided an abundance of underground access points for foraging and resting (Brainerd et al. 1995). Field layer varied with soil type, and in general pine-dominated forest occurred on xeric, lower 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 ≥ 20 m because of high site productivity indexes (cf. Hamilton 1986). By using tree height, rather than age, we were able to document that our pine martens consistently preferred later-successional seres of spruce-dominated forest and avoided open habitats throughout the year. These results agreed with winter studies in Scandinavia and northwestern Russia (Grakov 1972, Bjärvall et al. 1977, Degn and Jensen 1977, Pulliainen 1981a,b, Wabakken 1985, Eide 1995, Gundersen 1995). American martens (*Martes americana*) also generally select late-successional, mesic coniferous stands with high cover coefficients and avoid areas devoid of tree cover (see reviews in Buskirk and Powell 1994, Buskirk and Ruggerio 1994, Thompson and Harestad 1994).

Pine martens have many enemies, most notably the red fox (Lindström et al. 1995), and habitats such as clearcuts and openings were probably dangerous because of the scarcity 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 did not relax this avoidance of open habitats when an epizootic of sarcoptic mange reduced fox densities in the GWRA (Lindström 1991, Lindström et al. 1994). Gundersen (1995) found a significant nonparametric correlation between the ratio of pine martens to red fox relative to the proportion of spruce-dominated forest > 30 years, suggesting that pine martens are adapted to forests with greater cover and fewer enemies.

Pine martens and their primary prey species both preferred similar habitats during winter (Wabakken 1985, Eide 1995, Gundersen 1995). In the GWRA, pine martens fed upon a wide variety of food items, and diet varied seasonally and annually (Storch et al. 1990, Helldin in manus). The bank vole (*Clethrionomys glareolus*) was an important prey species during winter (Storch et al. 1990), and occurs in forest interiors and 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 utilized this species during summer, but not during winter (Storch et al. 1990, Jedrzejewski 1993) when snow cover may have prevented subnivean access in open areas (cf. Pulliainen 1981a, Buskirk 1984, Buskirk et al. 1989). Helldin (in manus), however, has shown that consumption of microtines was correlated with microtine density, and that alternate species, including mountain hares (*Lepus timidus*), Eurasian red squirrels (*Sciurus vulgaris*) , and forest grouse (subfamily Tetraoninae) were utilized more during microtine lows. Squirrels, hares, capercaillie grouse (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) are associated to varying degrees with mature, spruce-dominated forest (e.g. Wabakken 1985, Andrén and Lemnell 1992, Rolstad and Wegge 1987, Swenson 1991, Wegge et al. 1992, Swenson and Angelstam 1993, Andrén and Delin 1994, Eide 1995, Gundersen 1995). Habitat selection in the closely-related American marten can also parallel those of their preferred prey (Buskirk and MacDonald 1984, Koehler et al. 1990); however, since American martens are highly catholic in diet, it is doubtful that occurrence of individual prey species influences overall prey selection (Thompson and Harestad 1994). Thompson and Colgan (1987) suggested that American martens should forage where they can obtain the most prey, which is not necessarily where the most prey occur. Thus, habitats which increase foraging success should be preferred by pine martens.

Our data indicated that, in general, pine martens did not differentially select for habitats as a function of activity level. The notable exception to this is in the use of clearcut habitat. The primary differences in habitat selection between categories were between active and inactive pine martens′ use of open habitats during summer, as well as the relative use of clearcut and open habitats between winter and summer by active pine martens. Steventon and Major (1982) found that American martens in both activity modes showed similar preference hierarchies for habitat types and favored conifer-dominated stands. 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. Pine martens in our study relied heavily on the nests of Eurasian red squirrels in spruce trees as well as underground rock chambers as resting sites (Brainerd et al. 1995), and it was possible that the distribution of these microsites influenced pine marten habitat selection. American martens in Alaska often rested in red squirrel (*Tamiasciurus hudsonicus*) middens, which were concentrated in these white spruce stands (Buskirk 1984). From our data we conclude that pine martens were generally able to forage and rest in similar habitats, and that availability of resting sites was not limiting in the GWRA or VWRA.

We expected differential use of habitats between sexes on the basis of studies on the related American marten, which have shown that females were more selective of habitats than males (e.g. Buskirk and Powell 1994). This may indicate a strategy which simultaneously maximizes survival and reproduction while decreasing energetic costs. Our results do not support this hypothesis, and indicate that both sexes of pine martens utilized managed boreal forest in a similar manner. This does not contradict our data on resting site selection, which indicated that both sexes selected resting sites similarly throughout the year (Brainerd et al. 1995).

Pine martens in our study displayed a flexibility in habitat selection which allowed individuals to exploit the range of relatively fine-grained (Pielou 1974) mosaics of habitats occurring within our study areas. Reproduction and survival were probably maximized through preferential utilization of habitats affording the greatest opportunity for foraging, predator avoidance, and shelter (i.e. spruce-dominated forest with large, mature trees), and by avoiding of those habitats associated with the greatest risks and costs (i.e. clearcuts and open areas).

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Figure captions

Fig. 1. Composition of habitat types within the study areas in the VWRA, Norway and the GWRA, Sweden.

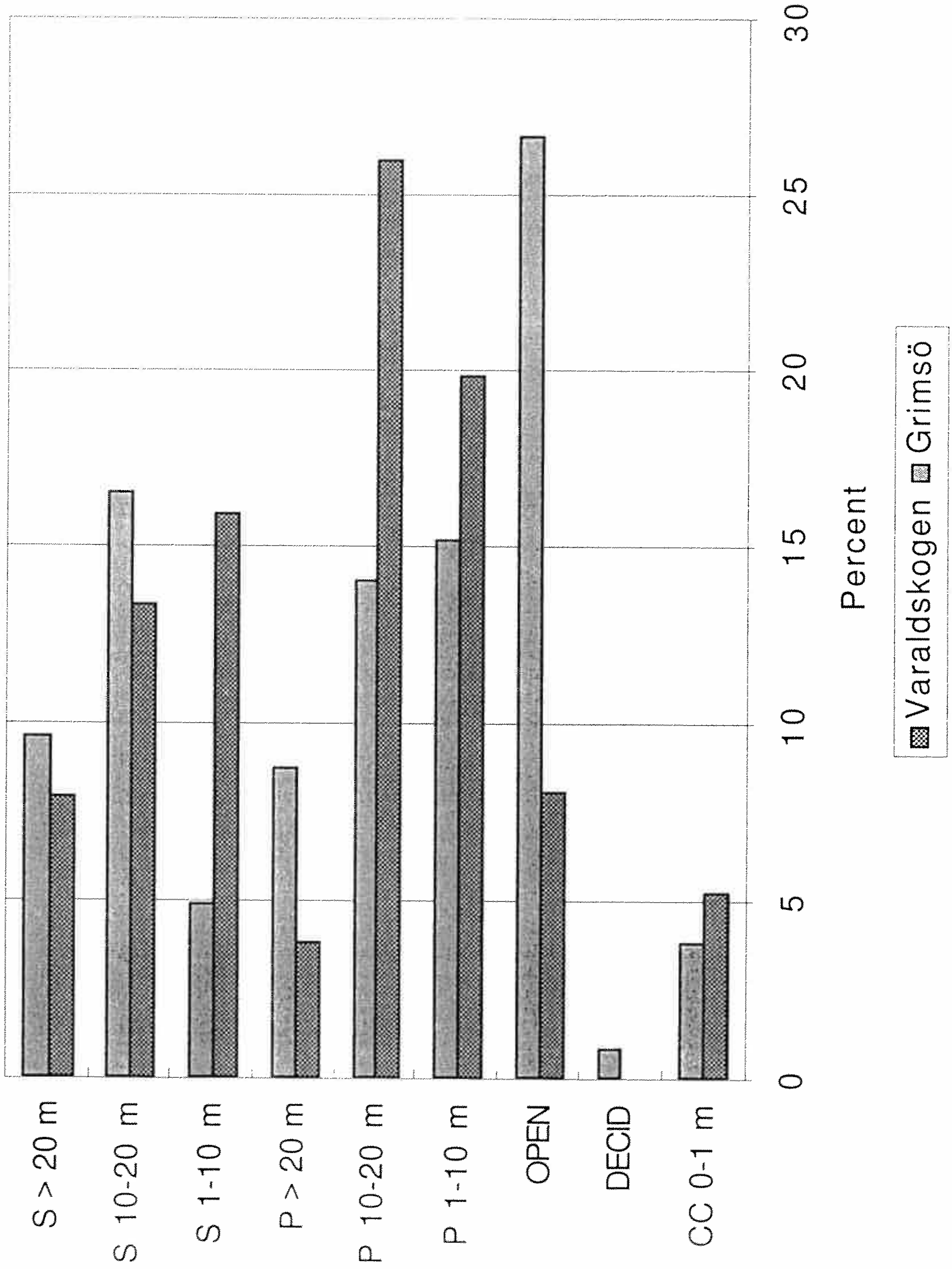
Fig. 2. *Ln*-transformed estimated probablities of selection ($ln\ X_i$) for different habitat types during the winter half-year by pine martens. The number of observations in each category are specified by their respective columns along the x-axis. Sample sizes are: active (12 martens, $n = 273$ locations); inactive (15 martens, $n = 418$ locations). Symbols indicate level of significance: $P < 0.05$ (*), $P < 0.01$ (*), $P < 0.001$ (***).

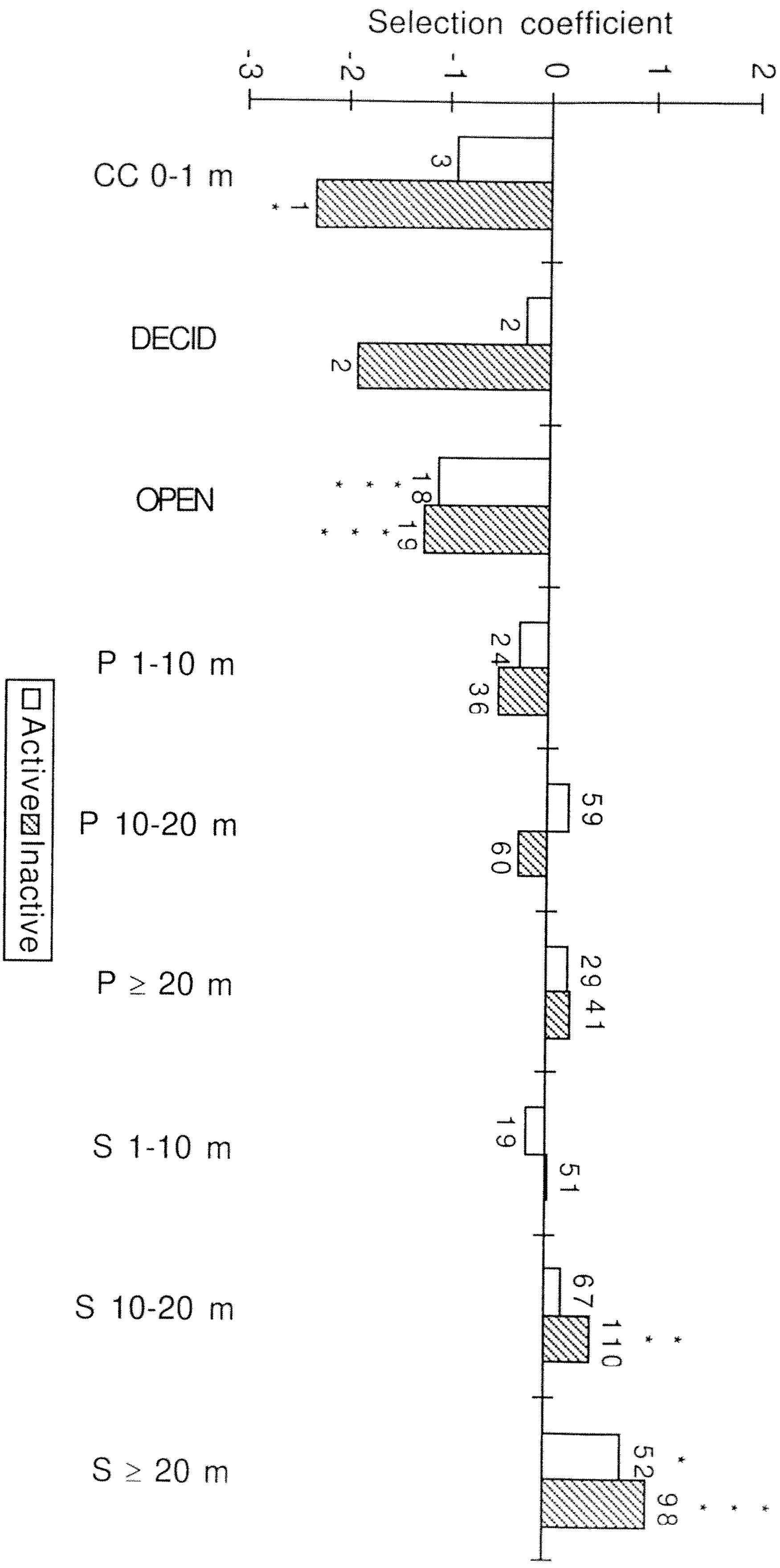
Fig. 3. *Ln*-transformed estimated probablities of selection ($ln\ X_i$) for different habitat types during the summer half-year by pine martens. The number of observations in each category are specified by their respective columns along the x-axis. Sample sizes are: active (11 martens, $n = 322$ locations); inactive (13 martens, $n = 415$ locations). Symbols indicate level of significance: $P < 0.05$ (*), $P < 0.01$ (*), $P < 0.001$ (***).

Table 1. Significant differences between estimated selection ratios computed by the Bonferroni inequality with k′= 36 comparisons when testing $H_0: X_a = X_b$ at the $\alpha = 0.10$ level for radio-locations ($n = 1495$) of 19 pine martens. Categories are ordered in ascending order of preference. The entry ′*′ indicates a significant difference between the row habitat and the column habitat, and the entry ′NS′ indicates no significant difference (*sensu* Manly et al. 1993).

Habitat	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

Fig. 1.


S > 20 m
S 10-20 m
S 1-10 m
P > 20 m
P 10-20 m
P 1-10 m
OPEN
DECID
CC 0-1 m
0
5
10
15
20
25
30
Percent
Varaldskogen
Grimsö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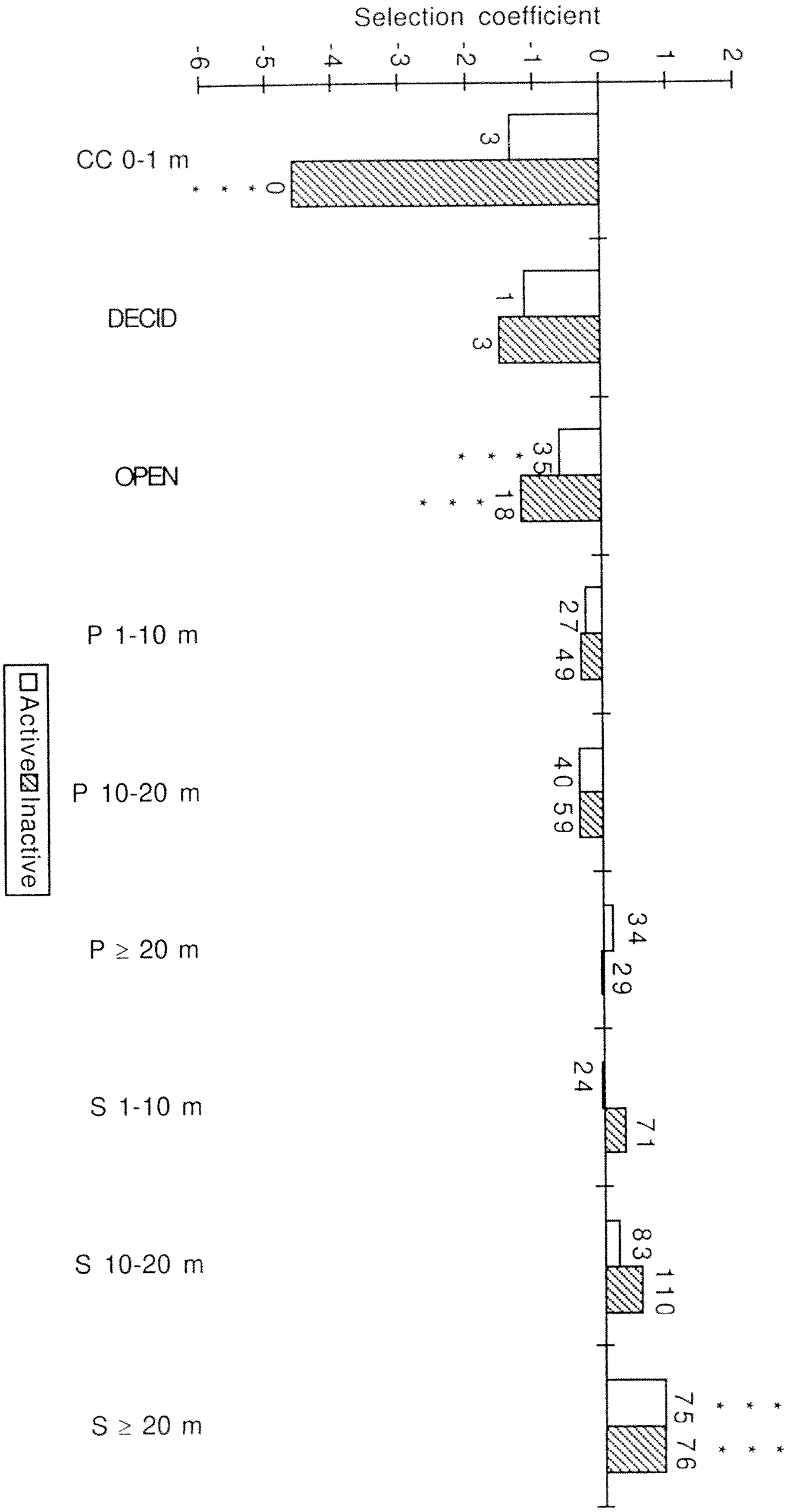
1
2
CC 0-1 m
3
1 *
DECID
2
2
OPEN
18 ***
19 ***
P 1-10 m
24
36
P 10-20 m
59
60
P ≥ 20 m
29
41
S 1-10 m
19
51
S 10-20 m
67
110 **
S ≥ 20 m
52 *
98 ***
□ Active ▨ Inactive

Fig. 2.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CC 0-1 m
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18
* * *
P 1-10 m
27
49
P 10-20 m
40
59
P ≥ 20 m
34
29
S 1-10 m
24
71
S 10-20 m
83
110
S ≥ 20 m
75
* * *
76
* * *
☐ Active ▨ Inactive

Fig. 3.

Paper V

Space use by the Eurasian pine marten (*Martes martes*) in relation to habitat quality in southern boreal Scandinavia

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Abstract

In order to investigate spacing and movements of pine martens (*Martes martes*) relative to habitat and landscape characteristics, we radio-tracked 19 radio-collared individuals captured in two study areas near the southern limit of the boreal zone in Scandinavia. Pine martens exhibited intrasexual territoriality, and spatial use patterns were similar between seasons and sexes. Home ranges (95% minimum convex polygon (MCP)) averaged 7.17 km^2 , adaptive kernel core areas averaged 3.22 km^2 and mean distance between consecutive movements $\geq$24 h averaged 1.47 km. Mean distance between consecutive movements $\geq$24 h were not related to the seasonal availability of bank voles (*Clethrionomys glareolus*) or field voles (*Microtus agrestis*). Core areas contained a greater proportion of preferred mature spruce forest than 95% MCP ranges, and 95% MCP ranges contained a higher proportion of this habitat than local 9.00 km^2 landscapes. Neither body mass (kg) nor sex were significantly related to 95% MCP range size, and interaction between sex and body mass was not significant. Multiple stepwise regression analysis demonstrated that the best predictors of pine marten 95% MCP range size were sampling duration, proportion and mean shape index of patches of preferred spruce-dominant forest $\geq$ 20 m tall within local landscapes. From this, we conclude that, at the landscape level, forest fragmentation may have a negative impact on pine marten densities.

Introduction

By the early 20th century, the pine marten was nearly exterminated in Norway and Sweden as the result of intensive fur trapping and predator control efforts (Modin 1915, Eliasson 1943, Selås 1990a, Helldin and Lindström 1992, Lindström 1997), and as a result protective measures were enacted, with this species receiving full protection in both countries by 1930 (Selås 1990a, Helldin and Lindström 1992, Lindström 1997). Pine marten numbers slowly recovered, and hunting seasons were eventually reinstated between 1939-1971 (Selås 1990a, Helldin and Lindström 1992, Lindström 1997). Harvests increased slowly until the beginning of the 1980´s, when a marked increase in pine marten numbers was observed throughout Fennoscandia (Krott and Lampio 1983, Storch et al. 1990, Brainerd 1990). This coincided with a concurrent decrease in populations of red fox (*Vulpes vulpes*) as a result of an epidemic of sarcoptic mange (Lindström and Mörner 1985, Lindström 1991, Lindström et al. 1995).

Researchers have hypothesized that the increase in pine marten numbers may have been related to decreased competition (Storch et al. 1990) or predation (Lindström et al. 1995) by red foxes. On the other hand, authors have hypothesized that fine-grained forest fragmentation has created favorable conditions for microtine rodents and medium-sized carnivores that prey upon them, including pine martens (Henttonen 1989, Brainerd 1990). However, forest cutting may also have a negative impact on pine marten populations as the scale and intensity of fragmentation increases, since elements of forest structure important in foraging, denning, thermoregulation, and predator avoidance are removed (see reviews in Lindström 1989, Brainerd 1990). In northern Sweden, research indicated that pine marten densities were significantly higher in a relatively intact and extensive old-growth forest preserve compared to surrounding forest fragmented by large-scale clearcutting (Bjärvall et al. 1977). Evidence from northwestern Russia indicates that such large-scale clearcutting practices can have a direct, negative impact on pine marten abundance (Aspisov 1959, Grakov 1972). Brainerd (1990) hypothesized that there may exist different levels of scale at which different processes may either benefit or incur costs to pine marten populations. Recent research has lent support for this theory for this species (Kurki et al. in press) and the closely-related American marten (*Martes americana*; Bissonette and Hargis 1995).

The pine marten is an important predator on capercaillie (*Tetrao urogallus,* Wegge et al. 1987), hazel grouse (*Bonasa bonasia*, Swenson 1991), as well as cavity nesting bird species such as the black woodpecker (*Dryocopus maritius*, Johnsson 1993, Rolstad et al. 1995). Recent research in Finland (Kurki et al. 1997) indicates that pine marten densities, along with those of red fox , are negatively correlated with reproductive success of black grouse (*Tetrao tetrix*). Increased pine marten densities has awakened a strong interest for trapping pine marten, primarily within the context of predator control.

In this paper, we test alternative hypotheses regarding possible determinants of the scale of spatial use in pine martens. We hypothesize that body mass should be a good predictor of home range size (McNab 1963, Harestad and Bunnell 1979). Since males are substantially larger than females, we also expect that males will range over larger areas in order to meet satisfy greater energy requirements (MacNab 1986) while simultaneously gaining access to females for breeding (Erlinge and Sandell 1986, Sandell 1986). Since microtine rodent populations are cyclic, and vary in density from year to year, we predict distance between consecutive movements will decrease within increased food availability. Since pine martens are territorial carnivores with low reproductive potential (Selås 1990b, Mead 1994) and clear habitat preferences (Brainerd and Rolstad in manus.), range size should decrease as quality of habitat within the local landscape increases (Van Horne 1983).

Methods

Study areas

Our research was conducted in 2 managed forests near the southern limit of the boreal zone (Ahti et al. 1968) of Sweden and Norway. The Grimsö Wildlife Research Area (GWRA: 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. Varaldskogen Wildlife Research Area (VWRA: 60° 10'N, 12° 30'E) is located on the Norwegian-Swedish border 175 km west of the GWRA, and covers approximately 100 km^2. The GWRA is relatively flat (75-125 m A.S.L.), whereas the topography in the VWRA is more hilly, varying between 200-400 m A.S.L. Both areas are dominated by commercial stands of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). 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. Lakes and rivers comprise approximately 5% of both study areas. A rocky glacial till, dominated by fields of large boulders in many places, dominates the substrate in both study areas. See Brainerd and Rolstad (in manus.) for a detailed description of these study areas.

Data collection and sampling

We captured and radio-collared pine martens during the winters of 1986-87, 1988-89, 1989-90 and 1990-91 in the GWRA and the winters of 1989-90 and 1990-1991 in the VWRA and monitored these by radio-telemetry (Table 1). Although we were able to determine ages through dental X-ray or cementum annuli counts for some individuals (Helldin 1997), this was not possible with all individuals and thus we do not differentiate between pine marten age categories. Only data from individuals displaying clearly sedentary (i.e. resident) behavior for ≥ 50 days were included in these analyses. In one case, a male of unknown age (M9005) shifted its home range 3 times over a two-year period. For this animal, we include the home range with the most locations ($n = 99$) and longest tracking period (251 days) utilized after 1 May, when the animal was ≥ 1 year old. For details on capture and monitoring methods, see Brainerd and Rolstad (in manus.).

Home range, core area and movements

Radio-locations included triangulations, cross bearings, close-tracking locations (≤ 500 m from the animal) and visual observations. We included only triangulations with the longest side ≤ 500 m from the furthest tracking station, or cross bearings with the longest distance ≤ 500 m from the pine marten for home range analysis. Angle between respective bearings was ≥ 45° for triangulations, and the angle between cross-bearings was 45°-135°. Error polygons were considered acceptable at the distances tracked in our study areas (see Cederlund and Lemnell 1979, Cederlund et al. 1979). Since we often radio-tracked pine martens continuously over 3-12 hour periods, our radio-fixes were not independent. We used only independent locations (Swihart and Slade 1985) for determining home range and core area sizes.

We estimated home ranges with 95% minimum convex polygons (MCP; Mohr 1947), and core areas by the adaptive kernel method (Worton 1989) with the Tracker Wildlife Tracking and Analysis Software (version 1.1, Camponotus AB, Sweden). We used the Ranges IV program (Kenward 1990) to plot the number of locations with 95% MCP area, and included data for those pine martens with clear asymptotes (between 25 and 35 locations) in these analyses.

We inspected utilization distributions (Ford and Krumme 1979, Kenward 1987) to identify the point of discontinuity (generally 65-75% of the total area) for each pine marten. This continuity provided a method for defining each pine marten´s core area (Kenward 1987). Core areas varied between 65-75% (median = 70) of fixes. The default settings in the Tracker program (density CV = 0.15, grid spacing = 0.05, margin = 30%) were used for determining adaptive Gaussian kernels, where the width of the kernel is adjusted to the density of observed points. We computed arithmetic centers for 95% MCP ranges for use in independence and fragmentation analyses. Pine martens were tracked for varying periods, and sample sizes were unequal (see Table 1).

We calculated mean distances between consecutive movements for locations separated by ≥ 24 hours during early winter (16 October-15 January), late winter (16 January-15 April), early summer (16 April-15 July) and late summer (16 July-15 October) in both study areas. Mean values were calculated for pine martens with ≥ 10 locations for each analysis. In order to avoid pseudoreplication (Hurlbert 1984), the sampling unit was the mean distance traveled for each pine marten. Vole indices in both study areas were based on the sum of the number of bank voles (*Clethrionomys glareolus*) and field voles (*Microtus agrestis*) captured per 100 trap (see Lindström et al. 1994, Wegge and Storaas 1990). Spring indices correspond roughly with the late winter-early summer seasons, and fall indices coincided with the late summer-early winter seasons.

Comparison of habitat content within core areas, home ranges and local landscapes

We measure habitat content within core areas, 95% MCP ranges and 9.00 km^2 local landscapes centered on arithmetic centers of 95% MCP ranges in order to test for selection of preferred habitat at different levels of scale. We chose to include local landscape samples in order to eliminate any biases associated with 95% MCP range size. The 9.00 km^2 (3.00 x 3.00 km) local landscapes encompass the daily cruising radius (see results) of pine martens in this study. We define habitats according to Brainerd and Rolstad (in manus.), where mature spruce-dominated forest (average tree height $\geq$20 m) was highly preferred, intermediate spruce forest (average tree height 10-20 m) was weakly preferred, and open habitats (including bogs and clearcut areas) were strongly avoided habitats. Matrix habitats include all pine-dominated forest, deciduous stands and spruce-dominated stands with dominant trees 1-10 m in height. We also included bodies of water in this analysis. We used the Wilcoxon signed rank test to test for differences in habitat content between pairs of observations in the different sampling areas.

Home range analysis

Habitats within each core area, 95% MCP range and corresponding local landscape were digitized from scanned, hand-drawn habitat maps using the MacGIS 3.0 software package (Department of Landscape Architecture, University of Oregon) on a Power Macintosh™ Performa 6200 computer. We considered a pixel size of 25 x 25 m as appropriate for these analyses. We used the FRAGSTATS program (McGarigal and Marks 1995) for creating output from core areas, 95% MCP ranges and local landscapes for each pine marten. This output was then used in statistical comparisons between landscape structure characteristics and measures of spatial use (Table 2). We set the edge parameter at 100 m for landscape analyses involving edge calculations, including estimates of habitat core area. An analysis of covariance was used to test the effects of ln-transformed body mass (kg) and sex and interaction of these variables on ln-transformed 95% MCP range size (km^2) in order to test the hypothesis that range area and body mass were positively correlated (McNab 1963, Harestad and Bunnell 1979). In order to further elucidate determinants of home range size, we used regressed the ln 95% MCP against input variables measured by the FRAGSTATS program within local landscapes, as well as sampling duration (in days). Throughout the text, means are stated with their standard deviations.

Results

We monitored 19 radio-collared pine martens from January 1987 through December 1991 in our two study areas (Table 1). Pine martens were monitored an average of 191.42 ± 88.32 days. A total of 3,545 radio-locations (x = 186.58 ± 168.89) met criteria for home range estimation; of these a subsample of 1,751 (x = 90.10 ± 48.94) independent locations were available for analyses (Table 1). Average body weights differed between sexes (Mann-Whitney U-test, $P = 0.0003$), and averaged 1.55 ± 0.12 kg for males and 0.99 + 0.09 kg for females (see Table 1).

Home range, core area, and movements

We observed some degree of intersexual overlap and little intrasexual overlap in 95% MCP ranges (Table 3, Fig. 1). 95% MCP range size, core area size, and distance between consecutive movements ≥24 h were highly correlated ($r^2 > 0.76$, $P < 0.0001$). We found no correlation between the number of independent locations with either 95% MCP range size ($r^2 = 0.14$, $P = 0.12$), although we did find a significant correlation between sampling duration and 95% MCP range ($r^2 = 0.54$, $P = 0.02$). We found no differences between study areas in 95% MCP range size for females (Mann-Whitney U-test, $n_G = 5$, $n_V = 3$, $P = 0.30$), males (Mann Whitney U-test, $n_G =$

8, $n_V = 3$, $P = 0.31$), or for sexes combined (Mann Whitney U-test, $n_G = 13$, $n_V = 6$, $P = 0.10$) and therefore we decided to pool animals for further analyses.

We compared 95% MCP range and core area size between sexes and seasons. We found no differences between sexes during either season or when these were combined (Fig. 2a, Mann-Whitney U-test, $P > 0.14$). Nor did we detect differences between seasons for either sex or for the pooled sample (Mann-Whitney U-tests, $P > 0.72$). Overall 95% MCP range size averaged 7.17 ± 4.93 km^2. Core area size did not differ between sexes during summer (Mann-Whitney U-test, $P = 0.78$), although these tended to do so in winter (Mann-Whitney U-test, $P = 0.08$). When seasons were combined, this tendency was strengthened (Fig. 2b, Mann-Whitney U-test, $P = 0.06$). We detected no differences for core area size between seasons for either sex or the pooled sample (Mann-Whitney U-test, $P > 0.73$). Overall size of core areas averaged 3.22 ± 1.79 km^2.

The number of core areas did not differ between sexes during either season or when these were combined (Mann-Whitney U-tests, $P \geq 0.46$), or between seasons for either sex or when sexes were pooled (Mann-Whitney U-tests, $P > 0.65$). This number averaged 2.05 ± 1.08 (range: 1-4) for all pine martens. Nearest neighbor distance between core areas averaged 1.91 ± 0.39 km (range: 1.25-2.60 km) and was similar between sexes for those pine marten with > 1 core area (Mann-Whitney U-test, $n_f = 4$, $n_m = 8$, $P = 0.44$).

Mean distance between consecutive movements ≥ 24 h were similar between sexes during 4 seasons (Mann-Whitney U-tests, $P > 0.16$). When sexes were combined, we found no differences between seasons (Kruskal-Wallis test, $P = 0.08$). This parameter was similar between sexes when seasons were pooled (Mann-Whitney U-test, $P = 0.80$) and averaged 1.47 ± 0.43 km (range: 0.80-2.60 km). Distances between consecutive movements ranged from 0.00-7.13 km ($n = 1133$ locations). Spearman´s rank correlation indicated that there was no correlation between mean distance between consecutive movements ≥ 24 h and vole index (Fig. 3) during any season in the GWRA ($P > 0.17$) or in the VWRA ($P > 0.32$).

Neither ln-transformed body mass (kg) nor sex were significantly related to ln-transformed 95% MCP range size (ANCOVA, effect of body mass: $F = 0.34$, $df_1=1, df_2=16$, $P = 0.56$; effect of sex: $F = 1.88$, d.f.$_1$ = 2, d.f.$_2$ = 16, $P = 0.18$). Furthermore, interaction between sex and body mass was not significant (ANCOVA, $F = 0.09$, d.f.$_1$ = 1, d.f.$_2$ = 15, $P = 0.77$).

Habitat content between core areas, home ranges and local landscapes

We compared the proportion of water surfaces and terrestrial habitat within core areas, 95% MCP ranges, and local landscapes (Fig. 4). We found no differences between sexes within any habitat between all possible pairs of sampling units (Mann-Whitney U-tests, $P \geq 0.14$). Core areas contained less water surface than local landscapes, and less open area and matrix habitat than either 95% MCP ranges or local landscapes. In contrast, core areas contained higher proportions of spruce-dominated forest with trees ≥ 10 m tall. 95% MCP ranges contained less matrix habitat than local landscapes, and a higher proportion of spruce-dominated forest ≥ 20 m in height compared to local landscapes. The amount of mature spruce forest ≥ 20 m tall averaged 39.7 ha within core areas, 73.3 ha within 95% MCP ranges and 71.2 ha within local landscapes.

Fragmentation analysis

We examined the influence of habitat and landscape variables on 95% MCP range size within local landscapes. Although some landscape variables were intercorrelated for this habitat (Table 4), they express different relationships and were therefore included in these analyses. In general, we found no clear relationships between habitat and landscape variables for habitats other than mature spruce habitat (simple regressions, $P > 0.10$). There were no clear relationships between either the number of core areas ($P \geq 0.14$, $n = 19$ pine martens) or nearest-neighbor distance between core area centers for pine martens with > 1 core area ($P \geq 0.38$, $n = 13$ pine martens) with any of the landscape variables in Table 1. Sampling duration (DAYS), %AREA and MSI explained 70.3% of the variation in 95% MCP range size (multiple stepwise regression model: ln 95% MCP = 1.747 + (0.005 x DAYS) - (0.100 x %AREA) + (3.249 x MSI) (Table 5).

Discussion

Spatial use patterns for both sexes were generally similar in magnitude to those reported in the literature for Eurasian pine martens (Marchesi 1989, Krüger 1990, Balharry 1991, Clevenger 1993, Zalewski et al. 1995), although one female in our study had a very large 95% MCP range (22.47 km^2). Resident pine martens in our study did not range over the large areas (> 80 km^2) reported in Pulliainen (1981, 1984), although 95% MCP ranges of some of our transient animals were of this magnitude (this study, unpubl. data). We found that 95% MCP range and core area sizes were similar between sexes, which generally contradicts the pattern observed elsewhere for the Eurasian pine marten (Pulliainen 1981, 1984, Marchesi 1989, Krüger 1990, Balharry 1991, Clevenger 1993, Zalewski et al. 1995) and the ecologically similar American marten (cf. Buskirk and McDonald 1989, Katnik et al. 1994, Powell 1994). The only other information on home range size for radio-tracked pine martens in Scandinavia (Overskaug et al. 1994) showed that one female had a home range larger than two males. Our pine martens had a radius of movement similar to findings from continental Europe (Marchesi 1989, Zalewski et al. 1995) but were less than those for pine martens in northern Finland (Pulliainen and Heikkinen 1980).

Size of 95% MCP ranges was influenced by sampling duration but not by the number of locations. In a review of the literature on home range size in American martens, Buskirk and McDonald (1989) found that although this parameter was not correlated with the number of locations, that there was a positive correlation with sampling duration. They conjectured that increased home range size may be attributable to shifts in territory boundaries over time, and this may also explain our similar results. The lack of correlation between number of locations and home range size in our study may be due to the fact that we used only independent (Swihart and Slade 1985) locations for delineating home ranges.

In general, we observed little intrasexual overlap in 95% MCP ranges between individuals that were monitored simultaneously, and there appeared to be relatively rigid boundaries even between individuals that were not tracked during the same year (Fig. 1). At the same time, there was a certain degree of overlap in 95% MCP ranges between sexes. These data support the general consensus that Eurasian martens (Marchesi 1989, Schröpfer et al. 1989, Krüger 1990, Balharry 1991, Clevenger 1993) and American martens (reviews in Buskirk and McDonald 1989, Powell 1994, Katnik et al. 1994) exhibit intrasexual territoriality. However, two males of unknown age apparently shared a large portion of the same range from late winter through late summer in this study. We strongly suspect that one of these individuals (M8902) may have been sexually immature (< 14 months for free-ranging animals, Krott 1973) during the tracking period (Helldin, pers. comm.). Studies on American martens (Archibald and Jessup 1984, Wynne and Sherburne 1984) indicate that ranges of adults and juveniles overlap, but no evidence of this phenomenon has been presented for Eurasian pine martens.

Mean distance between consecutive movements ≥ 24 h was 1.47 km, and was not related to the seasonal abundance of bank voles or field voles. The mean distance between consecutive locations separated by ≥ 24 h was also similar between seasons and sexes. Although Thompson and Colgan (1987) showed a functional relationship between home range size and resource abundance, we found no relationship between vole index and this parameter during any season, which may indicate that vole abundance was not great enough to influence movements in our areas. Although microtines were the single most important prey category in the winter diet of pine martens in the vicinity of the GWRA, condition and reproductive potential did not track microtine density (Helldin in manus). Helldin and Lindström (1993) concluded that pine martens do not experience food shortages during microtine lows, since they frequently feed on prey that fluctuate asynchronously with microtines. Our results support this notion, since no clear relationship between microtine abundance and movement patterns was observed in our study areas.

Other demands probably had an overriding influence on marten movements throughout the year. Such demands may include territorial maintenance (e.g. Pulliainen 1981, 1982, 1984), thermoregulation (e.g. Brainerd et al. 1995), predation risk (e.g. Buskirk and Powell 1994) or social contact (e.g. Helldin and Lindström 1995). It is possible that foraging tactics also play a key role in determining pine marten movements - recent research indicates that the scent produced by mustelid predators negatively influences the activity of bank voles (Jedrzejewski et al. 1993). Thus, pine martens may alternate between foraging areas in order to increase the element of surprise and thereby foraging success. Surprisingly, we found no decreased movement by lactating females during the early summer or increased movement during the breeding season (Katnik et al. 1994) for either sex relative to other seasons.

Pine marten densities in both study areas probably peaked during this study (Lindström et al. 1995) due to reduced populations of red fox in these areas (Lindström et al. 1994, Lindström et al. 1995). In the GWRA, pine marten populations were 5 times denser during this study than during a period of normal fox densities 10 years earlier (Lindström et al. 1995). As such, it is our impression that there may have been intense competition for available territories in both study areas, based on the behavior of transient individuals and home range shift in residents (unpubl. data), thus increasing the probability that the observed differences in marten territory sizes were related to habitat quality rather than social or energetic factors.

We did not find any relationship between the distance between core areas and indices of habitat quality or forest fragmentation. In Ontario, distances between core areas in home ranges were greater in uncut areas relative to cutover areas (Thompson and Colgan 1987, 1991, 1994). In our study, distance between nearest neighbor core areas was surprisingly similar for animals with >1 core area, which was similar to the daily movement interval for the sample. Such a separation in core areas may reflect mustelid foraging strategy or perhaps the distribution of key elements (den sites, thermal cover, prime foraging habitat) within pine marten home ranges. The lack of correlation between the number of core areas and habitat quality may also be related to microhabitat variables not measured in this study.

In general, pine martens had lower proportions of open habitats and water within core areas relative to 95% MCP ranges and local landscapes. The proportion of matrix habitats were similar between core areas and 95% MCP ranges. However, core areas and 95% MCP ranges had significantly lower proportions of pine-dominated forest and regenerating spruce forest compared to local landscapes, which suggests that although pine martens are indifferent to these habitats within 95% MCP ranges, they select against them at the landscape level. We found that pine martens selected core areas that had higher proportions of spruce-dominated stands ≥10 m tall than in either 95% MCP ranges or the surrounding landscape. This observation is consistent with selection displayed by our pine martens for such stands (Brainerd and Rolstad in manus.). Interestingly, although 95% MCP ranges varied greatly in size relative to standard-sized local landscapes, the area covered by preferred habitat within 95% MCP ranges was similar to the content within local landscapes. This may indicate that there is an optimal area of such habitat for this species in our study areas. Although no comparative data are available for Eurasian or American martens, similar relationships with regard to habitat content between home ranges and local landscapes have been reported for the capercaillie (Gjerde and Wegge 1989) and spotted owls (*Strix occidentalis*; Carey et al. 1990).

Our results indicated that pine marten home ranges varied over 15-fold in size, and that this variation could not be explained by sexual differences or energetic requirements based on body mass. Katnik et al. (1994) found no relationship between home range size and body mass for either sex in Maine, and a review by Buskirk and McDonald (1989) found that no relationship between male body mass and corresponding home range size, although a significant relationship was found for females.

We found that measures of local habitat quality coupled with sampling duration explained 70% of the variation in home range size. The Eurasian pine is a territorial species with low reproductive capacity (Selås 1990b, Mead 1994), strong habitat preferences (Brainerd and Rolstad in manus.), and thus the hypothesis that home range size should be strongly related to site conditions is applicable (Van Horne 1983, Lindstedt et al. 1986, Buskirk and McDonald 1989, Zielinski 1991). Indeed, proportion and degree of fragmentation of preferred habitat may influence population density in this species, since territorial spacing should have the effect of regulating population density (cf. Buskirk and McDonald 1989). Soutiere (1979) related home range size to site conditions for the cogenic American marten. In other studies, home range size was found to be inversely correlated with the size of forest patches for tawny owls (*Strix aluco*) in Great Britain (Redpath 1995) and positively correlated with proportion and amount of old forests within home ranges for Mexican spotted owls (*Strix occidentalis lucida*) in Northern Arizona (Ganey and Balda 1989). Capercaillie cocks compensated for a reduction in the amount of preferred habitat by having larger territories (Wegge and Rolstad 1986).

The predominant cause of forest fragmentation in our study areas was attributable to modern forestry practices. Although only a relatively small proportion of each study area was in clearcut, previous cutting had created a mosaic of patches of different habitat types, including preferred patches of mature spruce forest. In addition, large bogs in portions of our study areas superimposed a regime of natural fragmentation. Although we found no support for the hypothesis that size and proportion of open area in the landscape should negatively influence pine marten densities, it is clear that fragmentation of preferred habitat has a negative effect on pine martens. Although the cutting pattern in our study areas was relatively fine-grained, our data support findings elsewhere regarding pine marten densities and forest fragmentation (Aspisov 1959, Grakov 1972, Bjärvall et al. 1977). Large-scale cutting in North America has been shown to have a negative effect on American martens (Soutiere 1979, Steventon and Major 1982, Snyder and Bissonette 1987, Thompson and Colgan 1987, 1991, 1994, Thompson 1994, review in Thompson and Harestad 1994).

Brainerd (1990) reviewed the available literature on Eurasian pine martens, and discussed the trade-offs relative to forest fragmentation for this species. Clearcuts and early seres of regenerating stands provide an abundance of microtine rodents (e.g. Hansson 1978, Ims 1991) for predators like pine martens (Henttonen 1989) that, although opportunistic, prey to a significant extent on these species (Storch et al. 1990). However, conversion of mature forest to earlier successional stages also favors other generalist predators, including the red fox (Christensen 1979, Christiansen 1985). Data recently collected in Norway indicate that there is an inverse relationship between the ratio of red fox/pine marten tracks and the amount of spruce-dominated forest >30 years old in the landscape (Gundersen 1995), which may be due to differences in habitat selection and/or densities in this habitat. It is probable that red fox predation affects pine marten survival and thereby density (Lindström et al. 1995), and predation risk may be an important component in determining habitat quality, as suggested for American martens (Thompson 1994).

In conclusion, our results indicate that pine marten home ranges varied over 15-fold in size, and that this variation could not be explained by energetic requirements based on body mass, differences between sexes, or interaction between these factors. Habitat quality, in terms of availability of preferred habitat and its configuration in the landscape, were strong predictors of home range size, and conversely, pine marten density. However, although forest fragmentation may have a detrimental effect on pine marten populations by removing preferred habitat and increasing predation risk, pine martens in our study areas were able to survive and reproduce in landscapes with <10% coverage of preferred habitat (see Brainerd and Rolstad in manus). Indeed, during our study pine marten numbers were at or near a historical peak as a result of relaxed predation from red foxes (Lindström et al. 1995). At present, red fox and pine marten densities appear to be returning to levels observed prior to the outbreak of sarcoptic mange in the fox population during the 1980´s (Helldin, unpubl. data). In addition, interest in trapping of this species is again increasing as small game numbers decline concurrent with the increase in the fox population. Historic data show that pine marten populations are susceptable to overharvest (Dass ca.1670, in Selås 1990a and Lindström 1997, Modin 1915, Langley and Yalden 1977, Helldin and Lindström 1992, Lindström 1997), and modern forestry practices may compound this problem by increasing accessibility for trappers through construction of forest roads (cf. Hodgman et al. 1994). Given these perspectives, the fragmented forest may be in the process of becoming a more dangerous place for pine martens.

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Table 1. Summary of data on pine martens captured and radio-tracked in the GWRA and VWRA, 1987-1991.

Marten	Sex	Study area	Weight (kg)	Age (years)[1]	Age Criteria[2]	First tracking date	Last contact	Fate[3]	Days monitored	Total n	Indep. n[4]
F8702	Female	GWRA	1.00	≥ 2	R, TW	870131	870803	DD	184	134	91
F8704	Female	GWRA	1.10	≥ 1	BD	870318	870717	TF	121	122	63
			1.06	≥ 5	BD,R	910321	910913	TF	176	425	135
F8802	Female	GWRA	-	≥ 2	R	881219	890526	TF	158	88	60
			0.90	≥ 2	R	891213	900502	TF	140	112	79
F8803	Female	GWRA	1.14	3-4	CL	890316	890807	DD	144	78	65
F9004	Female	VWRA	0.95	≥ 2	R	900309	900808	TF	152	78	78
F9007	Female	VWRA	0.94	≥ 2	R	901225	910930	TF	279	119	103
F9102	Female	GWRA	1.03	≥ 2	R, DX	910201	910921	TF	232	605	143
F9106	Female	VWRA	0.88	≥ 2	R	910314	911029	TF	229	61	43
M8701	Male	GWRA	1.60	≥2?	W	870127	870322	TF	54	77	37
M8801	Male	GWRA	1.60	≥2?	W	881219	890514	TF	146	103	78
M8901	Male	GWRA	1.47	1	DX	890108	890920	TF	255	236	119
M8902	Male	GWRA	1.62	≥ 1	BD	891128	900823	TF	268	440	159
M8903	Male	GWRA	1.40	2-3	CL	891205	900127	DD	53	25	25
M8904	Male	GWRA	1.80	9	CL	891222	900321	DD	89	104	52
M9002	Male	GWRA	1.57	≥ 1	TW, BD	900610	900901	TF	83	100	41
M9003	Male	GWRA	1.53	≥ 1	BD	900319	900913	TF	178	301	80
M9005	Male	VWRA	1.45	≥ 1	BD	900510	910116	TF, DA	251	99	90
M9006	Male	VWRA	1.65	4-5	CL	900301	910306	TF, DA	370	172	172
M9105	Male	VWRA	1.40	1?	W	910130	910520	DD	110	66	38

1/ Age during tracking interval. Some animals aged ≥ 1 year were <1 year when captured. Question marks (?) indicate uncertainty in age estimation.

2/ BD = tracking period intersected theoretical birth-date (where no change in home range use was observed), CL = post-mortem cementum layer count (see Helldin 1997), DX = dental x-ray, R = reproduced, TW = tooth wear, W = weight.

3/ DA = died and recovered after study, DD = died during tracking period, TF = transmitter failure.

4/ Independent locations (see Swihart and Slade 1985).

Table 2. Overview of class index variables for mature spruce forest (≥20 m in height) used in fragmentation analyses (see McGarigal and Marks 1995).

Parameter	Abbreviation	Description[1]	Units
Percent area	% AREA	Percent coverage.	Percent
Patch density	PD	The number of patches per square kilometer.	No./km^2
Mean patch size	MPS	The sum of the area of all patches divided by the number of patches.	km^2
Landscape shape index	LSI	Relationship between landscape edge and area, which increases as landscape shape becomes more irregular and/or as the length of edge increases.	None
Mean shape index	MSI	The average shape (perimeter divided by square root of patch area for each patch) of patches, which increases as patch shapes become more irregular.	None
Total habitat core area index	TCAI	The percentage of the patch type in the landscape that is habitat core area.	Percent
Number of habitat core areas	NCA	The number of habitat core areas in the landscape.	None
Mean nearest neighbor distance	MNND	The sum of the distance to the nearest neighboring patch divided by the number of patches.	km

1/ Descriptions refer to measurements within habitat types only.

Table 3. Overlap between 95% MCP ranges for adjacent pine martens monitored simultaneously in the GWRA and VWRA (1987-1991).

Relationship	Marten individuals	Years	% overlap
Female:female			
	F8802:F8803	1988-89	0.00
	F8704:F9102	1990-91	2.06
	F9106:F9007	1990-91	0.00
	F9004:F9007	1990-91	0.00
	F9106:F9004	1990-91	0.00
		Average:	0.41
		Median:	0.00
Male:female			
	F8704: M8701	1986-87	10.24
	M8801:F8802	1988-89	0.00
	M8901: F8802	1988-89	81.25
	F9007: M9105	1990-91	35.87
	F9106: M9105	1990-91	2.01
		Average:	25.87
		Median:	10.24
Male:male			
	M8801:M8901	1988-89	3.75
	M9003::M8904	1989-90	0.00
	M8904:M8902	1989-90	0.00
	M8902:M9003	1989-90	76.29
	M9005:M9006	1990-91	0.00
		Average:	16.01
		Median:	0.00

Table 4. Correlation matrix for landscape variables associated with mature spruce-dominated forest ($\geq$ 20 m in height) within local landscapes. Underlined text indicates statistical significance at $P <$ 0.05.

	%AREA	TCAI	NCA	Ln MPS (km^2)	PD	Ln MNND (km)	MSI	LSI
%AREA	1.00	0.74	0.64	0.60	-0.04	-0.19	0.22	-0.44
TCAI		1.00	0.46	0.87	-0.54	0.18	-0.05	-0.72
NCA			1.00	0.39	-0.05	-0.23	0.37	-0.33
Ln MPS (km^2)				1.00	-0.79	0.17	0.11	-0.64
PD					1.00	-0.37	-0.03	0.53
Ln MNND (km)						1.00	-0.32	-0.58
MSI							1.00	0.09
LSI								1.00

Table 5. Multiple stepwise regression of ln 95% MCP against input variables measured within local landscapes. Input variables used as independent variables included 1) sampling duration in days (DAYS), 2) % area (%AREA) and 3) mean shape index (MSI) of spruce-dominated forest $\geq$ 20 m tall.

Variable	**Estimate**	**Step**	**F**	**Partial r^2**	**Model r^2**	**P**
Intercept	1.747					
DAYS	0.005	1	10.8	0.389	0.389	0.004
%AREA	-0.100	2	4.1	0.203	0.513	0.003
MSI	3.249	3	9.6	0.391	0.703	<0.001

Multiple regression model: ln 95% MCP = 1.747 + (0.005 x INTERVAL) - (0.100 x %AREA) + (3.249 x MSI) $r^2 = 0.703$

Figure captions

Fig. 1. Representative total 95% MCP ranges for pine martens in the GWRA (a: males, b: females) and c) VWRA. Marten identification numbers are cross-referenced with Table 1.

Fig. 2. Plots of total 95% MCP range sizes (a) and core area sizes (b) by sex for pine martens in the GWRA and VWRA, 1987-1991.

Fig. 3. Relationship between vole index (number trapped/100 trap-nights) during spring (late winter/early summer) and fall (late summer /early winter) and seasonal means for distances between consecutive movements $\geq$ 24 h for pine martens in two study areas in southern boreal Scandinavia. Symbols and sample sizes: GWRA: Early winter (□):$n = 1$, late winter (◇): $n = 12$, early summer (○):$n = 7$, late summer (△):$n = 6$; VWRA: Early winter (■):$n = 2$, late winter (◆):$n = 5$, early summer (●):$n = 6$, late summer (▲):$n = 4$.

Fig. 4. Relationship between a) proportion and b) area of different habitats between adaptive kernel core areas, 95% MCP ranges and local landscapes for radio- monitored pine martens ($n = 19$) in the GWRA and VWRA, 1987-1991. Symbols represent levels of significance with paired Wilcoxon signed-rank tests: $P < 0.05$ (*), P < 0.01 (*), P < 0.001 (***).

Fig. 1a.

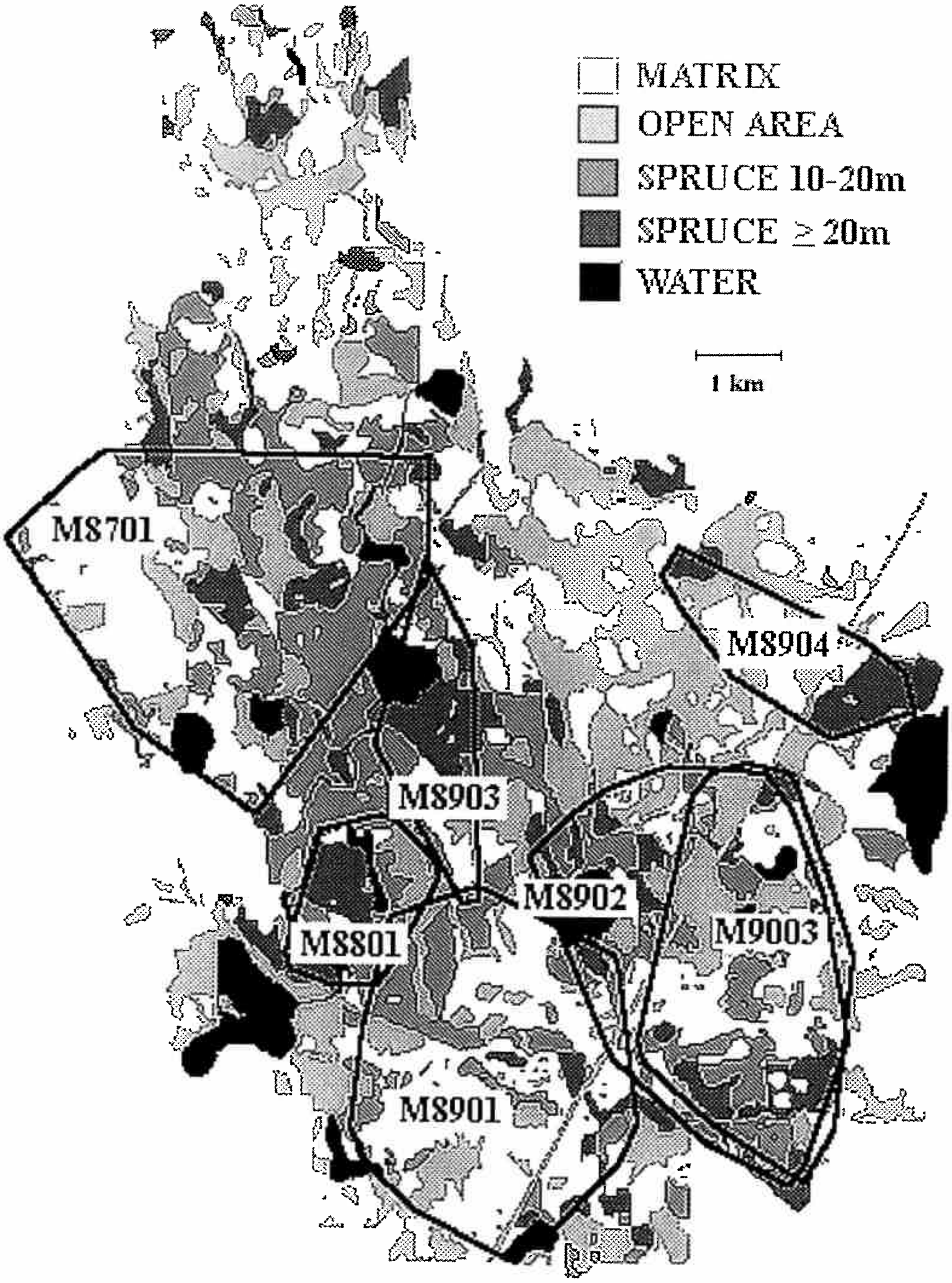

MATRIX
OPEN AREA
SPRUCE 10-20m
SPRUCE ≥ 20m
WATER
1 km
M8701
M8904
M8903
M8902
M8801
M9003
M8901

Fig. 1.6.

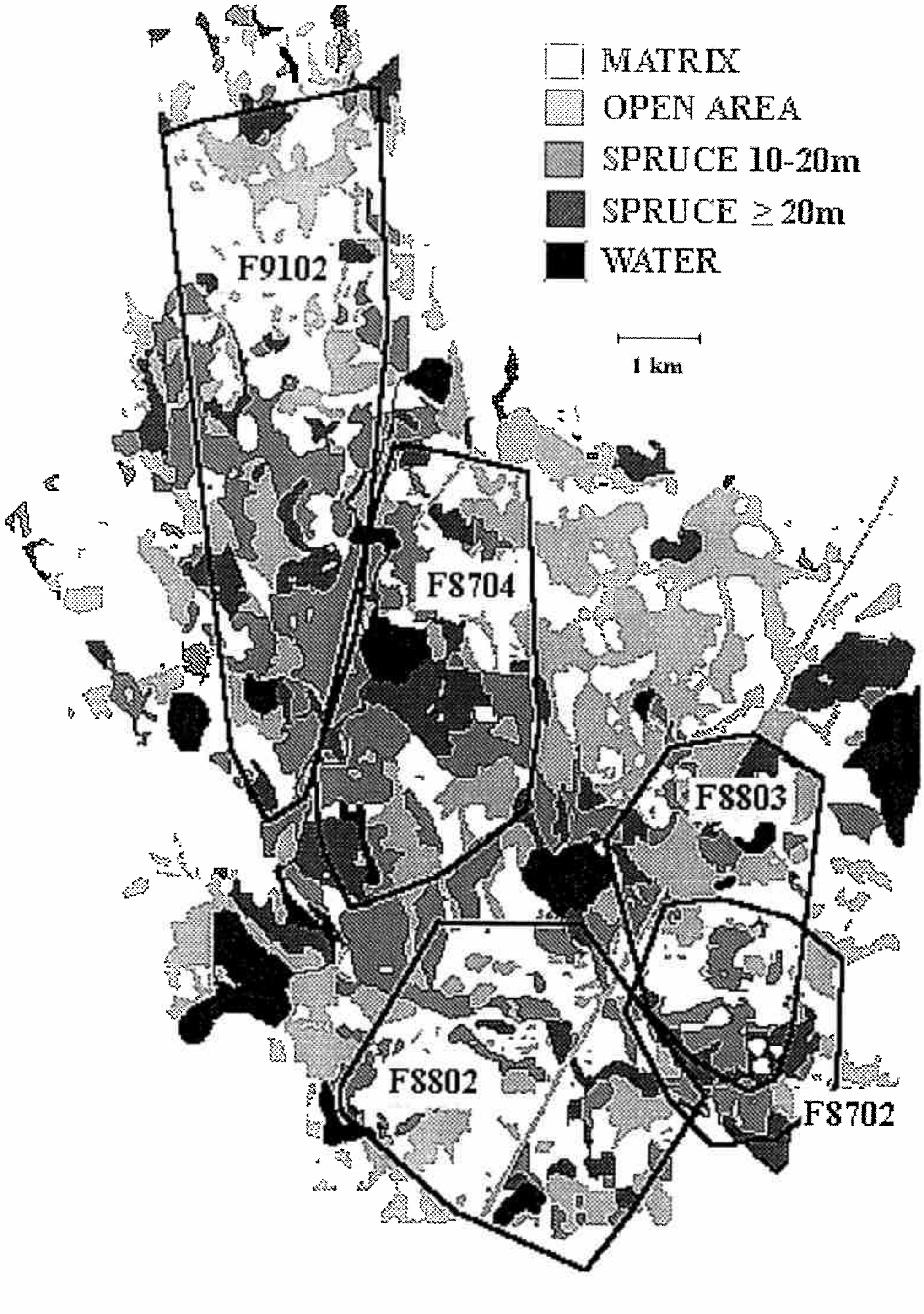

MATRIX
OPEN AREA
SPRUCE 10-20m
SPRUCE ≥ 20m
WATER
1 km
F9102
F8704
F8803
F8802
F8702

Fig. 1c.

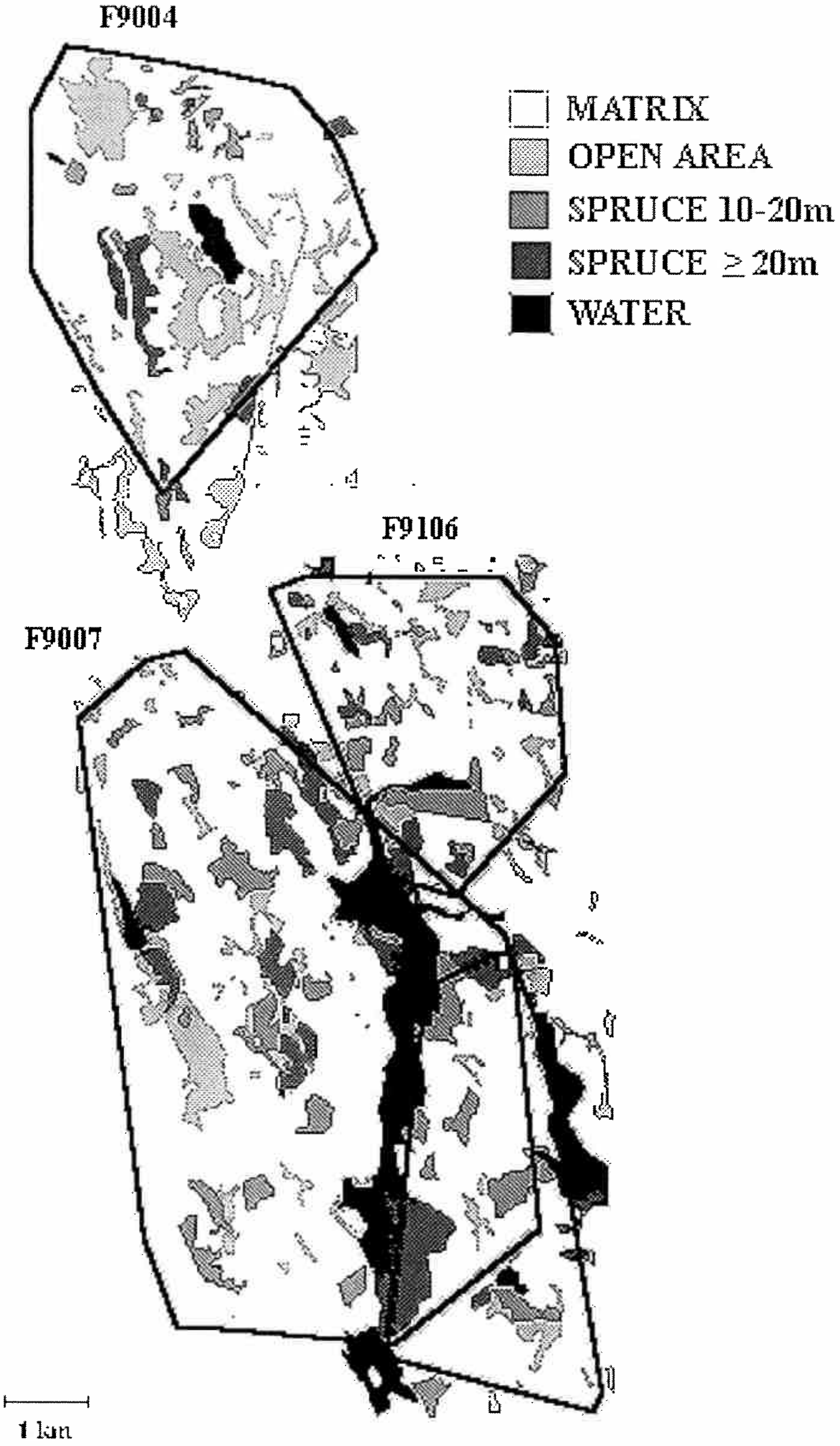

F9004
F9106
F9007
MATRIX
OPEN AREA
SPRUCE 10-20m
SPRUCE ≥ 20m
WATER
1 km

Fig. 2.

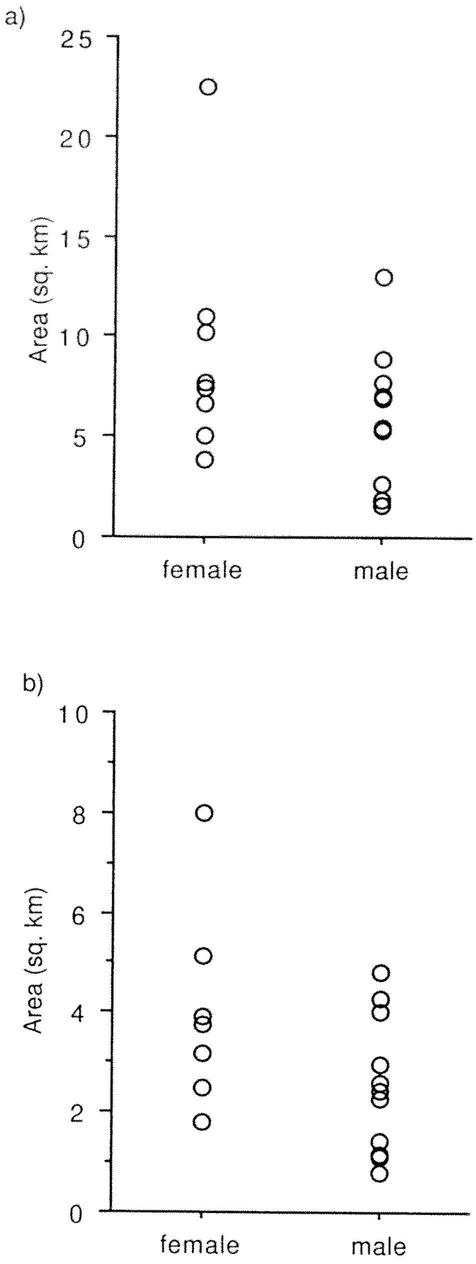

a)
25
20
15
10
5
0
Area (sq. km)
female
male
b)
10
8
6
4
2
0
Area (sq. km)
female
male

Fig. 3.

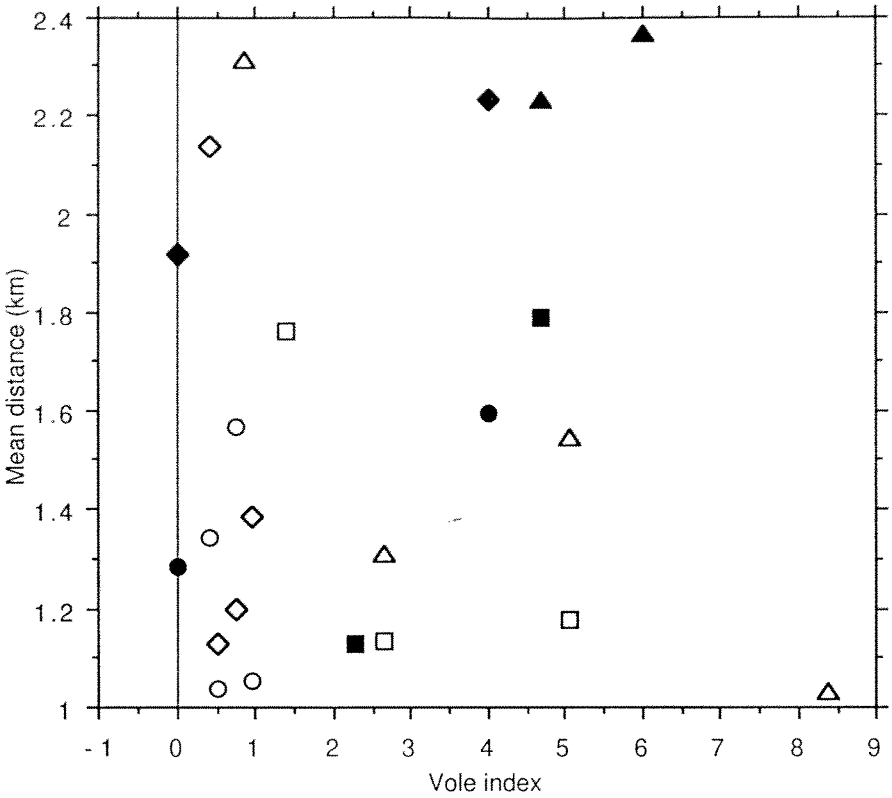
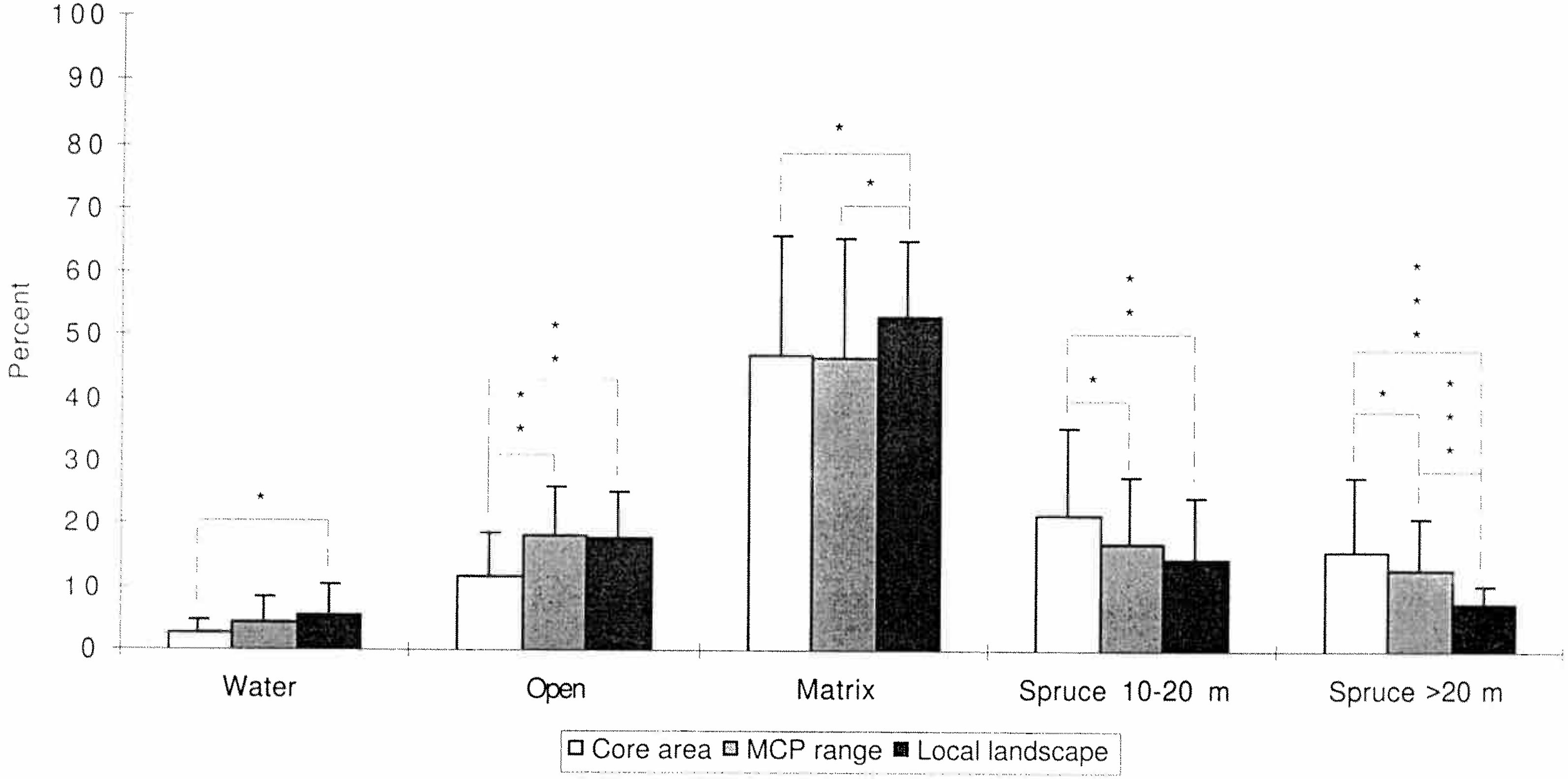


Fig. 4.


Percent
100
90
80
70
60
50
40
30
20
10
0
Water
Open
Matrix
Spruce 10-20 m
Spruce >20 m
*
□ Core area ▨ MCP range ■ Local landscape