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Research article

Forestry and environmental conditions as determinants of pine marten *Martes martes* occurrence in Norway

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The European pine marten *Martes martes* is often associated with late seral stage coniferous forest stands. Earlier research has indicated that this species may be negatively influenced by clearcutting practices. However, the effects of current clearcutting methods on pine marten occurrence in conjunction with changing environmental conditions are not well known. In this study, we combined four complete years of nationwide data collected during a long-term camera trap (CT) monitoring program in Norway. We employed a multi-scale occupancy model to investigate the relationship of pine marten occurrence to clearcuts (regenerating stands ≤ 10 years old) and forests ≥ 120 years old. We also examined pine marten detection in relation to habitat features (i.e. dominant microsite characteristics) and to varying snow depths and temperatures. We found no relationship between pine marten occurrence and the proportions of old forest and clearcuts at the landscape scale. At the habitat-patch scale, pine marten occurrence was positively associated with the presence of old forest patches and terrain ruggedness, but not with clearcuts ≤ 100 m from sites. At CT sites near clearcuts, the detection probability was negatively correlated with snow depth. In contrast, pine marten occurrence was positively associated with snow depth at CT sites > 100 m from clearcuts. Furthermore, the detection probability increased with temperature and the presence of boulders at CT sites. Boulders may provide important access points for foraging, and cover for resting and predator avoidance. While previous studies indicate that pine martens prefer older forest and avoid clearcuts, the current level and scale of clearcutting in Norway does not appear to influence its occurrence at the landscape scale.

Keywords: clearcutting, *Martes martes*, multi-scale occupancy model, Norway, old forest, pine marten

Introduction

The European pine marten *Martes martes* is an opportunistic mesocarnivore and forest specialist (Storch et al. 1990, Brainerd and Rolstad 2002, Proulx et al. 2004, Monakhov 2022) that occurs through Europe, including the British Isles, Scandinavia and the Balearic Islands, eastward to the Ural Mountains and parts of southwest Asia and the Middle East (Herrero et al. 2016, Monakhov et al. 2020, Monakhov 2022; Supporting information, for geographical range of pine marten). The latitudinal distribution of this species aligns with the boundaries of the forest zone (Monakhov 2022). In Fennoscandia, studies have shown that pine martens prefer mature coniferous forest stands (Storch et al. 1990, Brainerd and Rolstad 2002). However, pine martens are associated with a variety of habitat types throughout their range (Birks et al. 2005, Pereboom et al. 2008, Balestrieri et al. 2010, Mergey et al. 2011, Caryl et al. 2012, Lombardini et al. 2015, Moll et al. 2016, Remonti et al. 2022). In intensively cultivated areas of southern Europe, for example, pine martens use riparian woodland corridors and hedgerows (Pereboom et al. 2008, Balestrieri et al. 2010). However, modern forestry practices, whereby mature forest stands are clearcut for economic purposes, may negatively impact pine marten occurrence in Scandinavia (Brainerd 1990, 1997, Brainerd and Rolstad 2002).

Clearcutting forestry practices have predominated in Scandinavia since the 1950's (Hoen and Winther 1993, Gustafsson et al. 2010). This intensive model of forest management is characterised by even-aged, homogeneous, and sharply delineated stands with a rotation cycle between 60 and 120 years (Kuuluvainen 2009, Kuuluvainen and Gauthier 2018). Clearcuts and early seral stages generally lack canopy cover, understory layers, or dead wood compared to old forests (Esseen et al. 1997, Fisher and Wilkinson 2005). A lack of such habitat features, in addition to snags and arboreal cavities, can be detrimental to the persistence of forest-adapted species, such as pine marten, that rely on them for foraging and cover (Thompson 1994, Brainerd et al. 1995, Fridman and Walheim 2000, Brainerd and Rolstad 2002, Kuuluvainen 2009). In open areas such as clearcuts, pine martens are more vulnerable to predation by the red fox *Vulpes vulpes* or golden eagle *Aquila chrysaetos* due to the lack of vertical escape possibilities and structural cover (Lindström et al. 1995, Linnell et al. 1998, Smedshaug et al. 1999, Brainerd and Rolstad 2002, Lyly et al. 2015). Thompson and Colgan (1994) found that the congeneric American marten *Martes americana* had higher prey encounter rates and hunting success in old forest stands compared to clearcuts. In boreal Scandinavia, red squirrels *Sciurus vulgaris* prefer middle- and old-spruce-dominated forests (Andrén and Delin 1994) and are directly important to pine martens as prey (Storch et al. 1990, Helldin 2000) and indirectly because squirrel's nests provide cover for resting and birthing young (Brainerd et al. 1995). Habitats with high structural complexity, such as rugged terrain with rocky areas may to some extent mitigate the lack of important old forest structural features by providing access to subterranean and subnivean spaces used for foraging, resting, reproduction and escaping predators (Buskirk et al. 1988, Jędrzejewski et al. 1993, Thompson and Colgan 1994, Brainerd et al. 1995).

Seasonally changing environmental conditions, such as snow depth, may also mitigate some of the potential effects of clearcutting and hence influence pine marten dependence on old forest patches. Cano-Martínez et al. (2021) found a positive association between snow depth and pine marten presence in Norway. Pine martens may prefer areas with deeper snow to avoid red foxes which are correspondingly disadvantaged (Willebrand et al. 2017). However, snow may restrict subterranean and subnivean access to prey such as field voles *Microtus agrestis* which occur primarily in clearcuts (Wegge and Rolstad 2018). Hence, the prey-mediated effect of snow depth on pine marten occurrence may depend on habitat type (e.g. clearcut or old forest stands).

Temperature is another factor that may influence pine marten detection. Thompson and Colgan (1994) found that American marten activity substantially decreased during cold temperatures (i.e. $< -15°C$). Brainerd et al. (1995) found that pine martens consistently sought thermal shelter underground at temperatures $< -5°C$. Hence, it may be harder to detect pine martens if cold temperatures limit their activity.

Most habitat studies on pine martens in Scandinavia have been conducted at a single spatial scale, often at the home range level (Storch et al. 1990, Brainerd and Rolstad 2002). However, species-habitat associations can vary with spatial scales since habitat selection processes are often scale-dependent (Orians and Wittenberger 1991, Devictor et al. 2010). In Scotland, pine martens select for forested habitats and avoid agricultural areas at the landscape scale but use these habitats in proportion to their availability within home ranges (Caryl et al. 2012). At the landscape scale (50 000 km²), Moll et al. (2016) found that pine marten occurrence was not negatively influenced by other available habitat types where structurally complex woodland remained in the landscape. Thus, it is important to consider multiple spatial scales when investigating wide-ranging species and their habitats to ensure that conclusions are biologically relevant. Adopting a multi-scale approach could reduce the influence of human perceptional bias of scale on such studies (Johnson 1980, Alldredge and Gwiswold 2006).

In Norway, forests constitute 37.6% (121 000 km²) of the country's total surface area and of the forested area, 68.1% are subject to commercial harvest (Statistics Norway 2022). As the forest industry anticipates a four-fold increase in the annual turnover by 2045 (Olofsson 2015), a better understanding of how pine martens are affected by clearcuts in the landscape may be important. Also, the effect of clearcuts may differ depending on spatial scale. Here, we assessed how pine marten occurrence is influenced by clearcuts and old forest stands, at multiple spatial scales. Our study was conducted in a managed forested landscape in Norway and we used incidental observations recorded during a long-term camera trap

(CT) survey (see SCANDCAM project; https://viltkamera. nina.no). Forest habitat suitability for pine martens may vary with a gradient of forest age and stand structure. However, previous studies (Thompson 1994, Brainerd and Rolstad 2002, Fisher and Wilkinson 2005) indicate a clear contrast in pine marten use of clearcuts vs old forests and we focus on these two forest categories for our analysis. Our objectives are to examine pine marten occurrence relative to clearcut and old forest stands at the landscape and habitat-patch scales, as well as the influence of habitat characteristics, such as terrain ruggedness and rocky areas. In addition, we examine how detection probability of pine martens at CT sites is influenced by temperature and snow depth.

Material and methods

Study area

Our study areas (Fig. 1) extend from Troms og Finnmark County in northern Norway (68°N, 16°E) to Agder County in the south (58°N, 8°E) and encompass a range of sub-arctic – boreal climates with varying degrees of oceanic/continentality influence (CCKP 2021). The study areas fall within the boreo-nemoral (Fig.1; study areas 1–2) and boreal (Fig. 1; study areas 2–5) vegetation zones (Sjörs 1963, Ahti et al. 1968) and are characterised by intensively managed forest landscapes consisting of mixed stands of Scots pine *Pinus*
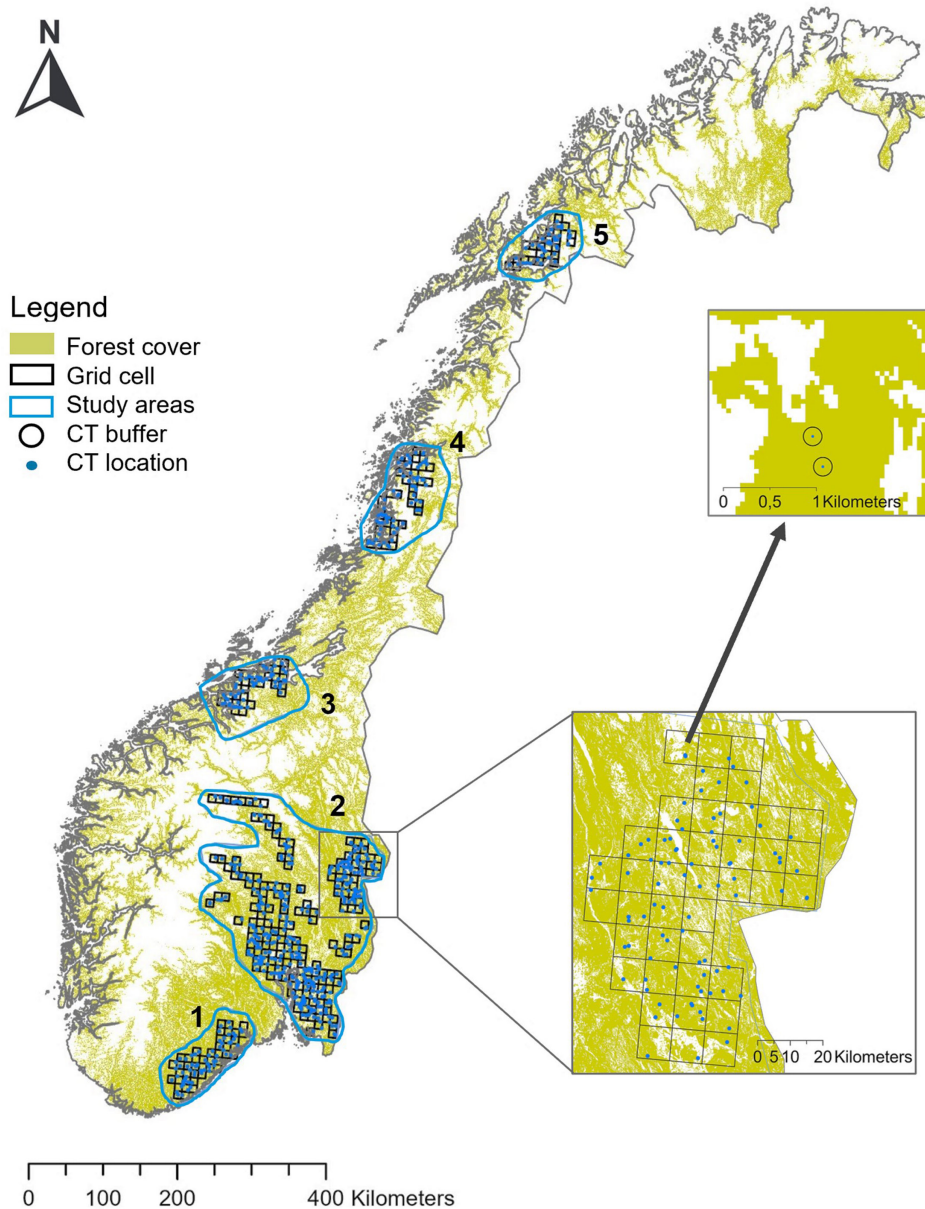

Figure 1. Study areas (labeled 1–5) and location of grid cells and camera traps (CTs). Lower right panel shows the grid cell (100 km²) at the landscape scale and top right panel shows two CTs at the habitat-patch scale (100 m radius around CT site dot).

sylvestris, Norway spruce *Picea abies*, birch (*Betula* spp.), grey alder *Alnus incana*, willow *Salix caprea*, aspen *Populus tremula,* and rowan *Sorbus aucuparia* (Bendiksen et al. 2008). During this study, the annual mean temperature varied from 0.52°C in study area five (Fig. 1) to 5.64°C in study area one (Fig. 1; CCKP 2021).

Camera trap survey

We obtained CT data for pine martens from a long-term survey conducted as part of the SCANDCAM project (https://viltkamera.nina.no). Trained project volunteers and technicians deployed and operated CTs (HC500, HC600, PC800, PC850, PC900 and HP2X, Reconyx, Holmen, Wisconsin, USA) year-round since the winter of 2010/2011. Data for this study were collected during 1 January 2018–31 December 2021. The CT sites were chosen to monitor Eurasian lynx *Lynx lynx* for management purposes (Hofmeester et al. 2021). Hofmeester et al. (2021) recorded high detection probability of multiple carnivore species at lynx-targeted CTs and concluded that these can be used to study occupancy of non-target species, including pine martens, in boreal systems. All CTs were placed in forest habitats and targeted microsites that lynx use (e.g. wildlife trails, forest roads, and along the base of cliffs/boulders). One CT was typically deployed within 50 km^2 grid cells although in a few cases two or more CTs were placed in a single grid cell. To ensure the presence of multiple CTs within a grid cell for our multi-scale modelling approach (see below), we generated a new grid with 100 km^2 grid cells. Each 100 km^2 grid cell contained between 1 and 8 CTs and averaged 1.99 CTs per grid cell. Moreover, for the landscape scale analysis, we would ideally utilize a grid cell size that can encompass several pine marten home ranges. Pine marten home ranges vary between 2–25 km^2 and averaged 7 km^2 in southern boreal Scandinavia (Brainerd 1997). Therefore, we used a grid cell size of 100 km^2. Grid cells were then grouped into larger study areas based on geographical location and discontinuities within our sampling design (Fig. 1). Each CT was programmed to be motion-triggered to rapidly take three consecutive images, in addition to a daily time-lapsed test picture. We classified CT images by species (Hofmeester et al. 2021). We summarized CT data as a detection history per CT describing the detection (1) or non-detection (0) of pine marten per five-day survey period as commonly done for CT studies of mobile species (Burton et al. 2015, Hofmeester et al. 2021). We chose a five-day survey period compared to actual observations or days of observations in order to reduce the influence of outliers and random events (e.g. scavenging of carcasses and caching of meat near CT that could lead to many images from the same individual) on detection probability.

Hierarchical framework

We adapted the conceptual framework developed by Hofmeester et al. (2019) to link pine marten detection to different orders of habitat selection (c.f. Johnson 1980). We investigated pine marten occurrence at two spatial scales:

second-order selection at the landscape scale and third-order selection at the habitat-patch scale (c.f. Hofmeester et al. 2019). We refer to pine marten occurrence at the landscape scale and the habitat-patch scale as occupancy and site use, respectively (Efford and Dawson 2012, Steenweg et al. 2018). Furthermore, detection probability was used to account for imperfect detection when estimating occupancy and site use.

We modeled pine marten occupancy and site use in a multi-scale occupancy model (Mordecai et al. 2011, Kery and Royle 2015) as adapted by Hofmeester et al. (2021) to CT data. Our hierarchical model included two levels (spatial scales) for the 'biological state' (i.e. occupancy and site-use) and one detection process level (i.e. detection probability).

We described occupancy of pine martens in each 100 km^2 grid cell as:

$$z_i \sim \text{Bernoulli}(\psi i) \qquad (1)$$

where z_i represents the observed occupancy state in each 100 km^2 grid cell i, and is Bernoulli distributed with a probability ψ_i, such that z_i is 1 if a grid cell i is occupied. We then described site use as:

$$a_{ij} \mid z_i \sim \text{Bernoulli}(z_i \times \theta_{ij}) \qquad (2)$$

where $a_{ij}|z_i$ represents the observed site use at CT site j in grid cell i conditional on the occupancy state (z_i) of the grid cell. Site use is Bernoulli distributed with a probability θ_{ij}. Finally, detection probability, was included to the model as such:

$$y_{ijk} \mid a_{ij} \sim \text{Bernoulli}(a_{ij} \times p_{ijk}) \qquad (3)$$

where the detection or non-detection of pine marten during the kth period at CT site j in grid cell i conditional on the site-use state, a_{ij} was denoted as $y_{ijk}|a_{ij}$. The detection probability for CT site j in grid cell i at the kth survey is Bernoulli distributed with probability p_{ijk}. Detection probability in occupancy models that use CT data is calculated based on the number of repeated detections at a survey site. The repeated detections at survey sites depend on a combination of technical CT factors linked to the functioning of the PIR (passive infra red) sensor (e.g. ambient temperature, visibility, etc.) and species biological characteristics related to how often individuals of the species visit the CT site (e.g. species density and habitat use; Hofmeester et al. 2019). However, it is not possible to distinguish between these technical and biological factors using an occupancy modelling framework. We thus interpret detection probability as a combination of technical CT factors and species biology.

Covariates

We selected relevant covariates and interaction term (i.e. clearcut, old forest, total forest, study area, terrain ruggedness, habitat features, temperature, snow depth and snow depth

× clearcut) based on the literature and our experience, and identified their expected effect (Table 1). We defined clearcut habitats as regenerating stands ≤ 10 years old and old forest habitats as forests ≥ 120 years. To create the clearcut and old forest covariates, we used state forest maps that included forest age, at a spatial resolution of 25 m (Gjertsen and Nilsen 2012) in combination with the Global Land Survey Landsat data (spatial resolution of 30 m; lossyear and treecover2000 raster maps; Hansen et al. 2013).

At the landscape scale, we extracted covariates for entire 100 km² grid cells, within which CT(s) were located (Fig. 1). For each year of the study (between 2018 and 2021), we calculated the clearcut covariate as the proportion of total forest that had been clearcut (i.e. clearcut area/total forest area) in each grid cell (Table 1; clearcut_grid covariate). We calculated the annual proportion of old forest area over total forest area for each grid (Table 1; old_forest_grid covariate). Total forest (including clearcuts and old forest) was calculated as the proportion of total forest area over terrestrial area (Table 1; total_forest covariate). The total_forest covariate was based on Landsat forest data (spatial resolution of 30 m) available from the Global Land Survey datasets (treecover2000 raster map;

Hansen et al. 2013), and terrestrial area obtained from the AR50 (spatial resolution of 50 m) nationwide land resources map (Heggem et al. 2019). We also combined multiple 100 km² grid cells into five study areas (Table 1; study_area covariate) based on the geographic clusters in which the grid cells were located (Fig. 1). We added study area to the model to correct for potential differences in occupancy at the landscape scale among the study areas and account for other varying factors (e.g. dominant tree species, vegetation zones, latitude) that were not incorporated as part of the selected model covariates.

At the habitat-patch scale, we described the habitat surrounding a CT site (i.e. habitat-patch) within a circular buffer (Fig. 1; radius = 100 m). Within each CT site buffer, we quantified average terrain ruggedness using a Terrain Ruggedness Index (TRI; average terrain ruggedness as an average of all TRI values per 50 m pixel in the buffer; Table 1; ruggedness covariate) developed by Riley et al. (1999) and a digital elevation model raster with a 50 m pixel spatial resolution (Kartverket 2016). TRI was calculated to quantify topographic heterogeneity at CT sites and represented the sum change in elevation between a pixel and its eight neighbouring pixels. We created a binary categorical variable denoting if

Table 1. Habitat covariates for calculating occupancy, site use and detection probability of pine marten *Martes martes* in Norway.

Covariate	Description	Expected effect	References
total_forest	Forest with > 30% canopy cover formed by > 5 m trees (Scots pine, Norway spruce, and/or deciduous trees) + clearcuts (stands 0–10 years, no canopy cover)	+ve on occupancy	Potvin et al. (2000), Brainerd and Rolstad (2002)
clearcut_grid	Proportion of stands 0–10 years with no canopy cover	−ve on occupancy	Potvin et al. (2000), Brainerd and Rolstad (2002)
old_forest_grid	Proportion of stand ≥ 120 years with > 30% canopy cover. Comprised of Scots pine, Norway spruce, and/or deciduous trees	+ve on occupancy	Storch et al. (1990), Brainerd and Rolstad (2002)
study_area	Artificial delineations with CT sites clusters. Areas 1–5 (Fig. 1) range from southern to northern Norway. Added to correct for potential differences among study areas that was not incorporated in the covariates	Control variable	
ruggedness	Terrain ruggedness index in each CT buffer from digital elevation model with a 50 m spatial resolution	+ve on site-use	Jędrzejewski et al. (1993), Pulliainen (1981)
clearcut_site	Clearcut stand of 0–10 years with no canopy cover. Binary categorical variable: 1 = clearcut, 0 = no clearcut for each CT buffer	−ve on site use	Potvin et al. (2000), Brainerd and Rolstad (2002)
old_forest_site	Old forest stand of ≥ 120 years with > 30% canopy cover formed by > 5 m trees (Scots pine, Norway, and/or deciduous trees). Binary categorical variable: 1 = old forest, 0 = no old forest for each CT buffer	+ve on site-use	Storch et al. (1990), Brainerd and Rolstad (2002)
feature	Dominant habitat feature present in the field of view of each CT (i.e. boulders, dense vegetation, open area, or sparse vegetation)	Higher detection probability with boulders	Jędrzejewski et al. (1993), Pulliainen (1981)
temperature	Mean temperature calculated over a five day period for each period that a CT was active	+ve on detection probability	Buskirk et al. (1988), Zalewski (2006)
snow	Mean snow depth calculated over a five day period for each period that a CT was active	+ve on detection probability	Cano-Martínez et al. (2021)
clearcut_detection	Clearcut stand of 0–10 years with no canopy cover	−ve on detection probability	Potvin et al. (2000), Brainerd and Rolstad (2002)
snow×clearcut_detection	Snow interaction with clearcut. Mean snow depth calculated over a five day period for each period that a CT was active	−ve with clearcut on detection probability	Storch et al. (1990), Pulliainen and Ollinmäki (1996)

there was a clearcut within each CT site buffer (0 = no clearcut, 1 = clearcut; also referred to as clearcut nearby hereafter, Table 1; *clearcut_site* covariate). We also created a binary categorical variable for old forest denoting if there was a patch of old forest within each CT site buffer (0 = no old forest, 1 = old forest; also referred to as old forest nearby hereafter, Table 1; *old_forest_site* covariate).

We included a habitat feature covariate (Table 1; *feature* covariate) as a variable on the detection probability as the CTs faced different types of dominant habitat features (e.g. sparse vegetation compared to dense vegetation) which may make pine martens more visible to CTs (Hofmeester et al. 2019). We classified (by visual inspection of CT site images) the dominant habitat features at each CT site as 1) boulders, 2) dense vegetation, 3) open area and 4) sparse vegetation, based on the presence of such features in the field of view of the CT (Supporting information, for image classification example). We obtained temperature and snow depth data from the Norwegian Meteorological Institute (2022). We included a five-day mean daily temperature as a temporally varying covariate on the detection probability (Table 1; *temperature* covariate). The *temperature* covariate was used to control for reduced marten activity at low temperatures (Buskirk et al. 1988, Thompson and Colgan 1994, Zalewski 2006), as well as to help account for the varying ability of CTs to detect pine marten at different temperatures (McIntyre et al. 2020). Pine marten activity is the most important factor here, as we aggregate over five days period, and there can be variations in temperature within this period. We also included the five-day mean daily snow depth as a temporally varying covariate (Table 1; *snow* covariate). Snow depth may increase detection of pine marten if individuals are elevated and can be better detected by CT, while pine martens might prefer or avoid locations with deep snow with respect to prey accessibility/predator avoidance (Willebrand et al. 2017, Cano-Martínez et al. 2021). Moreover, we used temperature and snow depth covariates to account for seasonal effects as these can better represent the range of environmental conditions experienced over the spatial range of our study areas (Fig. 1). Also, compared to equinox seasons, temperature and snow depth are more biologically relevant to our study species across such a wide latitudinal gradient. The clearcut covariate used to calculated the detection probability (Table 1; *clearcut_detection* covariate) was generated in the same way as the *clearcut_site* covariate (see above). We also included an interaction between snow depth and clearcut (Table 1; *snow×clearcut_detection* covariate). This was to determine if the effect of snow depth on the detection probability at a CT site was influenced by the presence of a clearcut nearby. All habitat covariates were extracted using ArcGIS Pro (ESRI 2020; ver. 2.5) and R (www.r-project.org; ver. R-4.1.2).

Model implementation

We used the following logistic regression equations in our multi-scale occupancy model:

$$\text{logit}\left(\psi_{iy}\right) = a_{0y} + a_1 \text{ total.forest}_i + a_2 \text{ clearcut.grid}_{iy} + a_3 \text{ old.forest.grid}_{iy} + a_4 \text{ study} \cdot \text{area}_i \tag{4}$$

$$\text{logit}\left(\theta_{ijy}\right) = \beta_{0y} + \beta_1 \text{ ruggedness}_{ij} + \beta_2 \text{ clearcut.site}_{ijy} + \beta_3 \times \text{old} \cdot \text{forest} \cdot \text{site}_{ijy} \tag{5}$$

$$\text{logit}\left(\rho_{ijky}\right) = \delta_{0y} + \delta_1 \text{ temperature}_{ijk} + \delta_2 \text{ feature}_{ijk} + \delta_3 \text{ snow}_{ij} + \delta_4 \text{ clearcut} \cdot \text{detection}_{ijy} + \delta_5 \text{ snow}_{ijk} \times \text{clearcut} \cdot \text{detection}_{ijy} \tag{6}$$

We included an intercept per year to estimate an average occupancy (α_{0y}), site use (β_{0y}) and detection (δ_{0y}) probability per year. Parameters $\alpha_1 - \alpha_4$, $\beta_1 - \beta_3$, and $\delta_1 - \delta_5$ represent the slopes for the different covariates, the interaction between covariates is denoted by '×'.

Using the z-transformation (i.e. subtracting the mean and dividing by the standard deviation of variable), we standardized all continuous covariates (Supporting information, for the range of unscaled covariates). Within each hierarchical level in the model, we checked for collinearity. We made sure that the Pearson correlation coefficient for the pairs of continuous covariates at each scale was below 0.6 (Zuur et al. 2010) to reduce collinearity issues. We calculated the variance inflation factors (VIFs) between multiple covariates at each scale and we checked that all covariate VIFs were below 3.0 (Zuur et al. 2010).

We estimated the multi-scale occupancy model in a Bayesian framework using Markov chain Monte Carlo (MCMC), ran in JAGS (Plummer 2003; ver. 4.3.0), and called from R (www.r-project.org; ver. R-4.1.2) through the jagsUI package (Kellner 2021; ver. 1.5.2). We used non-informative priors for all parameters (i.e. a uniform distribution from 0 to 1 for all intercepts (before logit transformation) and a normal distribution with a mean of 0 and a precision of 0.2 for all slopes). We ran 60 000 iterations (+burn-in of 20 000) and thinned by 10 on three chains. We determined if the model converged by assessing convergence statistic R-hat ($R < 1.1$; Gelman and Hill 2007) and trace plots (Brooks and Gelman 1998). We estimated the highest density interval (HDI) using the bayestestR package (Makowski et al. 2019) and reported the estimates of the slope for the change in occurrence on a logit scale (median and 89% credible interval; McElreath 2020) for all parameters. We interpreted any non-overlapping 89% credible intervals as evidence for a difference between estimates (Schenker and Gentleman 2001, McElreath 2020). Model code and data for the analyses are provided in Zenodo repository (Angoh et al. 2023).

Results

We obtained a total of 1 819 pine marten observations at 281 CT sites in 192 out of 323 grid cells. The total number of

camera trap days (sum of days for all 641 CT sites) was 384 428 days with a mean of 604.45 trap days per CT site.

Occupancy of 100 km² grid cells (landscape scale)

There was weak evidence for increased pine marten occupancy with proportion of forest cover in a 100 km² grid cell (α_{total_forest} = 0.42, 89% HDI = −0.09 to 0.98; Fig. 2a). We detected no clear association between pine marten occupancy and the proportion of old forest ($\alpha_{old\_forest\_grid}$ = 0.62, 89% HDI = −0.46 to 1.98; Fig. 2b) or the proportion of clearcuts in the landscape ($\alpha_{clearcut\_grid}$ = 0.38, 89% HDI = −0.52 to 1.26; Fig. 2c). The mean occupancy probability was high across all years (between 0.86 and 0.94) and study areas (between 0.78 and 0.94; Supporting information).

Site use at CT locations (habitat-patch scale)

When CTs were ≤ 100 m from old forest patches, site use probability was higher ($\beta_{old\_forest\_site}$ = 0.49, 89% HDI = 0.19 to 0.80; Fig. 3a). Site use probability of pine martens did not differ regardless of clearcut proximity ($\beta_{clearcut\_site}$ = 0.02, 89% HDI = −0.22 to 0.28; Fig. 3b). We found strong support for increased site use with increasing ruggedness at CT sites ($\beta_{ruggedness}$ = 0.38, 89% HDI = 0.27 to 0.49; Fig. 3c).

Detection probability

Detection probability of pine martens increased with snow depth at CT sites > 100 m from clearcuts (δ_{snow} = 0.19, 89% HDI = 0.15 to 0.22; Fig. 4a, blue line). In contrast, detection probability decreased with snow depth at CT sites ≤ 100 m from clearcuts ($\delta_{snow \times clearcutdetection}$ = −0.02, 89% HDI = −0.03 to −0.01; Fig. 4a, black line). Detection probability increased with increasing temperature ($\delta_{temperature}$ = 0.40, 89% HDI = 0.37 to 0.42; Fig. 4b). Cover type significantly affected detection probability (Fig. 4c). Pine martens were detected more frequently at sites with CTs facing towards boulders compared to sites with CTs that were aimed at sparse or dense vegetation or open areas. Furthermore, the detection probability at sites with CTs aimed at sparse vegetation was higher than sites with CTs pointed at dense vegetation. We found no differences in detection probabilities between CTs aimed at dense vegetation or open areas.

Discussion

In this study, we used a multi-year nation-wide camera trapping effort to study the effects of clearcutting practices on the occurrence of pine martens at multiple spatial scales. We found that pine martens have a broad tolerance for current forestry practices at the landscape scale in Norway. There was only marginal change in probability of pine marten occupancy at the landscape scale. However, at the habitat-patch scale, pine marten site use was greater in or near old forest patches compared to sites without old forests. At both the habitat-patch and landscape scales, there was no effect of recent clearcuts on site use and occupancy, respectively. The detection probability decreased with increasing snow cover only at sites proximal to clearcuts.

Our findings at the habitat-patch scale (Fig. 3a), corroborate earlier studies conducted in Scandinavia, which document pine marten preference of late seral stage forests at fine spatial scales (Storch et al. 1990, Brainerd and Rolstad 2002). In a study based on radiotelemetry in Norway and Sweden, Brainerd and Rolstad (2002) found that mature (≥ 20 m tall) spruce-dominated forest was strongly preferred by pine martens year-round. Nevertheless, an analysis of forest age alone did not indicate strong and consistent preference for forests ≥ 70 years old (Brainerd et al. 1994). Compared to Brainerd et al. (1994), we described old forest as ≥ 120 years old forest, which would be the forest type with habitat structures most similar to natural old growth forests in Norway. This could have contributed to the clearer pattern with increased site use of pine marten in old forest habitats that we observed, suggesting that pine martens might prefer old forest habitats. However, this does not hold at the landscape scale (Fig. 2b) and suggests that pine martens can live in a mixed landscape of old forests and other habitat types at the scale of landscape fragmentation that occurs in Norway. In accordance with Moll et al. (2016) and similar findings in other studies in Europe (Birks et al. 2005, Pereboom et al. 2008, Balestrieri et al. 2010, Mergey et al. 2011, Caryl et al. 2012, Lombardini et al. 2015, Remonti et al. 2022), our results at a broader spatial scale support growing concensus that pine martens can occupy a broad range of forest/land use types in Norway.

We also found that pine marten site use was not affected by clearcut proximity (Fig. 3b). In line with other studies (Pulliainen and Ollinmäki 1996, Sidorovich et al. 2010, Caryl et al. 2012), our results suggest that pine martens do not avoid areas near clearcuts. Pine martens could be using clearcut edges to take advantage of the higher availability of small mammalian prey relying on open habitats (e.g. field voles), while still having access to important structures and forest-associated prey in older forests (Brainerd 1990, Thompson and Harestad 1994, Pulliainen and Ollinmäki 1996, Sidorovich et al. 2010, Caryl et al. 2012). Moreover, as the proportion of clearcuts increase at the landscape scale, the occupancy probability of pine marten remained constant. The proportion of clearcuts (i.e. between 0 and 0.22 of total forest per grid cell) in our study is less than the minimum forest cover removal of 20–30% beyond which Thompson and Harestad (1994) predicted a decline in the carrying capacity for American martens. Moreover, the average size of a clearcut (0.08 km²; Statistics Norway 2003) in Norway is relatively small compared to the reported home range sizes of pine marten in Scandinavia (between 2–25 km²; Brainerd 1997). When interspersed in a matrix containing adequate forest cover, clearcuts could be creating biotic diversity in the landscape and this could benefit pine martens (Brainerd 1990, Hansson 1994, Caryl et al. 2012). However, with an anticipated increase in Norwegian timber harvest in the next
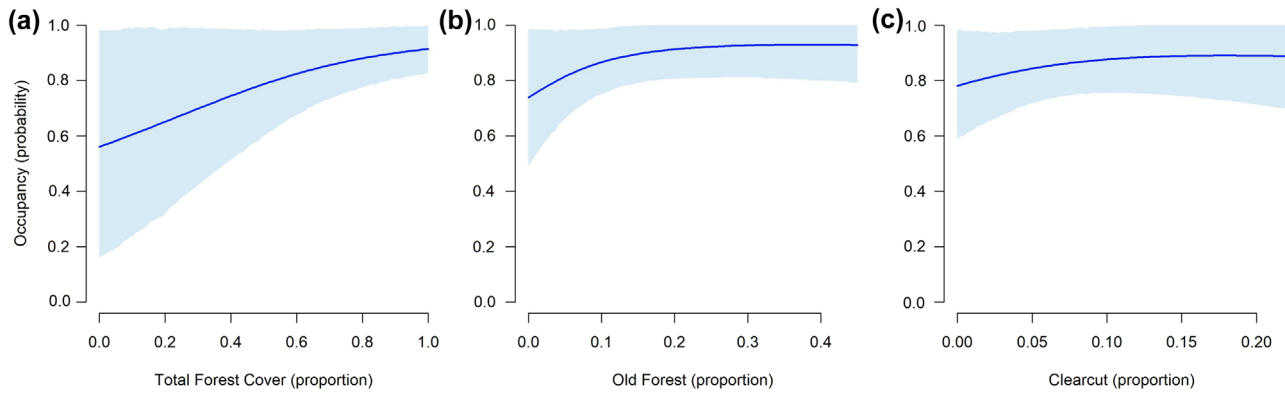
Figure 2. Relationship between occupancy probability and (a) total forest cover, (b) old forest and (c) clearcuts proportions. The line indicates the mean estimates of occupancy probability (for year 2021), 89% credible interval (highest density interval) included (polygon). The posterior estimates (log odds) of the covariates relative to the intercept was back transformed to obtain occupancy probability.

two decades (Olofsson 2015) and subsequent intensification of forest management, maintaining connectivity and preserving older forest habitats will be of essence to limit potential effects of fragmentation and forest loss by clearcuts on pine martens.

Our CTs were only placed in forest habitats (rather than random placement in the landscape). We were therefore unable to determine how different measures of habitat fragmentation may influence pine marten occurrence. Hargis et al. (1999) found that an increasing degree of forest fragmentation had a negative influence on American martens as measured by capture rates. The effects of forest fragmentation at the landscape scale on pine marten occupancy warrants further research throughout its distributional range. Further investigation would also be required to separate the effects of habitat loss and effects of landscape patterns (e.g. forest interior, forest edge, forest patch size, and forest aggregation) on pine martens. Another caveat is that

we did not use finer forest habitat age classes other than ≤ 10 years (clearcuts) and ≥ 120 years (old forest habitat) in this study. Forest between 11 and 119 years old likely contain much variation in their suitability for pine martens, but this variation is not captured by our study. Brainerd and Rolstad (2002) found that although pine martens selected mature spruce-dominated industrial forest and avoided clearcuts, they were able to exploit a wide range of forest stand classes. More research is needed to determine whether loss and fragmentation of forests at intermediate growth stages influence pine marten occupancy at the landscape scale, given a rotation cycle between 60 and 120 years in boreal Scandinavia (Kuuluvainen 2009).

In addition to the effects of forest habitat types on pine marten occurrence, we also tested if terrain ruggedness influenced site use by pine martens. We found that site use probability increased with higher terrain ruggedness (Fig. 3c). Similarly, pine martens were detected more frequently at
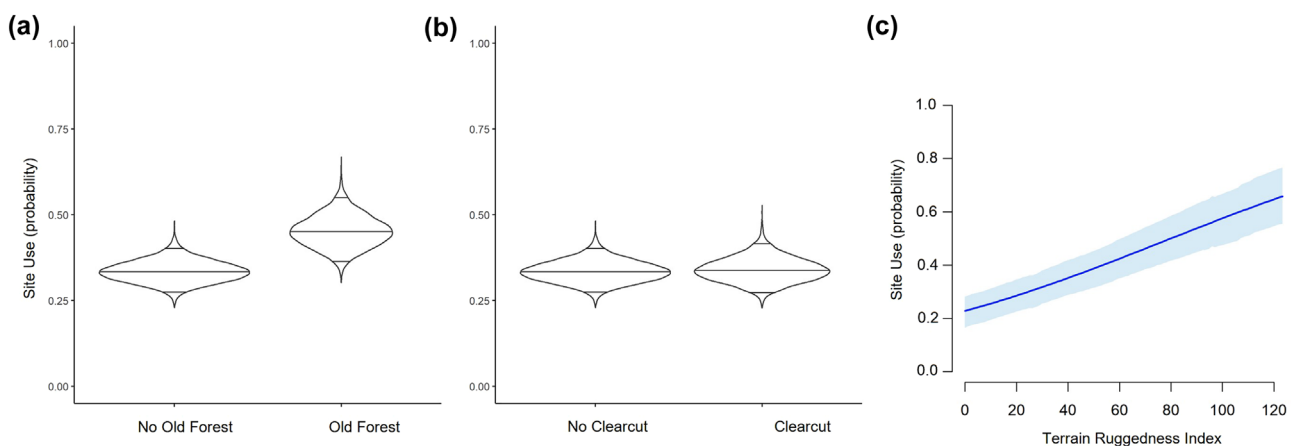

Figure 3. Violin plot of the site use probability for (a) old forest and (b) clearcut at the habitat-patch level. The posterior estimates of each parameter relative to the intercept were back transformed to obtain the site use probabilities. The middle horizontal bar on each violin curve indicates the median and the horizontal bars on either side indicate the upper and lower limit of the 89% credible interval (highest density interval). (c) Relationship between site use and terrain ruggedness index. The line indicates the mean estimates of site use probability (for year 2021), 85% credible interval (highest density interval) included (polygon). The posterior estimates (log odds) of the covariates relative to the intercept was back transformed to obtain site use probability.
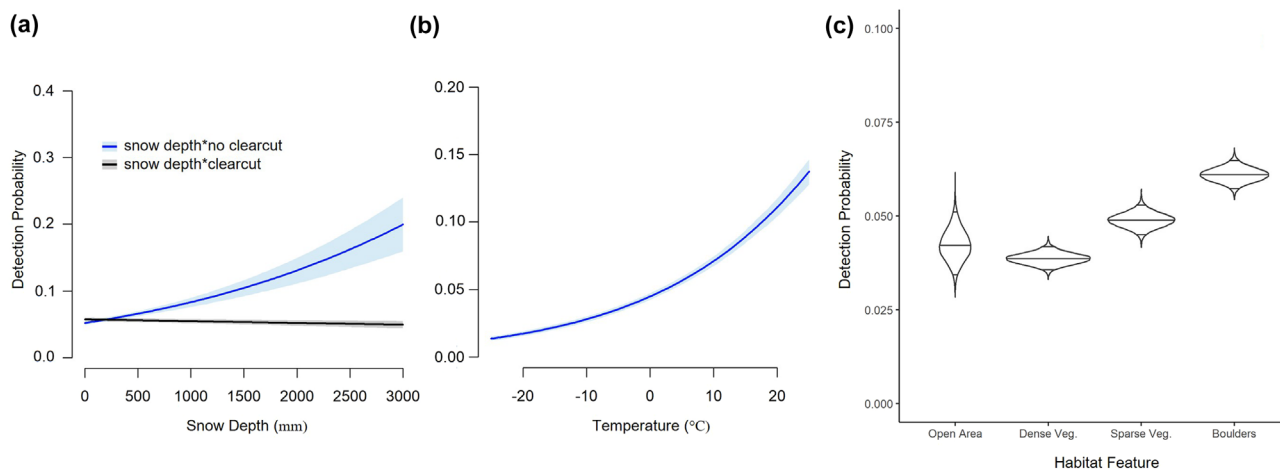
Figure 4. Relationship between detection probability and (a) snow × clearcut (black line) and snow × no clearcut (blue line), and (b) temperature. The line indicates the mean estimates of detection probability, 89% credible interval (highest density interval) included (polygon). The posterior estimates (log odds) of the temperature, snow, and snow × clearcut covariates relative to the intercept was back transformed to obtain detection probability. (c) Violin plot of the detection probability for habitat feature type. The posterior estimates of each parameter relative to the intercept were back transformed to obtain the detection probability. The middle horizontal bar on each violin curve indicates the median and the horizontal bars on either side indicate the upper and lower limit of the 89% credible interval (highest density interval).

CTs facing rocky boulder patches (Fig. 4c). Rugged terrains and rocky boulder patches, may provide greater access to subterranean and subnivean spaces. Attributes of subnivean spaces, such as thermal resistance, depth, and structural stability (Glass et al. 2021), may be crucial for foraging success, thermoregulation, reproduction (denning), and predator avoidance (Lindström et al. 1995, Wilbert et al. 2000). Jędrzejewski et al. (1993) found that pine martens take advantage of subnivean spaces which are used by preferred prey such as *Clethrionomys* voles. Also, given their elongated body, short fur, high surface to volume ratio, and resulting high lower critical body temperature (16°C), pine martens are sensitive to cold temperatures (Worthen and Kilgore 1981, Buskirk et al. 1988, Harlow 1994). Hence, thermal shelter provided by subterranean and subnivean dens may be essential for pine martens especially in winter (Buskirk et al. 1988, Brainerd et al. 1995, Zalewski 1997). Access to underground sites may complement the use of arboreal cavities in large trees (for shelter and cover, Pulliainen 1981, Wilbert et al. 2000) where these are scarce. Hence, the lack of adequate overhead cover and above-ground forest structures in clearcuts (Fisher and Wilkinson 2005) may to some extent be mitigated by access to subterranean and subnivean spaces (Brainerd et al. 1995).

The presence of clearcuts near a CT site negatively affected detection probability as snow depth increased. We did not observe this negative relationship between detection probability and snow depth in the absence of nearby clearcuts (i.e. detection probability increased with increasing snow depth and no clearcut; Fig. 4a). As snow depth increases, subnivean access to rodents is reduced in more open areas (Jędrzejewski et al. 1993, Pulliainen and Ollinmäki 1996, Zalewski et al. 2006, Willebrand et al. 2017). In north-central Idaho, Koehler and Hornocker (1977) found that American marten used forests with low canopy cover

(< 30%) more often when snow depth is low compared to when it is high. When snow cover is deep in open areas, the American marten can less easily dig through and hunt rodents (Koehler and Hornocker 1977, Steventon and Major 1982, Thompson and Colgan 1994). During the winter, field voles in clearcuts may not be accessible to pine martens if snow depth is high and snow is impenetrable. This may make clearcuts less attractive to pine martens (Storch et al. 1990, Pulliainen and Ollinmäki 1996, Helldin 2000). Hence, within a matrix containing clearcuts, late seral stage forests which typically harbour other important prey species (e.g. mountain hares *Lepus timidus*, red squirrels, bank voles *Clethrionomys glareolus*, capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix* and hazel grouse *Tetrastes bonasia*) that are accessible during heavy snow conditions are essential (Swenson and Angelstam 1993, Hansson 1994, Pulliainen and Ollinmäki 1996, Olsson et al. 2005, Willebrand et al. 2017). Lush canopy cover in old forests (especially spruce-dominated stands) can influence snow hardness and depth, making the excavation of small mammals easier for pine martens (Wabakken 1985). Moreover, Willebrand et al. (2017) found that with increasing snow depth, red foxes exhibit lower hunting success compared to pine martens in conifer forests (> 1.5 m) where both mesocarnivore species occur. This and our finding that pine marten detection probability increased with increasing snow depth only in forests with no clearcuts nearby (Fig. 4a) suggest that this species may take advantage of areas with deeper snow in older forest stands to avoid competition with red fox.

Finally, we found that pine marten detection probability was positively correlated with temperature (Fig. 4b). As previously mentioned, pine martens are sensitive to cold temperatures, and they may reduce their activity and seek shelter to conserve energy as temperature decreases (Worthen and Kilgore 1981, Buskirk et al. 1988). Accordingly, at locations

where cold temperatures are experienced, pine martens would be captured on CTs less often. Therefore, we interpret this response as a biological response in the activity of pine martens. In contrast, we interpret the differences in detection probability among microsites as a combination of technical CT and biological factors. Areas with sparse vegetation or many boulders may make pine martens more visible to CTs compared to dense vegetation (Fig. 4c) (Hofmeester et al. 2019). However, detection probability was lower in open areas, and this is presumably caused by lower pine marten use of open areas.

In light of our findings, we conclude that in a forest dominated landscape fragmented by clearcutting practices, pine martens occur widely, although we do see some associations with older forest habitats. We suggest that habitat structure (e.g. terrain ruggedness and the presence of rocky fields) could mitigate a lack of important old forest attributes, possibly via providing access to subnivean and subterranean spaces. We observed that temporal changes in environmental conditions (e.g. snow depth and temperature) influence how often a pine marten is detected in different types of habitats . Hence, while assessing the effects of forestry practices on pine marten populations, such temporal changes in environmental conditions should also be accounted for in order to minimise biases while evaluating pine marten detection and subsequent occurrence estimates. These findings may be relevant to the conservation of pine martens and other forest-dependent species that are found within intensively managed forests.

Author contributions

Siow Yan Jennifer Angoh: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Neri H. Thorsen**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – review and editing (supporting). **Tim R. Hofmeester**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Writing – review and editing (supporting). **John Odden**: Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Methodology (supporting); Project administration (supporting); Writing – review and editing (supporting). **John D. C. Linnell**: Conceptualization (equal); Data curation (supporting); Writing – review and editing (supporting). **Scott M. Brainerd**: Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Project administration (lead); Supervision (lead); Writing – review and editing (supporting).

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Data availability statement

Data and code are available from the Zenodo Repository: https://zenodo.org/badge/latestdoi/581188687 (Angoh et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ahti, T., Hämet-Ahti, L. and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. – Ann. Bot. Fenn. 5: 169–211.

Alldredge, J. R. and Gwiswold, J. 2006. Design and analysis of resource selection studies for categorical resource variables. – J. Wildl. Manage. 70: 337–346.

Andrén, H. and Delin, A. 1994. Habitat selection in the Eurasian red squirrel, *Sciurus vulgaris*, in relation to forest fragmentation. – Oikos 70: 43–48.

Angoh, S. Y. J., Thorsen, N. H., Hofmeester, T. R., Odden, J., Linnell, J. D. C. and Brainerd, S. M. 2023. Data from: Forestry and environmental conditions as determinants of pine marten *Martes martes* occurrence in Norway. – Zenodo Repository, https://zenodo.org/badge/latestdoi/581188687.

Balestrieri, A., Remonti, L., Ruiz-González, A., Gómez-Moliner, B. J., Vergara, M. and Prigioni, C. 2010. Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). – Mamm. Biol. 75: 412–419.

Bendiksen, E., Brandrud, E. and Røsok, Ø. 2008. Boreale lauvskoger i Norge Naturverdier og udekket vernebehov (in Norwegian). – NINA Report 367, 331 pp.

Birks, J. D. S., Messenger, J. E. and Halliwell, E. C. 2005. Diversity of den sites used by pine martens *Martes martes*: a response to the scarcity of arboreal cavities? – Mamm. Rev. 35: 313–320.

Brainerd, S. M. 1990. The pine marten and forest fragmentation a review and general hypothesis. – In: Myrberget, S. (ed.), Transactions of the nineteenth international conference of game biologists. pp. 421–434.

Brainerd, S. M., Helldin, J. -O., Lindström, E. R. and Rolstad, J. 1994. Eurasian pine martens and old industrial forest in southern boreal Scandinavia. – In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. and Powell, R. A. (eds), Martens, sables, and fishers: biology and conservation. Cornell University Press, pp. 343–354.

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. Fenn. 32: 151–157.

Brainerd, S. 1997. Habitat selection and range use by the Eurasian pine marten (*Martes martes*) in relation to commercial forestry practices in southern boreal Scandinavia. – PhD thesis, Agriculture University of Norway, Norway.

Brainerd, S. M. and Rolstad, J. 2002. Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. – Wildl. Biol. 8: 289–297.

Brooks, S. P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. – J. Comput. Graph. Stat. 7: 434–455.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E. and Boutin, S. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. – J. Appl. Ecol. 52: 675–685.

Buskirk, S. W., Harlow, H. J. and Forrest, S. C. 1988. Temperature regulation in American marten (*Martes americana*) in winter. – Natl Geogr. Res. 4: 208–218.

Cano-Martínez, R., Carricondo-Sanchez, D., Devineau, O. and Odden, M., 2021. Small rodent cycles influence interactions among predators in a boreal forest ecosystem. – Mamm. Res. 66: 583–593.

Caryl, F. M., Quine, C. P. and Park, K. J. 2012. Martens in the matrix: the importance of non-forested habitats for forest carnivores in fragmented landscapes. – J. Mamm. 93: 464–474.

CCKP. 2021. Climate change knowledge portal for development practitioners and policy makers. – https://climateknowledge-portal.worldbank.org/country/norway.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villeger, S. and Mouquet, N. 2010. Defining and measuring ecological specialization. – J. Appl. Ecol. 47: 15–25.

Efford, M. G. and Dawson, D. K. 2012. Occupancy in continuous habitat. – Ecosphere 3: 32.

ESRI. 2020. ArcGIS Pro, ver. 2.5. – Environmental Systems Research Institute Inc. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Esseen, P. -A., Ehnström, B., Ericson, L. and Sjöberg, K. 1997. Boreal forest. – Ecol. Bull. 46: 16–47.

Fisher, J. T. and Wilkinson, L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. – Mamm. Rev. 35: 51–81.

Fridman, J. and Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. – For. Ecol. Manage. 131: 23–36.

Gelman, A. and Hill, J. 2007. Data analysis using regression and multilevel/ hierarchical models. – In: Alvarez, R. M., Beck, N. L. and Wu, L. L. (eds). Cambridge University Press, pp. 352–358.

Gjertsen, A. K. and Nilsen, J. -E. 2012. SAT-SKOG. Et skogkart basert på tolking av satellittbilder (in Norwegian). – Norsk institutt for skog og landskap Report 23, 54 pp.

Glass, T. W., Breed, G. A., Liston, G. E., Reinking, A. K., Robards, M. D. and Kielland, K. 2021. Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. – Oecologia 195: 887–899.

Gustafsson, L., Kouki, J. and Sverdrup-Thygeson, A. 2010. Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. – Scand. J. For. Res. 25: 295–308.

Hansen, M. C., Potapov, P., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., Kommareddy, A., Egorov, A., Chini, L., Justice, C. and Townshend, J. R. 2013. High-resolution global maps of 21st century forest cover change. – Science 342: 846–850.

Hansson, L. 1994. Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. – Landsc. Ecol. 9: 105–115.

Hargis, C. D., Bissonette, J. A. and Turner, D. L. 1999. The influence of forest fragmentation and landscape pattern on American martens. – J. Appl. Ecol. 36: 157–172.

Harlow, H. J. 1994. Trade-offs associated with the size and shape of American martens. – In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. and Powell, R. A. (eds), Martens, sables and fishers: Biology and conservation. ComelI University Press, pp. 391–403.

Heggem, E. S. F., Mathisen, H. and Frydenlund, J. 2019. AR50–Arealressurskart i målestokk 1:50 000. Et heldekkende arealressurskart for jord-og skogbruk (in Norwegian). – NIBIO Report 5, 41 pp.

Helldin, J. -O. 2000. Population trends and harvest management of pine marten *Martes martes* in Scandinavia. – Wildl. Biol. 6: 111–120.

Herrero, J., Kranz, A., Skumatov, D., Abramov, A. V., Maran, T. and Monakhov, V. G. 2016. The IUCN red list of threatened species 2016. – International Union for Conservation of Nature (IUCN).

Hoen, H. F. and Winther, G. 1993. Multiple use forestry and preservation of coniferous forests in Norway: a study of attitudes and willingness to pay. – Scand. J. For. Res. 8: 266–280.

Hofmeester, T. R., Cromsigt, J. P. G. M., Odden, J., Andrén, H., Kindberg, J. and Linnell, J. D. C. 2019. Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. – Ecol. Evol. 9: 2320–2336.

Hofmeester, T. R., Thorsen, N. H., Cromsigt, J. P. G. M., Kindberg, J., Andrén, H., Linnell, J. D. C. and Odden, J. 2021. Effects of camera-trap placement and number on detection of members of a mammalian assemblage. – Ecosphere 12: e03662.

Jędrzejewski, W., Zalewski, A. and Jędrzejewski, B. 1993. Foraging by pine marten *Martes martes* in relation to food resources in Bialowieza National Park, Poland. – Acta Theriol. 38: 405–426.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.

Kartverket. 2016. Høyde prosjekter WMS. – https://www.kartverket.no/api-og-data/terrengdata#_ga=2.104350472.984423700.1671528033-891813748.1671528033.

Kellner, K. 2021. jagsUI: a wrapper around 'rjags' to Streamline 'JAGS' analyses, ver. 1.5.2. – https://CRAN.R-project.org/package=jagsUI.

Kery, M. and Royle, J. 2015. Modeling static occurrence and species distributions using site-occupancy models. – In: Kery, M. and Royle, J. (eds), Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS, 1st ed., vol. 1. Academic Press, pp. 600–608.

Koehler, G. M. and Hornocker, M. G. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. – J. Wildl. Manag. 41: 500–505.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. – Ambio 38: 309–315.

Kuuluvainen, T. and Gauthier, S. 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. – For. Ecosyst. 5: 26.

Lindström, E., Brainerd, S., Helldin, J. O. and Overskaug, K. 1995. Pine marten–red fox interactions – A case of intraguild predation? – Ann. Zool. Fenn. 32: 123–130.

Linnell, J. D. C., Odden, J., Pedersen, V. and Andersen, R. 1998. Records of intra-guild predation by Eurasian Lynx, *Lynx lynx*. – Canad. Field Nat. 112: 707–708.

Lombardini, M., Cinerari, C. E., Murru, M., Vidus Rosin, A., Mazzoleni, L. and Meriggi, A. 2015. Habitat requirements of Eurasian pine marten *Martes martes* in a Mediterranean environment. – Mamm. Res. 60: 97–105.

Lyly, M. S., Villers, A., Koivisto, E., Helle, P., Ollila, T. and Korpimäki, E. 2015. Avian top predator and the landscape of fear: responses of mammalian mesopredators to risk imposed by the golden eagle. – Ecol. Evol. 5: 503–514.

Makowski, D., Ben-Shachar, M. and Lüdecke, D. 2019. bayestestR: describing effects and their uncertainty, existence and significance within the bayesian framework. – J. Open Source Softw. 4: 1541.

McElreath, R. 2020. Statistical rethinking: a Bayesian course with examples in R and Stan – In: McElreath, R. (ed), 2nd ed., Chapman and Hall/CRC Press, 469 pp.

McIntyre, T., Majelantle, T. L., Slip, D. J. and Harcourt, R. G. 2020. Quantifying imperfect camera-trap detection probabilities: implications for density modelling. – Wildl. Res. 47: 177–185.

Mergey, M., Helder, R. and Roeder, J. J. 2011. Effect of forest fragmentation on space-use patterns in the European pine marten (*Martes martes*). – J. Mamm. 92: 328–335.

Norwegian Meteorological Institute. 2022. – https://www.met.no/.

Moll, R. J., Kilshaw, K., Montgomery, R. A., Abade, L., Campbell, R. D., Harrington, L. A., Millspaugh, J. J., Birks, J. D. S. and Macdonald, D. W. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. – J. Zool. 300: 177–185.

Monakhov, V. G., Bondarev A. Y., Tyutenkov O. Y. 2020. On the pine marten (*Martes martes*) morphology in the upper Ob River basin (in Russian with English summary). – Tomsk State Univ. J. Biol. 49: 91–106.

Monakhov, V. G. 2022. *Martes martes* (Carnivora: Mustelidae). – Mamm. Species 54: seac007.

Mordecai, R. S., Mattsson, B. J., Tzilkowski, C. J. and Cooper, R. J. 2011. Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. – J. Appl. Ecol. 48: 56–66.

Olofsson, G. 2015. SKOG22 nasjonal strategi for skog- og trenæringen (in Norwegian). – Norges forskningsråd – Report SKOG22, 48 pp.

Olsson, G. E., White, N., Hjältén, J. and Ahlm, C. 2005. Habitat factors associated with bank voles (*Clethrionomys glareolus*) and concomitant hantavirus in northern Sweden. – Vector-Borne Zoon. Dis. 5: 315–323.

Orians, G. H. and Wittenberger, J. F. 1991. Spatial and temporal scales in habitat selection. – Am. Nat. 137: 29–49.

Pereboom, V., Mergey, M., Villerette, N., Helder, R., Gerard, J. F. and Lode, T. 2008. Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. – Can. J. Zool. 86: 983–991.

Plummer, M. 2003. JAGS: a program for analysis of bayesian graphical models using Gibbs sampling. – In: Hornik, K., Leisch, F. and Zeileis, A. (eds), Proceedings of the 3rd international workshop on distributed statistical computing (DSC 2003), pp. 1–10.

Potvin, F., Bélanger, L. and Lowell, K. 2000. Marten habitat selection in a clearcut boreal landscape. – Conserv. Biol. 14: 844–857.

Proulx, G., Aubry, K., Birks, J., Buskirk, S., Fortin, C., Frost, H., Krohn, W., Mayo, L., Monakhov, V., Payer, D., Saeki, M., Santos-Reis, M., Weir, R. and Zielinski, W. 2004. World distribution and status of the genus *Martes* in 2000. – In: Harrison, D. J., Fuller, A. K. and Proulx, G. (eds), Martens and fishers (*Martes*) in human-altered environments: an international perspective. Springer, pp. 21–76.

Pulliainen, E. 1981. Winter habitat selection, home range, and movements of the pine marten (*Martes martes*) in a Finnish Lapland forest. – In: Chapman, J. and Pursley, D. (eds), Worldwide Furbearer Conference Proceedings. Frostburg, pp. 1068–1087.

Pulliainen, E. and Ollinmäki, P. 1996. A long-term study of the winter food niche of the pine marten *Martes martes* in northern boreal Finland. – Acta Ther. 41: 337–352.

Remonti, L., Ruiz-González, A. and Balestrieri, A. 2022. Colonization of agricultural landscapes by the pine marten. – In: Do Linh San, E., Sato, J. J., Belant, J. L. and Somers, M. J. (eds), Small carnivores: evolution, ecology, behaviour, and conservation. Wiley Blackwell, pp. 275–291.

Riley, S., Degloria, S. and Elliot, S.D. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. – Int. J. Sci. 5: 23–27.

Schenker, N. and Gentleman, J. F. 2001. On judging the significance of differences by examining the overlap between confidence intervals. – Am. Stat. 55: 182–186.

Sidorovich, V. E., Sidorovich, A. A. and Krasko, D. A. 2010. Effect of felling on red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) diets in transitional mixed forest in Belarus. – Mamm. Biol. 75: 399–411.

Sjörs, H. 1963. Amphi-Atlantic zonation, Nemoral to Arctic. – In: Love, A. and Love, D. (eds), North Atlantic biota and their history. Pergamon Press, pp. 109–125.

Smedshaug, C. A., Selås, V., Lund, S. E. and Sonerud, G. A. 1999. The effect of a natural reduction of red fox *Vulpes vulpes* on small game hunting bags in Norway. – Wildl. Biol. 5: 157–166.

Statistics Norway. 2003. Harvested areas, by harvesting type (acres) (F) (completed series) 1999–2003: table 05349. – https://www.ssb.no/statbank/table/05349/tableViewLayout1.

Statistics Norway. 2022. Facts about forestry. – https://www.ssb.no/jord-skog-jakt-og-fiskeri/faktaside/skogbruk.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P. and McKelvey, K. 2018. Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. – Ecology 99: 172–183.

Steventon, J. D. and Major, J. T. 1982. Marten use of habitat in a commercially clear-cut forest. – J. Wildl. Manage. 46: 175–182.

Storch, I., Lindström, E. and de Jounge, J. 1990. Diet and habitat selection of the pine marten in relation to competition with the red fox. – Acta Theriol. 35: 311–320.

Swenson, J. E. and Angelstam, P. 1993. Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. – Can. J. Zool. 71: 1303–1310.

Thompson, I. D. 1994. Marten populations in uncut and logged boreal forests in Ontario. – J. Wildl. Manage. 58: 272–280.

Thompson, I. D. and Colgan, P. W. 1994. Marten activity in uncut and logged boreal forests in Ontario. – J. Wildl. Manage. 58: 280–288.

Thompson, I. D. and Harestad, A. S. 1994. Effects of logging on American martens, and models for habitat management. – In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. and Powell, R. A. (eds), Martens, sables, and fishers: biology and conservation. Cornell University Press, pp. 355–367.

Wabakken, P. 1985. Vintermæring, habitatbruk og jaktatferd hos mår (*Martes martes*) in sørøst-norsk barskog (in Norwegian). – MSc thesis, University of Oslo, Norway.

Wegge, P. and Rolstad, J. 2018. Cyclic small rodents in boreal forests and the effects of even-aged forest management: patterns and predictions from a long-term study in southeastern Norway. – For. Ecol. Manage. 422: 79–86.

Wilbert, C. J., Buskirk, S. W. and Gerow, K. G. 2000. Effects of weather and snow on habitat selection by American martens (*Martes americana*). – Can. J. Zool. 78: 1691–1696.

Willebrand, T., Willebrand, S., Jahren, T. and Marcström, V. 2017. Snow tracking reveals different foraging patterns of red foxes and pine martens. – Mamm. Res. 62: 331–340.

Worthen, G. L. and Kilgore, D. L. 1981. Metabolic rate of pine marten in relation to air temperature. – J. Mamm. 62: 624–628.

Zalewski, A. 1997. Factors affecting selection of resting site type by pine marten in primeval deciduous forests (Białowieża National Park, Poland). – Acta Theriol. 42: 271–288.

Zalewski, A. 2006. Factors affecting the duration of activity by pine martens (*Martes martes*) in the Białowieża National Park, Poland. – J. Zool. 251: 439–447.

Zalewski, A., Jędrzejewski, W. and Kelt, D. 2006. Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieża Forest (E Poland) compared with other European woodlands. – Ecography 29: 31–43.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol. 1: 3–14.