Inland Norway
University of
Applied Sciences

Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

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Which environmental factors influence pine marten populations and predation patterns in the boreal forest landscape?

PhD in Applied Ecology and Biotechnology
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Abstract

The pine marten (*Martes martes*) is commonly associated with mature coniferous forest stands at the northern extent of its range. Anthropogenic landscape alterations, including clearcutting and forest conversion to agricultural land, may negatively impact this species although information on this is limited. Hence, in this dissertation, my aim was to identify important environmental factors influencing pine marten occurrence, abundance and predation in a boreal forest landscape altered by forestry and agriculture. In **Paper I,** I analysed four years of nationwide data collected using camera traps deployed across Norway. I used a multi-scale occupancy model to investigate how pine marten occurrence at multiple spatial scales is related to clearcuts and old forests (≥120 years). At the landscape level, pine marten occupancy was independent of either of these habitat types. At the habitat patch level, pine marten site use was positively associated with the presence of old forests and terrain ruggedness but not associated with nearby clearcuts. The presence of boulders, snow depth, and temperature influenced the detection of pine martens. While previous studies suggest that pine martens prefer older forests and avoid clearcuts, current clearcutting practices in Norway do not appear to influence their occupancy at a broad scale. **Paper II** focused on the influence of environmental factors and microtine rodent abundance on pine marten population growth rates and abundance. Based on analyses of snow tracking indices, I found no evidence of cyclicity in pine marten populations in Hedmark, Norway, although their annual growth rates correlated positively with microtine rodent abundance as a function of increasing elevation. Pine marten abundance increased with elevation, snow depth, density of mature spruce forest, and microtine rodent abundance, but decreased with increased agricultural land density. Microtine rodents are important prey species, potentially influencing pine marten population dynamics in less productive, higher elevation areas with limited alternative prey. In **Paper III**, I used data from camera traps placed at capercaillie (*Tetrao urogallus*) nests to investigate how different landscape factors influence the risk of nest predation by pine martens and red foxes (*Vulpes vulpes*). Rates of nest predation by pine martens declined with increasing agricultural land density and tended to increase along gradients from clearcuts to forest interiors, while predation rates by red foxes were not influenced by these factors. The conversion of forests to open habitats appears to place pine martens at a disadvantage relative to red foxes, which are habitat generalists. This dissertation provides insights regarding the influence of biotic and abiotic factors on pine martens over time and space in human-modified landscapes. My findings could be instrumental in the effective management and conservation of pine martens and analogous species in Norway.

Sammendrag

Skogsmår (*Martes martes*), heretter kalt mår, er en art tilknyttet eldre barskog innenfor den nordlige delen av sitt utbredelsesområde. Flatehogst og andre menneskeskapte endringer i skogstruktur kan derfor påvirke denne arten negativt, men det foreligger fortsatt begrenset kunnskap om disse forholdene. Jeg ville derfor belyse ulike faktorers påvirkning på mårens romlige fordeling, bestandsdynamikk og deres innvirkning på byttedyr innenfor boreale barskoger preget av skog- og landbruk. I min første artikkel (**Artikkel 1**) analyserte jeg data fra viltkamera med flerskala occupancy-modeller for å undersøke hvordan mårens fordeling i landskapet var påvirket av blant annet forekomst av hogstflater og eldre barskog (≥120 år). På landskapsnivå var forekomst av mår uavhengig av begge disse variablene. Innenfor en mindre skala (habitatnivå) var derimot forekomst av mår knyttet til eldre skog og kupert terreng, men avstand til hogstflater hadde ingen betydning. Ved hvert viltkamera hadde forekomsten av store steiner, og endringer i temperatur og snødybde, betydning for mårens oppdagbarhet. **Artikkel II** fokuserer på hvordan variasjoner i tilgang til viktige byttedyr – smågnagere - og ulike miljøfaktorer sammen påvirker abundans og dynamikk i mårbestanden. Basert på analyse av snøsporingsindekser fant vi ingen tydelig flerårig syklus i mårbestanden i Hedmark, Norge. Allikevel var mårens vekstrate positivt korrelert med smågnagere, og effekten av dette økte langs en høydegradient. Mårens bestandstetthet var høyest i områder med mye snø, smågnagere, eldre granskog, og i høyereliggende områder, mens bestandstettheten var lavest i områder preget av jordbruk. Måren er en generalistpredator, og smågnagere ser ut til å ha stor betydning for dens bestandsdynamikk og tetthet, spesielt i mindre produktive og høyereliggende områder med få alternative byttedyr. I **Artikkel III** brukte jeg data fra viltkamera for å undersøke hvordan ulike landskapsparametere påvirket risiko for reirpredasjon hos storfugl (*Tetrao urogallus*) forårsaket av rødrev (*Vulpes vulpes*) og mår. Reirpredasjon fra mår minket nær jordbruksarealer og hogstflater, og økte i områder med sammenhengende skog. Rødrevens predasjonsmønster var ikke påvirket av disse faktorene. Landskapsendringer fra skog til åpne områder ser ut til å være en ulempe for mår, i motsetning til rødrev, som er en utpreget habitatgeneralist. Samlet gir denne avhandlingen innsikt i hvordan endringer i biotiske og abiotiske faktorer påvirker mår i landskap preget av menneskelig aktivitet, og dette kan gi verdifull kunnskap for forvaltningen av mår og tilknyttede viltarter i Norge.

Preface

My deepest gratitude goes to Scott Brainerd, my main supervisor, for graciously taking me on as his student and providing unwavering support. His expertise and guidance were instrumental during the planning stages of this dissertation, and I deeply appreciate his editing of numerous drafts of the papers and synopsis. Scott has been an inspiring mentor and friend. I will forever be grateful to him for leading the way up steep cliffs and guiding me through rough terrain.

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List of Papers

This dissertation is based on the following publication and manuscripts:

Paper I

Angoh, S.Y.J., Thorsen, N.H., Hofmeester, T.R., Odden, J., Linnell, J.D.C., Brainerd, S.M. 2023. Forestry and environmental conditions as determinants of pine marten *Martes martes* occurrence in Norway. Wildlife Biology. 2023: e01113.

Paper II

Angoh, S.Y.J., Nergaard, P.J., Jahren, T., Odden, M., Brainerd, S.M. How do microtine rodent abundance, snow and landscape parameters influence pine marten *Martes martes* population dynamics? Manuscript.

Paper III

Angoh, S.Y.J., Brainerd, S.M., Odden, M., Devineau, O., Jahren, T. The influence of landscape factors on capercaillie nest predation rates by two competing mesopredators: pine marten versus red fox. Manuscript.

1. Introduction

1.1. General Background

1.1.1. Human-Modified Forest Landscapes

Each species occupies a distinct ecological niche and thrives when an optimal level of key resources is available (Cushman et al. 2010). Beyond the tolerance threshold of some species for certain environmental factors, they cannot persist (Cushman & Wasserman 2017). Anthropogenic landscape alteration, including habitat loss and fragmentation, typically reduces habitat suitability and connectivity (Haddad et al. 2015; Mullu 2016; Stevens et al. 2006). Given that a species' habitat is often characterised by a suite of specific environmental variables (Cushman & Wasserman 2017), the alteration and degradation of habitats important for habitat specialists will likely lead to biodiversity loss (Balmford et al. 2003; Brooks et al. 2002). Forest-dwelling species account for over 80% of all threatened species globally due to widespread habitat loss (Luther et al. 2020). Intensified land use activities, including agriculture, logging, mining, and road construction, result in a net loss of over 12 million hectares of forests every year (Curtis et al. 2018; Hansen et al. 2013). Remaining fragments of forested areas can be small and isolated in a matrix of anthropogenic land cover types and vary in their capacity to sustain forest specialist species (Andrén 1994, 1997; Harvey et al. 2006; Hendershot et al. 2020; Arroyo-Rodríguez et al. 2020).

1.1.2. Winners and Losers

Forest specialists can be negatively impacted by the fragmentation, degradation, and depletion of their preferred habitats. These same processes may benefit habitat generalists that are able to exploit and thrive in these anthropogenic landscapes (McPeek 1996; Hinsley et al. 2009; Clavel et al. 2011; Carrara et al. 2015; Sozio & Mortelliti 2016; Rocha et al. 2018). For example, deforestation of the Lacandona rainforest will likely lead to the decline of the Mexican deer mouse (*Peromyscus mexicanus*), a forest specialist, while habitat generalists, such as the Toltec cotton rat (*Sigmodon toltecus*) and rice rat (*Oryzomys* sp.), may increase in abundance (Arce-Peña et al. 2019). Some habitat generalists may thrive in human-modified forest landscapes due to their ability to exploit a variety of habitats and anthropogenic food sources (Andrén 1994; Bino et al. 2010, Presley et al. 2019). For instance, red foxes (*Vulpes vulpes*), which are habitat generalists, are known to capitalize on anthropogenic food sources (Bino et al. 2010). Hence, red foxes may benefit from the transformation of forested areas into landscapes dominated by farming and human settlements (Hradsky et al. 2017; Jahren et al. 2020). With increasing deforestation in Columbia, neotropical carnivore communities became increasingly dominated by highly adaptable habitat generalists (Boron et al. 2023). Furthermore, certain traits commonly observed in many carnivores, including low population densities, low reproductive output, and relatively large home range requirements, make some species more vulnerable to habitat alterations (Henle et al. 2004; Mergey et al. 2011). Biotic homogenization poses a significant conservation challenge due to its impact on intact wildlife communities, which are crucial for maintaining ecological resilience (Clavel et al. 2011; Boron et al. 2023).

1.1.3. Ripple Effects

The loss and degradation of natural habitats can have broad consequences for wildlife communities, potentially disrupting interspecific interactions such as competition and predation, and causing widespread trophic imbalances (Berger-Tal & Saltz 2019). In human-modified landscapes, where top predators have been displaced or driven to extinction, there is often a subsequent rise in the population of smaller predators, a phenomenon known as mesopredator release (Prugh et al. 2009). For example, in midwestern USA, the eradication of wolves (*Canis lupus*) has led to the release of coyotes (*Canis latrans*) from predation and competition pressures. This resulted in a significant increase in the population of coyotes, with notable impacts on their prey species (Jones et al. 2016). Moreover, in Alaska, wolf abundance was negatively correlated with non-apex predator abundance, although mesocarnivores were attracted to wolf-killed carrion (Sivy et al. 2017).

Boron et al. (2023) highlighted the importance of forest availability in carnivore coexistence, particularly between top predators and mesocarnivores. Additionally, the loss of structurally complex forests may jeopardize mechanisms of coexistence among mesocarnivores (e.g., niche partitioning at fine spatiotemporal scales), leading to competitive exclusion, displacement, and ultimately, extirpation (Boron et al. 2023). As important habitats for specialist mesocarnivores become fragmented and reduced, intraguild competition with habitat generalists occupying the same food niche can intensify and result in increased mortality (Lindström et al. 1995; Karanth et al. 2017; Gilbert et al. 2022).

1.1.4. The Norwegian Forest Context

The total land area of Norway is 323,808 km^2, with forests comprising 37.6% of its territory (Statistics Norway 2022). Over the past centuries, a need for arable land and pastures for livestock has driven extensive deforestation along most coastal areas in Western Norway (Hjelle et al. 2018). Largely concentrated in the southeastern region of the country (Helseth et al. 2022), the remaining forested areas are intensively managed, with 68.1% being commercially harvested (Statistics Norway 2022). Commercially important tree species include Norway spruce (*Picea abies)*, Scots pine (*Pinus sylvestris),* and birches (*Betula* spp.) (Svensson & Dalen 2021). Since the 1950s, extensive afforestation projects have been undertaken in western and northern Norway, resulting in about 4.5% (3,900 km^2) of today's productive forested area (Tomter & Dalen 2014). In recent years, a surge in timber prices has coincided with increased harvests (Helseth et al. 2022). In 2021, the timber harvest peaked at 11.57 million m^3, generating a turnover of approximately 5.4 billion NOK (around 460 million EUR) (Helseth et al. 2022; Norwegian Agriculture Agency 2024). Forest products are also being increasingly recognised as important renewable resources that can facilitate the "green shift" towards a more environmentally sustainable economy (Ministry of Agriculture and Food 2019). By 2045, the Ministry of Agriculture and Food strategic initiative, FOREST22, anticipates a four-fold increase in the annual turnover of the forest industry (Olofsson 2015).

Since the 1950s, clearcutting has been the dominant silvicultural practice for forest management in Norway (Hoen & Winther 1993; Gustafsson et al. 2010; Storaunet & Rolstad 2020). This approach often involves cutting and replanting entire forest stands on a rotation cycle typically lasting between 60 and 120 years (Kuuluvainen 2009; Kuuluvainen & Gauthier 2018; Helseth et al. 2022). Large-scale forestry operations in neighbouring Sweden and Finland have resulted in significant landscape transformation, characterized by a sharp decline in the proportion of old forest and a concurrent increase in the proportion of young forest stands (Östlund et al. 1997; Kuuluvainen & Gauthier 2018). In contrast, forest management in Norway operates on a smaller scale due to topographical and land ownership constraints (Yrjölä 2002; Mezzera & Sæther 2016), with the average clearcut size being 0.08 km^2 (Statistics Norway 2003). But, even when clearcutting is conducted on a small scale, it can still impact forest characteristics, altering tree species composition and structural diversity within stands (Kouki et al. 2001; Kuuluvainen & Gauthier 2018).

While Norwegian forests have grown in biomass and area due to the expansion of semi-natural forests and forest plantations over the past 70 years, there has also been a concurrent depletion of old forests (Helseth et al. 2022). Clearcuts and young seral stage stands do not have the heterogeneous canopy cover, large snags, arboreal cavities, developed understory layers, and abundant downed woody materials found in old forests (Esseen et al. 1997; Fisher & Wilkinson 2005). The lack of such habitat features can be detrimental to the persistence of forest species that rely on them (Kuuluvainen 2009; Framstad et al. 2022). Forest-dwelling species account for nearly half (48%) of all red-listed species in Norway (Artsdatabanken 2021). Moreover, forest landscapes have been further modified through the construction of infrastructures, such as roads, recreational homes, and power lines, resulting in habitat loss and fragmentation (Norwegian Environment Agency 2018; Helseth et al. 2022). In 2020, the Norwegian Nature Index classified the biodiversity status of Norwegian forests as relatively poor, with a value of 0.41 compared to a reference value of 1.7 (Certain et al. 2011; Storaunet & Framstad 2020).

1.2. The Focal Species

1.2.1. Pine Marten: Range and Status

The European pine marten (*Martes martes*; hereafter "pine marten") ranges from Mediterranean biotopes to Fennoscandian taiga, and to western Siberia and Iran (Figure 1; Monakhov 2022). This species uses habitats such as mature coniferous and mixed forests, insular wooded areas, and shrublands (Clevenger 1993; Brainerd & Rolstad 2002; Herrero et al. 2016; Remonti et al. 2022). While pine martens are thought to be adaptable, in most part of their range, they are seldom found in agricultural or urbanised areas, and avoid open areas, including clearcuts (Storch et al. 1990; Brainerd & Rolstad 2002; Proulx et al. 2005; Pereboom et al. 2008).

Figure 1. From Monakhov (2022): geographic distribution of pine marten (green area).

Historically, the pine marten has been subject to severe population declines due to persecution and overharvesting (Langley & Yalden 1977; Helldin 2000a). In the 1930s, pine martens received full protection in Norway and Sweden following heavy persecution due to high pelt prices and bounties (Helldin 2000a). As their populations recovered, protections were gradually lifted. Nonetheless hunting seasons were designed to protect pine martens during the breeding season (Helldin 2000a). Globally, the pine marten is classified as a species of Least Concern on the IUCN Red List (Herrero et al. 2016). In most countries where the hunting of pine martens is permitted, their populations remain stable (Proulx et al. 2005). Nevertheless, threats such as habitat loss and landscape alterations may pose potential long-term challenges to pine martens (Brainerd 1990; Proulx et al. 2005; Virgós et al. 2012).

1.2.2. A Forest Denizen

Pine martens are congeneric with American martens (*Martes americana*) and fishers (*Martes pennanti*), and these mustelids have similar ecological niches and responses to habitat loss and fragmentation (Proulx et al. 2005). Alterations in the composition and structure of forested landscapes in North America have had an impact on the habitat selection and resource availability of both the American marten and fisher (Payer & Harrison 2005; Spencer et al. 2015). Following clearcutting in North America, researchers have observed reductions in canopy cover, coarse woody debris, and riparian dispersal zones (Ruggiero et al. 1994). Since American martens and fishers rely on diverse structural elements from where they can access small mammalian prey (Potvin et al. 2000), they require and often occupy mature coniferous forests (Chapin et al. 1998; Suffice et al. 2020). In Scandinavia, Brainerd & Rolstad (2002) hypothesized that pine marten fitness could be maximised in spruce-dominated forest with large, mature trees and by avoiding clearcuts and open areas.

Given their elongated bodies and conductive fur, pine martens have a high lower critical body temperature, and they rely on insulated resting sites during cold winters (Pulliainen 1981; Harlow 1994; Brainerd et al. 1995). Brainerd et al. (1995) found that underground cavities in rocks provide thermal shelter during cold weather. They also found that mature pine and aspen trees with woodpecker cavities are strongly preferred as natal den sites, while underground sites are used by family groups once kits become mobile (Brainerd et al. 1995). Inhospitable open habitats may be more often crossed or temporarily inhabited by dispersing individuals traversing the landscape in search of vacant territories rather than by resident individuals within their established home range (Croose et al. 2014).

Nonetheless, in areas with high resource availability and low predation risks, such as La Selva forest and Elba Island in central Italy, pine martens display plasticity in habitat selection and occupy many different landcover types including deciduous forests, open fields, rural areas, and shrubland (De Marinis & Masseti 1993; Manzo et al. 2018; Mori et al. 2022). Studies conducted in other parts of Europe also indicate a greater habitat flexibility for this species than previously thought (Birks et al. 2005, Pereboom et al. 2008, Balestrieri et al. 2010, Mergey et al. 2011, Caryl et al. 2012, Virgós et al. 2012, Lombardini et al. 2015, Remonti et al. 2022). In areas where pine marten populations are well-established, they can be found in various non-woodland habitats in Scotland, including montane habitats in the Cairngorms, coastal habitats in Wester Ross and peatland blanket bog in the Flow Country (Croose et al. 2013). Agricultural matrices containing remnant forest patches may also be important for providing pine martens with essential resources such as food, den sites, and additional habitats (Pereboom et al. 2008; Balestrieri et al. 2010; Mergey et al. 2011). In highly fragmented landscapes, such as the Ardennes in northeastern France, Pereboom et al. (2008) found that pine martens were not restricted to large forests and used small woods and hedgerows. Moreover, they recorded faster movement of pine martens in large, forested areas compared to smaller forests and hedgerows. Slower movement indicates a preference for foraging in these habitat types (Pereboom et al. 2008), which typically exhibit high diversity and availability of small mammals (Thompson & Harestad 1994; Huggard 1999). Remonti et al. (2022) found that expanding pine marten populations in northern Italy relied on residual forest patches and riparian wood corridors to colonise heavily cultivated areas in the Po-Venetian plain. The significant increase in commercial forest plantation and resulting forest cover has also contributed to the natural range expansion of core pine marten populations and their re-colonisation of large areas in Scotland and Ireland (O'Mahony et al. 2012; Croose et al. 2013; Croose et al. 2014).

In southern boreal Scandinavia, pine martens used a variety of forest age classes and types relative to their availability, but strongly avoided open areas such as clearcuts and agricultural fields and preferred mature stands of spruce-dominated forest (Brainerd 1997; Brainerd & Rolstad 2002). Their home range size also varied significantly with the size and distribution of mature forest patches in a matrix of young forest and clearcuts (Brainerd 1997). Depending on the scale and degree of forest fragmentation, pine marten abundance may be either positively or negatively affected (Brainerd 1990, 1997). Pine martens may benefit from using forested landscapes that are interspersed with fine-grained open habitats (Virgós et al. 2012). However, Brainerd (1990) argued that significant forest patch size reduction and increased isolation of forests within a matrix of clearcuts and human dominated open areas may be detrimental to pine martens.

1.2.3. Food and Foes

In Scandinavia, pine martens are generalist predators with a diverse diet consisting of small mammals, birds, eggs, carrion, insects, and fruits (Storch et al. 1990; Helldin 2000b). These mustelids are notorious predators of forest grouse, frequently targeting the eggs and chicks of species such as capercaillie grouse (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) (Jahren 2017). Their arboreal adaptations also enable them to hunt prey species inhabiting tree canopies, such as red squirrels (*Sciurus vulgaris*) and various bird species (Lindström 1989; Helldin 2000b). Pine martens are known to cache food in preparation for reduced prey availability during winter months (Twining et al. 2018).

Pine martens can adapt their diet in response to changes in food abundance and availability (De Marinis & Masseti 1995; Pulliainen & Ollinmäki 1996). Notably, studies have observed that pine martens exhibit functional responses to the availability of microtine rodents (Jedrzejewski et al. 1993; Helldin 1999; Zalewski 2005; Rosellini et al. 2008), including bank voles (*Myodus glareolus*) and lemmings (*Lemmus lemmus*). Microtine rodent populations in boreal Scandinavia and Eurasia follow cyclic patterns, fluctuating in abundance every 3–5-years (Elton 1924; Korpimäki et al. 1991; Lindström et al. 2001; Krebs 2013; Kleef & Wijsman 2015). Lindström (1989) and Storch et al. (1990) found that pine martens switched to more abundant red squirrels when voles were scarce. Wijsman (2012) found that in the Netherlands, pine martens increased predation on passerine nests during years of low abundance of wood mice (*Apodemus sylvaticus*). Furthermore, given that small rodents comprise a significant portion of the pine marten diet, the size and structure of their populations may be influenced by cyclic fluctuations in these prey species populations (Jedrzejewski et al. 1993; Pulliainen & Ollinmäki 1996; Helldin 1999, 2000b).

Previous research has documented trophic niche overlap between pine martens and other mesopredators, including stone martens (*Martes foina*), stoats (*Mustela erminea*), and red foxes (Storch et al. 1990; McDonald 2002; Granata et al. 2022). The coexistence of species within the same guild may be facilitated by the partitioning of resources based on prey size (McDonald 2002; Remonti et al. 2012), as well as habitat segregation (Fedriani et al. 1999) and interspecific differences in activity patterns (Kupferman et al. 2021). Nevertheless, Remonti et al. (2012) found that in a resource-poor area, where red foxes, pine martens, and stone martens coexisted, intensified interspecific competition over limited prey led to the habitat displacement of stone martens.

Red foxes not only compete with pine martens for prey, but occasionally kill them as intraguild competitors (Lindström et al. 1995). In Sweden and Norway, an epizootic of sarcoptic mange in red fox populations during the 1980s caused a significant decline in their numbers, leading to a concurrent surge in pine marten populations as indicated by harvest statistics (Lindström et al. 1995; Smedshaug et al. 1999; Willebrand et al. 2022). Red fox populations recovered in the mid-1990s and pine marten harvests in Norway subsequently declined (Smedshaug et al. 1999; Statistics Norway 2023), although it is uncertain if this is a causal relationship or a declining interest in marten trapping. Intensified forestry practices in Fennoscandia have also benefited red foxes through increased availability of microtine rodents associated with clearcutting (Henttonen 1989; Kurki et al. 1998). Increased abundance of red foxes and loss of forested habitat may suppress pine marten populations (Helldin 2000a; Lindström et al. 1995).

2. Objectives of Dissertation

Through this dissertation, I aim to examine factors influencing pine marten occurrence, abundance, and predation in landscapes modified by forestry and agriculture in Norway. I specifically address the following objectives:

1) To investigate the influence of forestry practices and environmental conditions on pine marten occurrence at multiple spatial scales (Paper I);
2) To evaluate the influence of landscape parameters and microtine rodent abundance on pine marten abundance and population growth rate (Paper II);
3) To evaluate capercaillie nest predation rates by pine martens and red foxes and determine how landscape factors influence nest predation by each species (Paper III).

3. Methods and Results: Overview of Papers

3.1. Paper I

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

My objective was to examine the effects of clearcutting practices and environmental conditions on the occurrence of pine martens at multiple spatial scales. I examined an extensive set of data spanning four years (from 2018 to 2021) and collected as part of the nationwide SCANDCAM camera trap monitoring project (see https://viltkamera.nina.no). The data included 1,819 observations of pine martens obtained from 281 camera trap sites distributed across a wide geographical area, spanning from Troms and Finnmark County in northern Norway to Agder County in the south.

In this paper, I refer to pine marten occurrence at the landscape scale and the habitat-patch scale as occupancy and site use, respectively (Efford & Dawson 2012, Steenweg et al. 2018). I modelled pine marten occupancy and site use in a multi-scale occupancy model (Mordecai et al. 2011, Kery & Royle 2015) as adapted by Hofmeester et al. (2021) to camera trap data. Furthermore, detection probability was used to account for imperfect detection when estimating occupancy and site use. Within this model, I also investigated the relationship between pine marten occupancy and site use relative to key habitat and landscape variables. These variables included measures of clearcuts (defined as regenerating stands ≤ 10 years old) and forests aged ≥ 120 years, and terrain ruggedness. Additionally, I investigated factors influencing pine marten detection, including dominant microsite characteristics (e.g., presence of boulders, sparse or dense vegetation, and open areas), snow depths, and temperatures.

Pine marten occupancy did not correlate with proportions of old forest or clearcuts at the landscape scale. However, at the habitat-patch scale, pine marten site use was positively correlated with the presence of old forest patches (≤ 100 m from sites) and terrain ruggedness, but not with the presence of clearcuts (≤ 100 m from sites). Temporal changes in environmental conditions (e.g., snow depth and temperature) influenced pine marten detection. Detection probability at sites near clearcuts (≤ 100 m from site) was negatively correlated with snow depth, while this parameter was positively correlated with forested sites farther from clearcuts. Finally, temperature, as well as presence of boulders positively influenced detection probability.

3.2. Paper II

How do microtine rodent abundance, snow and landscape parameters influence pine marten Martes martes population dynamics?

Paper II focused on identifying the drivers of spatiotemporal variation in pine marten populations in the Hedmark portion of Innlandet County, Norway. Specifically, I examined factors that may influence pine marten population dynamics, including microtine rodent abundance, densities of mature spruce forest and of agricultural land, snow depth, and elevation.

To investigate the temporal variation in pine marten populations, I first used tracking data from 600 unique snow transects to compute a pine marten abundance index for the years 2003 to 2014. These indices were then used in conjunction with a diagnostic tool, the Partial Rate Correlation Function, to identify potential density-dependent feedback/cyclicity in pine marten populations. I found no evidence of cyclicity in pine marten populations. Instead, their population growth was directly density-dependent.

To further examine temporal variations in population size, I used the instantaneous rate of increase between 2008 and 2014 as the response variable in a generalized linear mixed model (GLMM). This model incorporated several explanatory variables, including a microtine rodent abundance index, elevation, snow depth, and an interaction between the microtine rodent abundance index and elevation. Notably, the analysis for this model covered fewer years due to the unavailability of microtine rodent census data for the entire pine marten survey period. Moreover, to examine the influence of the above explanatory variables on the spatial variation in abundance of pine marten, a second GLMM was fitted. This model included two supplementary explanatory variables: mature spruce forest and agricultural land densities. The response variable for this model was the number of pine marten tracks observed per snow transect between 2007 and 2014.

There was no influence of the microtine rodent abundance index and snow depth on pine marten population growth rate. Pine marten population growth rate tended to increase with elevation. I found a positive association between pine marten population growth rate and microtine rodent abundance index with increasing elevation. Pine marten abundance increased with elevation, snow depth, density of mature spruce forest, and the index of microtine rodent abundance, but decreased in areas with a higher density of agricultural land.

3.3. Paper III

The influence of landscape factors on capercaillie nest predation rates by two competing mesopredators: pine marten versus red fox

To better comprehend the impact of anthropogenic land use on ground nest predation by pine martens and red foxes, capercaillie nests were monitored in Hedmark and Nord-Trøndelag, Norway, between 2009 and 2014. The monitoring involved the use of camera traps. Camera images (see Figure 2) and the interpretation of eggshell remains enabled the classification of nest fate as either successful (≥ 1 chick hatched), abandoned, or predated by either pine marten, red fox, or other predators. To evaluate competing risks of capercaillie nest mortality, I used the nest exposure time and fate of 156 nests in a cause-specific hazard model. This model examined nest predation by red foxes and pine martens relative to landscape covariates, including the distance from forest/clearcut edges or roads, as well as agricultural land density.

Figure 2. Image of pine marten predating on capercaillie nest from camera trap monitoring system.

Predation by pine martens and red foxes was the predominant hazard to capercaillie nests, followed by predation by other species and nest abandonment. Both mesopredators exhibited similar daily nest predation rates. Pine marten predation was negatively correlated with agricultural land density. The likelihood of nest predation by pine martens tended to increase along a gradient from clearcut to forest interior, while it tended to decrease with distance from roads. I found that nest predation by red fox only increased with distance from road in areas with high agricultural land density. No distinct relationship emerged between nest predation by red foxes and individual factors including agricultural land density or distance to forest-clearcut edges or distance from roads.

4. Discussion

Landscape modifications have often been associated with severe declines in various classes of terrestrial vertebrates (e.g., Andrén 1994; Gibbons et al. 2000; Stuart et al. 2004) as well as invertebrates (e.g., Didham et al. 1996) and plants (e.g., Hobbs & Yates 2003). Nonetheless, remnants of natural habitats and their surrounding altered land cover may provide suitable conditions for some wildlife species to persist (Arroyo-Rodríguez et al. 2020). Understanding how these species fare in modified landscapes can significantly enhance wildlife conservation and management strategies. This dissertation examined the environmental factors shaping pine marten populations and predation patterns within a landscape modified by forestry and agriculture.

4.1. Effects of Forestry

Both Paper I and II highlight a positive association between pine martens (i.e., site use and abundance) and old forests, particularly those dominated by spruce (Paper II). This corroborates earlier research conducted in southern boreal Scandinavia, which documented a preference for late seral stage forests (including mature spruce-dominated forests) by pine martens at fine spatial scales (Storch et al. 1990; Brainerd & Rolstad 2002). However, at a broader spatial scale, my findings indicate that these mustelids are not confined to old forest habitats. Moreover, I found that pine martens did not avoid areas near clearcuts within forest patches, and their occupancy remained constant even as the proportion of clearcuts increased in the landscape (Paper I). These results not only provide insights into the nuanced and scale-dependent responses of pine martens to landscape modification by forestry practices, but also support a growing consensus that pine martens are highly adaptable and can occupy a diverse range of forest and habitat types (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).

Nonetheless, it is important to note that the average size of a clearcut in Norway (0.08 km^2; Statistics Norway 2003) is relatively small compared to the reported home range sizes of pine marten in Scandinavia, which range between 2–25 km^2 (Brainerd 1997). A fine-grained pattern of forest clearcutting may be advantageous to pine martens since prey such as field voles (*Microtus agrestis*) are favoured by open grassy habitats in clearcuts (e.g., Hansson 1994). In such landscapes, pine martens might forage near clearcut edges to capitalize on this enhanced prey abundance without venturing far out of older forest stands that they are adapted to

(Brainerd 1990; Thompson & Harestad 1994; Pulliainen & Ollinmäki 1996; Sidorovich et al. 2010; Caryl et al. 2012).

4.2. Topography

Norway generally has a rocky and rugged topography with large expanses of glacial till comprised of jumbled, large boulders throughout much of the country (Olsen et al. 2013). In Paper I, I observed an increase in pine marten site use with terrain ruggedness. Additionally, pine martens were more frequently detected in rocky areas. Rugged terrain and rocky areas may provide better access to subterranean and subnivean spaces. Attributes including the structural stability, depth, and thermal insulation of such spaces (Glass et al. 2021) may enhance access to microtine rodents (see Jędrzejewski et al. 1993), thermoregulation, reproduction (denning), and predator avoidance (Brainerd et al. 1995; Lindström et al. 1995; Wilbert et al. 2000). The elongated body, short fur, and high surface-to-volume ratio of the analogous species, American martens, contribute to their high lower critical body temperature, making them particularly sensitive to cold temperatures (Worthen & Kilgore 1981; Buskirk et al. 1988; Harlow 1994). Thermal shelter provided by subterranean and subnivean dens may therefore be a critical factor for pine martens, especially during winter (Brainerd et al. 1995; Zalewski 1997). Underground sites can serve as an additional or alternative form of shelter and cover for denning females, particularly in locations where arboreal cavities in large trees are scarce and as kits become more mobile during the course of the summer breeding season (Pulliainen 1981; Brainerd et al 1995; Wilbert et al. 2000). Hence, enhanced access to subterranean and subnivean spaces in more rugged terrain and rocky areas could help offset the lack of old forest structures in industrial forests in Scandinavia (see Brainerd et al. 1995).

4.3. Predators and Prey

4.3.1. Capercaillie Nests

Paper III suggests a tendency for pine martens to predate more on capercaillie nests located deeper within forests and away from clearcuts. Pine martens might avoid open habitats due to limited options for vertical escape possibilities and lack of protective cover from predators like red foxes and golden eagles (*Aquila chrysaetos*) (Lindström et al. 1995; Sulkava et al. 1999; Brainerd & Rolstad 2002; Lyly et al. 2015). Sonerud et al. (2023) suggested that since pine martens are more restricted by forest cover, they would be more likely to encounter nests within forest interiors sooner than those in or closer to clearcuts. Nevertheless, I found no conclusive evidence indicating lower predation rates of nests closer to clearcuts. In contrast, Paper III clearly demonstrates that an increase in agricultural land density reduces nest predation by pine martens but not by red foxes. This is consistent with results from Paper II, which illustrate a decline in pine marten abundance with increasing agricultural land density. In Finland, Kurki et al. (1998) observed that areas with a high proportion of agricultural land had lower pine marten abundance when compared to the abundance of red foxes. While fragmentation often influences predator-prey relationships, predicting the direction of change may not be straightforward due to the varying influence of different landscape configurations and predator communities (Mullu 2016). Bayne & Hobson (1997) discovered that in central Canada, nests adjacent to agricultural land faced increased predation, whereas those near logged areas did not. They found no changes in the predator community in logged areas but noted higher densities of red squirrels preying on nests in forest patches adjacent to agricultural land (Bayne & Hobson 1997).

Moreover, given the distinct patterns in habitat use of pine martens and red foxes, I observed notable differences in nest predation rates between these mesopredators in relation to multiple landscape factors (Paper III). This highlights the importance of species partitioning when investigating the relationship between nest predation rate and environmental parameters. Not doing so may lead to underestimating the influence of some landscape and habitat factors on nest predation, potentially resulting in misguided conservation efforts (Maag et al. 2022). My findings offer valuable information about the landscape factors that influence capercaillie nest predation by two key mesopredators. They also have implications for the management of pine martens and red foxes in modified forest landscapes where capercaillie conservation is a priority. Further investigation that includes annual monitoring of predator and prey populations, along with quantitative measurements of anthropogenic habitat (e.g., clearcut and agricultural land) expansion would be needed to better disentangle the effects of landscape modifications on prey-predator relationships.

4.3.2. Microtine Rodents

Paper II suggests that pine marten populations in boreal forests experience direct density-dependent growth rather than the delayed density-dependence typical of cyclic populations (Row et al. 2014). This pattern may stem from the opportunistic, generalist diet of pine martens and their ability to cache food for later consumption (Andersson & Erlinge 1977; Helldin 2000b; Twining et al. 2018). In Sweden, Helldin (1999) found that microtines were important in the winter diet of pine martens. However, these mustelids switched to alternative prey during microtine lows, and their reproductive success and proportion of yearling appeared to be independent of microtine cycles (Helldin 1999). Moreover, pine martens exhibit strong territorial behaviours, delayed implantation, and relatively low reproductive potential (Monakhov 2022) that may contribute to a slow response to environmental changes (Labrid 1986).

Nevertheless, in Paper II, I found that pine marten abundance increased with the microtine rodent abundance index used. I also detected a positive trend between pine marten population growth rate and the microtine rodent abundance index at higher elevation. This suggests that microtine rodents are important prey whose influence on pine marten population dynamics potentially increases in less productive, higher elevation areas where there may be limited alternative prey.

4.4. Temporal Environmental Change

Similar to Cano-Martínez et al. (2021), I observed an increase in pine marten abundance with snow depth (Paper II). However, this relationship may not be straightforward and could also be modulated by habitat characteristics. In Paper I, the detection of pine marten decreased with increasing snow depth in areas with clearcuts nearby but increased with snow depth in the absence of clearcuts. As snow depth increases, access to subnivean rodents diminishes in more open habitats (Jędrzejewski et al. 1993; Pulliainen & Ollinmäki 1996; Zalewski et al. 2006; Willebrand et al. 2017). Koehler & Hornocker (1977) found that American martens used forests with low canopy cover (< 30%) more often when snow depths were relatively low in north-central Idaho. Deep snow in open areas without subnivean access points decreases the ability of American martens to penetrate the snow when foraging for small mammals (Koehler & Hornocker 1977; Steventon & Major 1982; Thompson & Colgan 1994). In winter, field voles in clearcuts may be inaccessible to pine martens if the snow is impenetrable, making clearcuts less appealing to these mustelids (Storch et al. 1990; Pulliainen & Ollinmäki 1996; Helldin 2000b). Late seral stage forests may be crucial within a landscape mosaic since they often contain important prey species that remain accessible to pine martens even during heavy snow conditions (Swenson & Angelstam 1993; Hansson 1994; Pulliainen & Ollinmäki 1996; Willebrand et al. 2017).

Moreover, dense canopy cover in old forests, particularly spruce-dominated stands, can affect snow hardness and depth, making it easier for pine martens to excavate small mammals (Wabakken 1985). Their relatively large paws and light body weight may also give pine martens an advantage for moving through and over snow (Koehler & Hornocker 1977; Steventon &

Major 1982; Jędrzejewski et al. 1993). Willebrand et al. (2017) found that with increasing snow depth, red foxes had diminished hunting success compared to pine martens in conifer forests (> 1.5 m). Pine martens may benefit from deeper snow conditions in forest stands with a canopy cover to avoid competition with the larger and heavier red foxes, their primary enemies in Scandinavia (Lindström & Hörnfeldt 1994; Willebrand et al. 2017).

4.5. Future Research

The data I used were collected as part of research and monitoring projects that were not specifically designed to test the effects of forest landscape fragmentation on pine marten occurrence and abundance. Hargis et al. (1999) found that an increasing degree of forest fragmentation had a negative influence on American marten abundances as measured by capture rates. Research is needed on the effects of forest fragmentation on pine marten occurrence and densities relative to forest patch size and isolation across Scandinavia (see Brainerd 1990, 1997). Such a study would require a design with random study locations in the landscape, including sites in clearcuts and other open areas. Moreover, a meta-analysis of environmental parameters that influence pine marten occurrence throughout its broad distributional range would provide a holistic basis for conservation of this species.

Although forestry in Norway is conducted on a smaller scale due to the size of individual properties when compared to Sweden and Finland, intensification of forest management and associated timber harvest is anticipated over the next two decades (Olofsson 2015). This may lead to further forest loss and fragmentation in Norway. A large-scale comparative study that examines the effects of different forestry regimes and clearcutting scales in Norway, Sweden and Finland on pine marten occurrence would contribute to a better understanding of the full extent to which landscape modifications influence this species.

4.6. Conservation and Management

In Norway, managed commercial forest habitats with a rotation cycle typically ranging between 60 and 120 years (Kuuluvainen 2009) constitute the primary forested habitat resource for pine martens. Given the current scale of forestry development in Norway, these dynamic habitats appear to be a sustainable resource for pine martens. However, given their low reproductive rates and susceptibility to anthropogenic change, it is unclear what effects more intensified forest management practices and timber harvest regimes will have on pine marten populations and ecology. Currently, harvest statistics are available for pine martens in Norway (see Statistics Norway 2023). However, there is a lack of information about whether these statistics accurately reflect pine marten population trends in Norway (Pedersen et al. 2021). Thus, a monitoring system that is designed to detect changes in pine marten distribution and abundance would be useful for conservation and management purposes.

Drawing from the current study and previous research (e.g., Wegge & Kastdalen 2007; Summers et al. 2009; Jahren 2017), it is evident that pine martens are highly effective predators which can potentially impact small game species, including capercaillie grouse. In Norway, management programs encourage the control of pine martens and red foxes in order to increase the abundance of grouse species populations (Jensen et al. 1998; Pedersen et al. 2021). Although pine marten populations in Scandinavia seem to be relatively stable (Helldin 2000a; Pedersen et al. 2016), intensive control within a modified landscape with suboptimal habitats could lead to significant population declines (Lande et al. 1995). Furthermore, in other regions where pine martens are legally protected, such as Scotland and Ireland, efforts to help their recovery and re-colonization of historical ranges have interfered with the management goals for other vulnerable species, such as capercaillie grouse (Mathews 2012; O'Mahony et al. 2012; Croose et al. 2013; Baines et al. 2016). In such areas, proposed management interventions should consider the natural levels of predation inherent in a stable predator-prey system (O'Mahony et al. 2012) and integrate an understanding of how specific predators and prey interact within a modified landscape.

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Dissertation articles

Paper I

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

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WILDLIFE BIOLOGY

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 $\leq$ 10 years old) and forests $\geq$ 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 $\leq$ 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

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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 km^2), 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 km^2) 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*

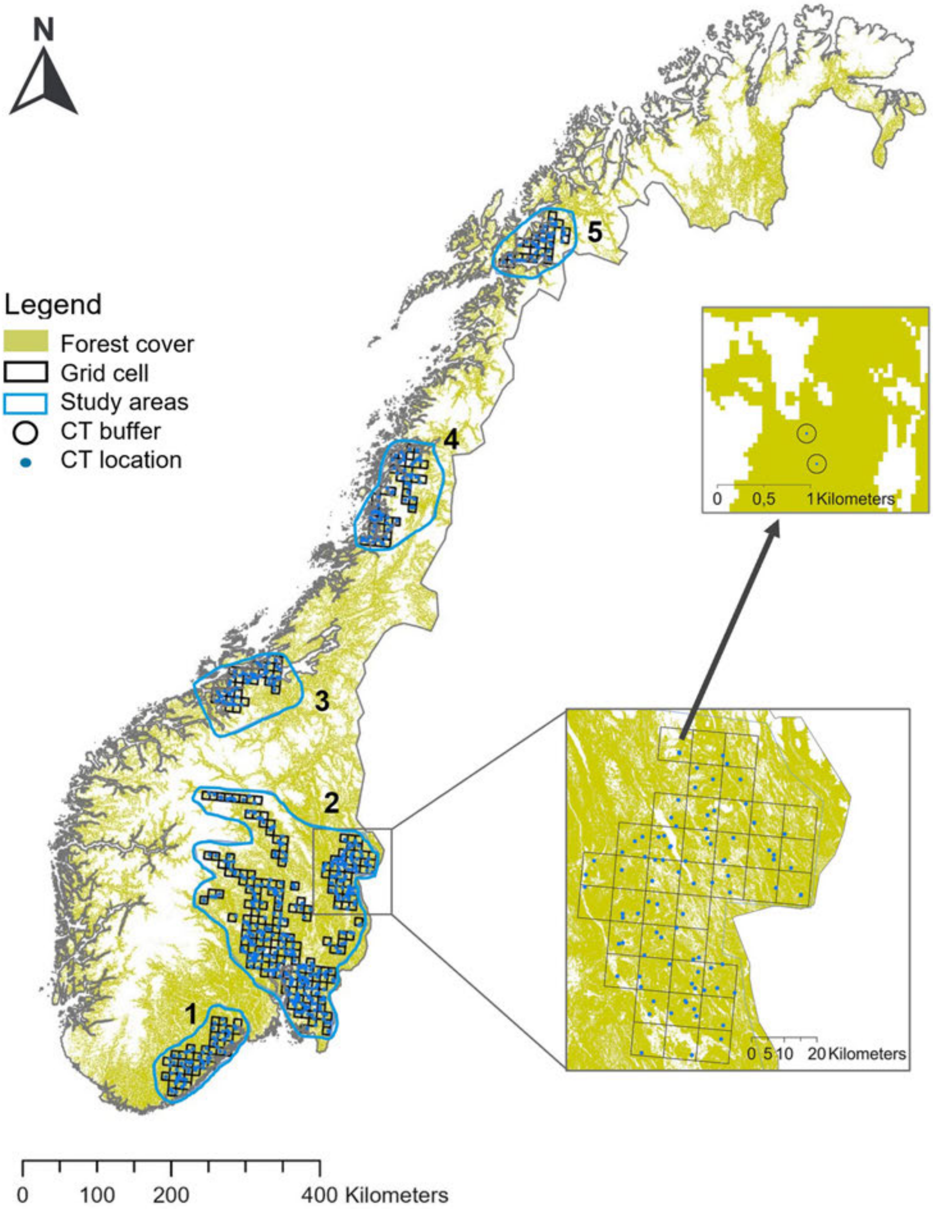

Figure 1. Study areas (labeled 1–5) and location of grid cells and camera traps (CTs). Lower right panel shows the grid cell (100 km^2) at the landscape scale and top right panel shows two CTs at the habitat-patch scale (100 m radius around CT site dot).

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:

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

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:

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

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:

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

where the detection or non-detection of pine marten during the k^{th} 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 k^{th} 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 km^2 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 km^2 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:

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

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

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

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 km^2 grid cells (landscape scale)

There was weak evidence for increased pine marten occupancy with proportion of forest cover in a 100 km^2 grid cell ($\alpha_{\text{total\_forest}} = 0.42$, 89% HDI $= -0.09$ to 0.98; Fig. 2a). We detected no clear association between pine marten occupancy and the proportion of old forest ($\alpha_{\text{old\_forest\_grid}} = 0.62$, 89% HDI $= -0.46$ to 1.98; Fig. 2b) or the proportion of clearcuts in the landscape ($\alpha_{\text{clearcut\_grid}} = 0.38$, 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 $\leq$ 100 m from old forest patches, site use probability was higher ($\beta_{\text{old\_forest\_site}} = 0.49$, 89% HDI $= 0.19$ to 0.80; Fig. 3a). Site use probability of pine martens did not differ regardless of clearcut proximity ($\beta_{\text{clearcut\_site}} = 0.02$, 89% HDI $= -0.22$ to 0.28; Fig. 3b). We found strong support for increased site use with increasing ruggedness at CT sites ($\beta_{\text{ruggedness}} = 0.38$, 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 ($\delta_{\text{snow}} = 0.19$, 89% HDI $= 0.15$ to 0.22; Fig. 4a, blue line). In contrast, detection probability decreased with snow depth at CT sites $\leq$ 100 m from clearcuts ($\delta_{\text{snow x clearcutdetection}} = -0.02$, 89% HDI $= -0.03$ to -0.01; Fig. 4a, black line). Detection probability increased with increasing temperature ($\delta_{\text{temperature}} = 0.40$, 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 ($\geq$ 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 $\geq$ 70 years old (Brainerd et al. 1994). Compared to Brainerd et al. (1994), we described old forest as $\geq$ 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 km^2; Statistics Norway 2003) in Norway is relatively small compared to the reported home range sizes of pine marten in Scandinavia (between 2–25 km^2; 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

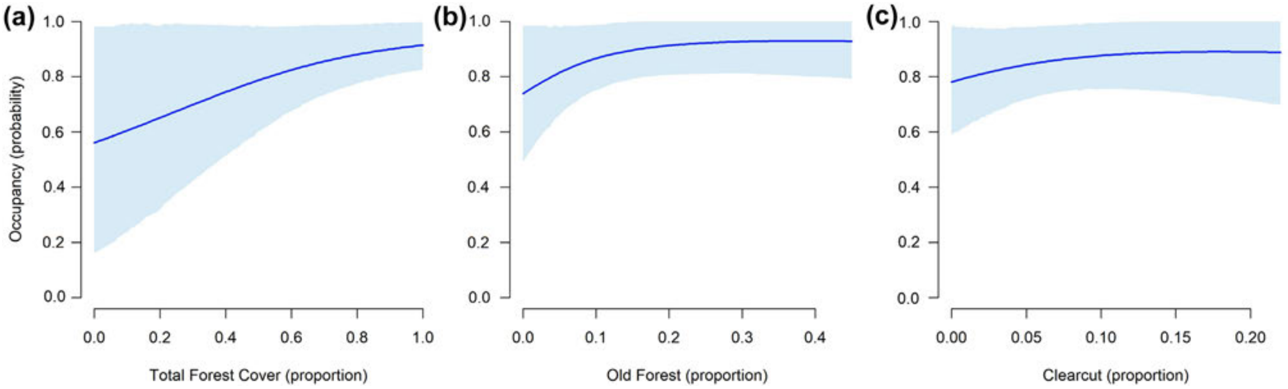

Figure 2. Relationship between occupancy probability and (a) total forest cover, (b) old forest and (c) clearcuts proportions. The line indicates the mean estimates of occupancy probability (for year 2021), 89% credible interval (highest density interval) included (polygon). The posterior estimates (log 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

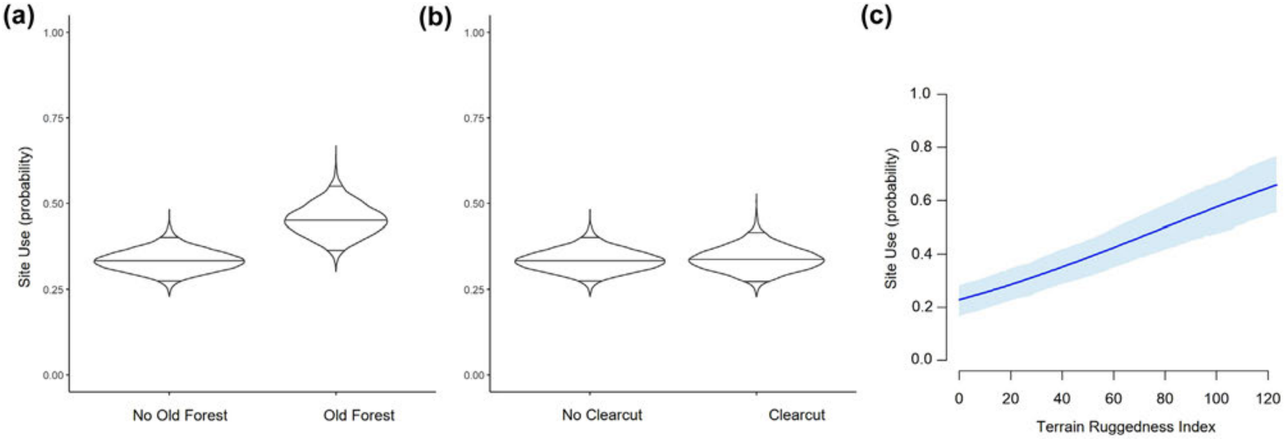

Figure 3. Violin plot of the site use probability for (a) old forest and (b) clearcut at the habitat-patch level. The posterior estimates of each parameter relative to the intercept were back transformed to obtain the site use probabilities. The middle horizontal bar on each violin curve indicates the 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.

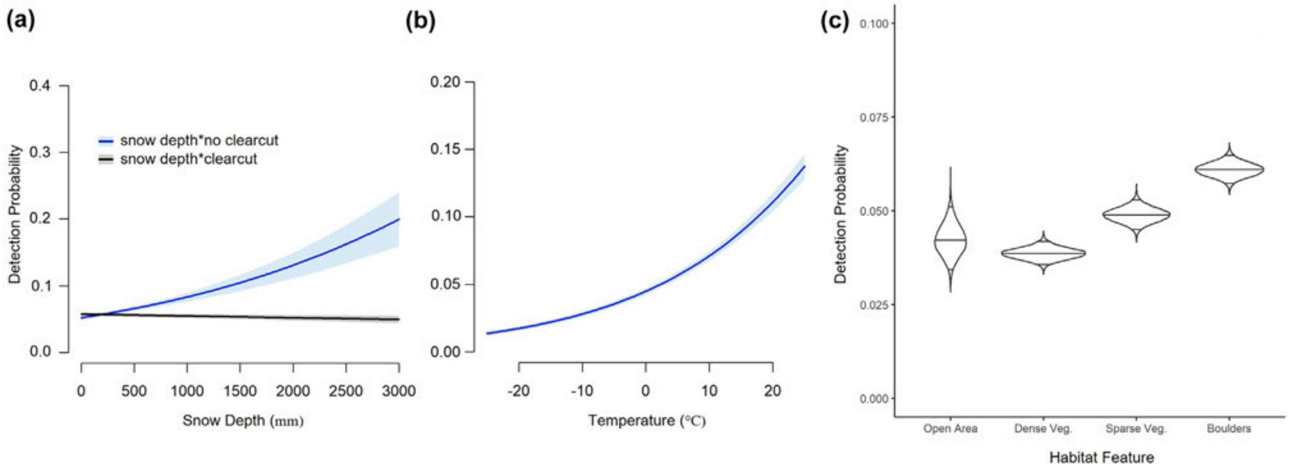

Figure 4. Relationship between detection probability and (a) snow × clearcut (black line) and snow × no clearcut (blue line), and (b) temperature. The line indicates the mean estimates of detection probability, 89% credible interval (highest density interval) included (polygon). The posterior estimates (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.

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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.

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2

Paper II

Manuscript

How do microtine rodent abundance, snow and landscape parameters influence pine marten *Martes martes* population dynamics?

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3

Paper III

Manuscript

The influence of landscape factors on capercaillie nest predation rates by two competing mesopredators: pine marten versus red fox

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Applied Sciences

Limited information indicates that pine martens in Scandinavia depend on late seral forests and are negatively impacted by clearcutting. The objective of this thesis is to identify important environmental factors influencing pine marten occurrence, population dynamics, and predation in Norwegian boreal forest landscapes altered by forestry and agriculture.

In Paper I, pine marten occupancy was independent of clearcuts and old forests at the landscape level based on camera trap data collected across Norway. At the habitat patch level, pine martens were associated with old forests and rugged terrain. Detection was influenced by snow depth, temperature, and boulder presence.

Paper II found no evidence of cyclicity in pine marten populations based on snow-tracking data collected in southeastern Norway. Nevertheless, the population growth rate of this mustelid increased with microtine rodent abundance at higher elevations. Pine marten spatial abundance increased with elevation, snow depth, mature spruce forest density, and microtine rodent abundance, but decreased with agricultural land density.

Camera trap data was used in Paper III to study how landscape factors influence predation by pine martens and red foxes on capercaillie nests. Pine marten nest predation declined with increasing agricultural land density and tended to increase along gradients from clearcuts to forest interiors, while red fox nest predation was unaffected by these factors. Thus, the conversion of forests to open habitats may place pine martens at a disadvantage relative to red foxes. Overall, this thesis sheds light on how biotic and abiotic factors may influence pine martens in human-modified landscapes.