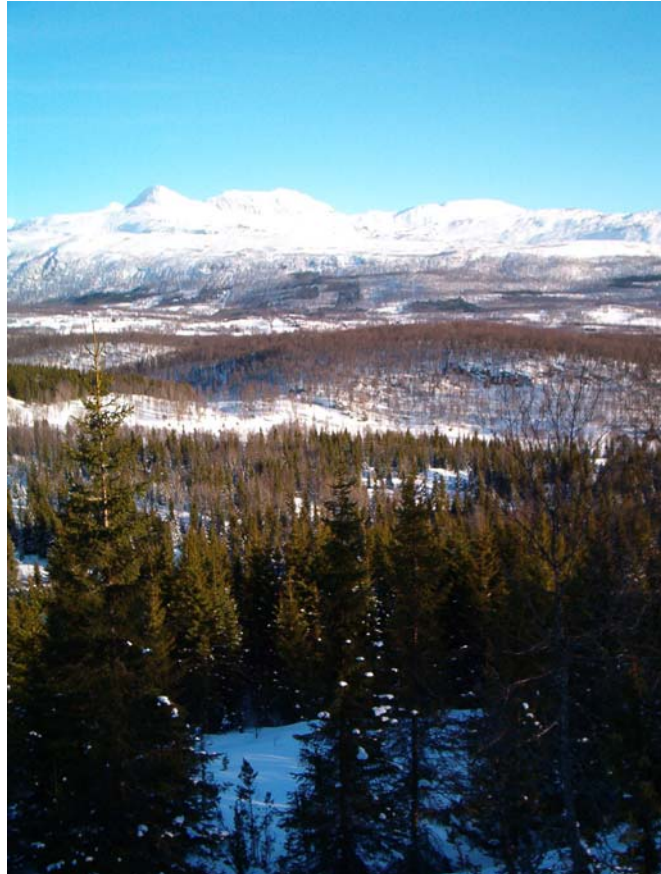


Master's Thesis in Ecology

Spatial distribution of mammals in relation to spruce plantations in birch forests of northern Norway



Kristoffer Hovind Juell

November 2007



Department of Biology · Faculty of Science

University of Tromsø, N – 9037 Norway

Bio – 3910

Master's Thesis in Ecology

**Spatial distribution of mammals in relation to spruce plantations
in birch forests of northern Norway**



Kristoffer Hovind Juell

November 2007

Department of Biology · Faculty of Science

University of Tromsø, N – 9037 Norway

Forord

Og plutselig kom den dagen da jeg kunne skrive forordet ☺ hehe.. Ja, det er mye jobbing som ligger bak disse få sidene du nå holder i hånda. Det begynte med et flott feltarbeid på ski, deretter var det mye transformering av data og grubling over diverse kreative feilmeldinger ifra statistikkprogrammet R. Men etter en stund ble jeg faktisk god venn med R og ting startet å falle på plass i hodet såvel som på arket. I denne prosessen har jeg lært mye, og det er mange å takke for det!

Jeg ønsker å takke Gud, som har båret meg gjennom denne prosessen, fra start til slutt. Jeg vil også takke Rolf Anker Ims, Nigel Gilles Yoccoz og Åshild Ønvik Pedersen for god veiledning! De har alle gitt grundige og konstruktive tilbakemeldinger, både i samtale og i høykvalitets kommentarer på oppgaven. Takk også til Mette Svenning og Anne Høydal for deres velvilje og hjelp under hele oppgavetiden. Takk til alle som hjalp meg i felt: Marie, Siw, Gjertrud og ikke minst Åshild! Og til alle som har lest igjennom oppgaven, Rolf, Nigel, Åshild, Siw og Mette, takk for verdifulle kommentarer! Jeg vil også takke alle på Rødbrakka, inkludert: Anne, EllenKathrine, Kjersti, Laffen, Gøril, Marika, Kristin (begge to), Ellen, Vegard, Trond, Johannes, Pieter, Iris, mfl... Mine romkamerater også: Migmar, Bjørnar og Victoria. Og til alle dere som har bedt for meg: Ann Brit, Kjetil, Gunn Marte, Rakel, Caroline, Øyvind Geronimo, Benedikte, Eva, Karla og hennes menighet, Endre, Lars, m.fl.. En spesiell takk til Martin André Heer og Mette Nielsen (jippi, en vaffel i døra!) for at dere fulgte meg opp nå i innspurten! Takk også til familien i Oslo for all støtte og oppmuntring!

Tromsø, November 2007

Kristoffer Hovind Juell ☺

Abstract

Spruce plantations in coastal birch forests of northern Norway might affect the spatial activity of mammals in the landscape. To investigate this relationship, I censused tracks of mammals in the winter according to the Finnish wildlife triangle method and analysed these at three spatial scales; tree stand level, landscape level and regional level, the two first being related to spruce. The spatial activity of mammals did not show any distinct responses to spruce plantations at the level of spruce stands or landscapes. There were, however, significant trends in spatial distribution of some species at the regional level, but these could not be attributed to structural alterations of the forest due to spruce plantations. There is still a lack of basic knowledge, requiring further research on the spatial ecology of mammals in birch forests of northern Norway.

Table of contents

1. Introduction	8
2. Materials and methods	11
2.1 Study area	11
2.2 Sampling design	12
2.3 Snow-track survey.....	13
2.4 Data treatment and statistical analysis	14
2.4.1 <i>Tree stand level</i>	14
2.4.2 <i>Landscape level</i>	15
2.4.3 <i>Regional level</i>	16
3. Results	17
3.1 Responses at the tree stand level	17
3.1.1 <i>Interspecific differences in edge response</i>	17
3.1.2 <i>Forest stand type response</i>	19
3.2 Responses at the landscape level.....	20
3.3 Regional level distributions.....	21
4. Discussion	23
4.1 Tree stand level	23
4.1.1 <i>Lack of interspecific differences in edge response</i>	23
4.1.2 <i>Lack of response to forest stand type</i>	24
4.2 Landscape level	25
4.3 Regional level.....	26
4.4 Conclusion.....	26
References	28
Appendix 1	32
Appendix 2	33
A) Tree stand level	33
B) Landscape level	33
Appendix 3	34
A) Tree stand level	34
B) Landscape level	35

1. Introduction

Large areas of coastal birch *Betula pubescens* forest in northern Norway have since the beginning of the 20th century gradually been replaced by non-native spruce plantations (mainly Norway spruce *Picea abies*) (Hausner et al. 2002). This extensive tree species conversion has altered the structure of the natural forest landscape, at least to the human eye, by loss and fragmentation of the birch forest. In recent years, more focus have been put on the ecological effects of spruce planting on vegetation communities and associated wildlife (e.g. Fremstad 1997, Gjerde & Saetersdal 1997, Sigurdson 2000, Hausner 2001, Gjerde et al. 2005, Einarsen 2007). The uncertainty of consequences for biodiversity (Hausner et al. 2002) calls for a better understanding of the ecological effects on several spatial scales.

The global distribution of birch forest is limited to Fennoscandia (Norway, Sweden, Finland and the Kola Peninsula), the Kamchatka Peninsula and some areas at Iceland, Greenland and Scotland (Nilssen and Vorren 1990, Hausner 2001), making this a sparse ecosystem. Northern Norway holds a large proportion of the Fennoscandian birch forest (Beckel 1995) making the country responsible for sustainable management of this ecosystem. Birch forests in the lowlands near the coast are typically single-stemmed and have a well developed understory (Hausner 2001), hence creating a suitable habitat for many forest living birds and mammals. Given its limited global distribution, there has been surprisingly little research on birch forests (Hausner 2001). This makes it hard to predict responses to spruce planting among mammals in this ecosystem. However, some studies have reported vertebrate responses to spruce plantations. Sigurdson (2000) reported a negative effect of rodent densities on spruce at stand level. Einarsen et al. (2007) found no effects of spruce edges on predation on artificial ground nests; the greatest variation in predation rates was rather found between landscape blocks, i.e. at a regional level. Still, predation rates appeared dependent on the successional stage of spruce plantations (Einarsen et al. 2007). Studies of communities of birds in birch (Hausner 2001) and pine *Pinus sylvestris* forests (Gjerde & Saetersdal 1997, Gjerde et al. 2005) have found plantations of spruce to reduce the diversity of birds locally at stand level, while increasing at the landscape and regional scale. Hence, they recommend researchers and managers to pay attention to habitat qualities at both local and regional level. No studies have previously evaluated the response of medium to large sized mammals to the spruce planting in birch forests of northern Norway. The purpose of the present study is

therefore to do this by analysing the spatial distribution of mammals in relation to spruce plantations in winter in a study area in northern Norway.

The Norway spruce came to southern Norway about 2500 years ago, but has not yet spread naturally to the coastline of western and northern Norway (Moen 1998). Planting of spruce in northern Norway was initiated in the beginning of the 20th century (mostly as small patches, less than 1 hectare), but the majority of planting took place after the 1950's (Hausner 2001). Consequently, there are only a few small patches of mature spruce in the landscape, while most plantations are in an early succession stage, spread throughout the landscape and mixed with birch trees (Hausner et al. 2002). Spruce planting may influence the spatial distribution of mammals both by altering the tree species composition and changing the structure of the forest. The structural element may influence herbivores such as mountain hares *Lepus timidus* and moose *Alces alces* in their dependence upon shelter in daytime (Hewson & Hinge 1990, Mysterud & Østbye 1999), and open areas during nighttime feeding (Telfer 1970, Lindlöf et al. 1974). Changing the tree species composition can affect the distribution of preferred food plants, as mountain hare and moose have been found to prefer deciduous trees, avoiding spruce, as forage in the winter (Pulliainen & Tunkkari 1987, Cederlund et al. 1980). Spruce plantations have also been found to increase the shading and acidification of the ground compared to the birch forest (Fremstad 1997). This can alter the habitat for the ground vegetation, leading to a shift in plant species composition and a reduction in biodiversity (Fremstad 1997, Saetre 1999). Studies from northern Norway indicate that spruce plantations reduce the diversity of grasses and herbs at the forest floor (Sætra 1971) as well as the epiphytic vegetation on trees (Nilsen 2007), compared to the adjacent native birch forest. This may affect herbivores in their need of both food and shelter (Thirgood & Hewson 1987, Hewson & Hinge 1990, Mysterud & Østbye 1999). Spatial distribution of herbivores inevitably affect their predators, as habitat selection for predators (e.g. red fox *Vulpes vulpes* and small mustelids *Mustela spp.*) mostly relates to prey availability (Carr & Macdonald 1986, Frafjord 2004, Hellstedt & Henttonen 2006).

The main objective of the present study was to see how the spatial distribution of tracks of mammals, set under snowy conditions during the winter, would relate to spruce. More specifically, at tree stand level I investigated the interspecific differences in track distance to spruce edge and the density of tracks in spruce relative to other stand types. At landscape level, I looked for trends in the density of tracks as a function of percentage spruce and the

amount of plantation edge habitat. At the scale of the entire study area (i.e. regional scale), I investigated the spatial distribution of tracks both within and among species.

2. Materials and methods

2.1 Study area

The study was conducted in the municipalities of Skånland and Evenes (68°30 N, 16°40 E) in northern Norway from 1st of March until 9th of April 2003 (Figure 1).

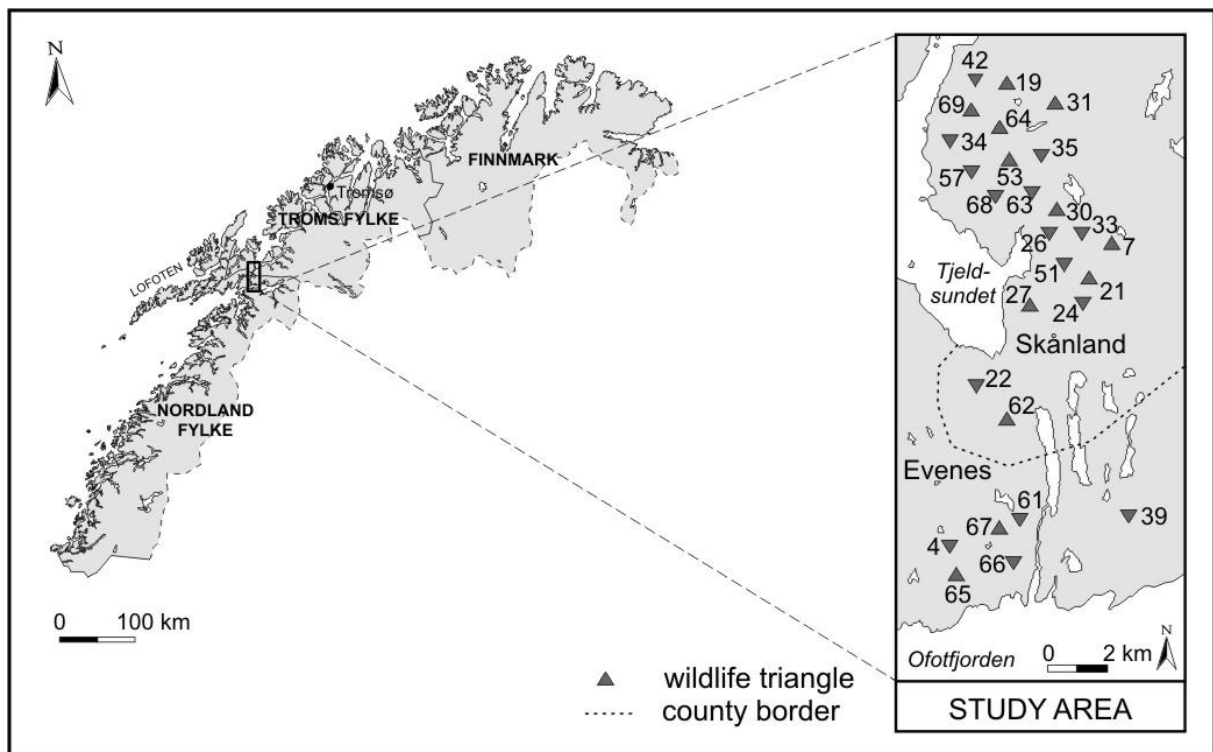


Figure 1. Left: Map of northern Norway showing Nordland, Troms and Finnmark County. The study area is marked by a rectangle. Right: An enlarged map of the study area showing the positions of the 27 wildlife triangles with numbers for identification (Illustration: T. Midthun).

The altitude in the study area extends from zero to 300 meters above sea level, forming a rolling topography of hills. The influence of the Gulf Stream makes the climate unusually favorable relative the latitude (Moen 1998). Evenes holds an average temperature of -4.2°C in January and 13.5°C in July, while the mean annual precipitation ranges from 800 to 1200 mm (1961-1990, Norwegian Meteorological Inst. 2006). The area is usually snow-covered from late October until April, but both temperature and precipitation show great variation between years in these coastal areas.

The study area is covered by approximately 76 km² of forest. Birch is the dominant species, with elements of willow *Salix spp.*, rowan *Sorbus aucuparia*, grey alder *Alnus incana*, aspen

Populus tremula and bird cherry *Prunus padus* in the deciduous forest (Fremstad & Normann 1982, Hausner 2001). The forest landscape is characterised by a well-developed undergrowth due to calcareous ground conditions (Gustavson 1974). The coastal deciduous forest is naturally fragmented on a large scale by mountains, fjords and marshes. Outbreaks of Geometric moths (*Epirrita autumnata* and *Operophtera brumata*) are significant disturbance factors with a period of approximately 10 years (Tenow 1996), but do not usually lead to large-scale death of the forest in the study area. Human disturbances in the forest, apart from planting of spruce, are mainly related to grazing, logging, and cultivation (Esseen et al. 1997) as well as the numerous forest roads fragmenting the landscape.

The oldest spruce plantations in the area are from the early 1900. However, most trees were planted in the 1950`s. Currently, about 10 % of the deciduous forest in the municipalities of Skånland and Evenes are converted to spruce plantations, covering approximately 25 % of the productive area (personal communication Øystein Kanstad, Skånland and Dag Grønnerød, Evenes, March 2003. The numbers are in accordance with Hausner 2001). Most plantations are relatively young and mixed with birch trees, while elderly plantations are more homogeneous. The old plantations are small in size, ranging from 0.008 km² to 0.170 km², averaging at 0.057 km² (Hausner et al. 2002).

The study area harbours an assemblage of mammal and bird species that is normal for the boreal forest in northern Fennoscandia (see Esseen et al. 1997). The most common mammal species, their trophic position and space use is given in Appendix 1.

2.2 Sampling design

My basic study unit is an equilateral triangle with 1 kilometer long compass-straight sides (transects), thus having a total perimeter of 3 kilometers. The starting points of 32 such triangular routes were selected from 60 randomly generated GPS positions. The criteria for selecting starting positions were that the triangles should not overlap in the terrain and be possible to walk on skis. However, the present study counts only 27 triangles, due to unusually warm climatic conditions, with much rain. March 2003 had an average temperature of +1.3°C and 227.3mm of precipitation at a meteorological station lying in the middle of the general study area (Evenes airport), whereas the long-term values of March are -2.5°C and 67mm of precipitation (Evenes airport in the period 1961 until 1990, Norwegian

Meteorological Inst. 2006). The nearly daily precipitation limited the number of days possible to track animals, and inevitably the number of triangles, since my method require at least one snow (and rain) free night for tracks to set. Periods of hard crusted snow, when no tracks are set except for the heavy moose, is another factor limiting the sample size. This factor can also bias my corrections of “tracking nights since last snowfall”, and triangles skied at different dates will suffer differently in this respect. From the selected positions, the surveys were started 20 meters into the closest spruce plantation in order to cover the ecotones between spruce plantations and birch forest. The triangles were systematically placed in the terrain with one transect line going east/west (see Figure 1 for placement of triangles in the study area). The regular shape and systematical placement of the wildlife triangle, the randomly generated starting points and selection of these based upon no triangle overlap all help to guarantee the randomness of habitats along the triangle sides.

2.3 Snow-track survey

Several studies have used snow tracking to estimate abundance, activity and spatial distribution of mammals (e.g. Helle et al. 1996, Kurkki et al. 1998, D'Eon 2001). Thompson et al. (1989) found that track counts for marten *Martes americana*, snowshoe hare *Lepus americanus* and red squirrel *Tamiasciurus hudsonicus* were correlated with live-trapping data, suggesting that abundance of tracks can be used as an index of population density and habitat preferences for these species. The snow-track survey in the present study is based on the Finnish wildlife triangle method described in detail by Lindén et al. (1996) and Högmänder & Penttinen (1996). Animal tracks and vegetation changes, scored as a change from absence to presence of spruce trees >2 meters tall, intercepting the triangle sides were recorded in UTM coordinates using a hand-held GPS-receiver (Garmin GPS12XL). Positions were noted with an accuracy of 20 meters. The coordinates of animal crossings and vegetation changes served as basis for statistical analysis. Spruce percentage was calculated for each triangle by comparing the share of spruce vegetation to the total length of the respective triangle. Only fresh tracks (set after the last snowfall) were identified according to Aronson & Eriksson (1992). All crossings were counted, even if the observer could easily notice all tracks to be left by the same individual. This is important when converting track numbers into animal densities (Högmänder & Penttinen 1996).

2.4 Data treatment and statistical analysis

Choosing the appropriate study scale (level), covering the effect of interest, is crucial in landscape ecology. Forestry acts mainly on stands and landscapes (Niemelä 1999) and the sampling design allowed the snow-track data to be analysed at these levels. The basic unit at the tree stand level was a part of a triangle side with a continual presence or absence of spruce. The triangle is the unit at landscape level. Responses at the stand and landscape level can be influenced by the size and spatial distribution of the spruce stands, as well as the different mammals' perception of the landscape (Wiens 1976). In my study, the plantations of spruce were smaller than the home range requirements and cruising radii of the observed mammals (Appendix 1), hence suggesting a fine-grained response to spruce for these species (Wiens 1976). Regional variations between triangles were also evaluated, since they have been found to play an important role for species owing to high mobility and large homeranges (Wiens 1976, Rolstad 1991, Gjerde & Saetersdal 1997, Hausner et al. 2002).

The data were analysed with respect to the response of individual species. However, stoat *Mustela erminea* and weasel *Mustela nivalis* are ecologically similar species (Aunapuu & Oksanen 2003), and they were grouped as mustelids in all analysis in order to increase sample size. Only species with more than 100 tracks were included in the analysis, for the same reason (Appendix 1).

2.4.1 Tree stand level

Two different possible effects of spruce were examined at the tree stand level. First, I wanted to see if the species would respond differently in terms of tracks distance to spruce edge. Secondly, I compared the density of tracks in spruce to other stand types, to see if spruce stands were avoided or preferred relative to the surrounding forest.

2.4.1.1 Differences in edge response

In this analysis, I focused on interspecific differences in response to spruce plantation edges. The analysis required a calculation of each track's distance to the nearest edge of a spruce stand. The GPS positions of tracks and vegetation changes served as basis for estimating 95% confidence intervals for the mean of each species distribution of distances relative to

spruce plantation edge. Nonparametric bootstrap was used for estimating robust confidence limits (Efron & Tibshirani 1991), and implemented by the statistical software R, version 2.6.0 (R Development Core Team 2007, function `abcnon{bootstrap}`).

2.4.1.2 Forest stand type effects

My second objective was to see if there were significantly less tracks set in spruce than in other forest types and if there were major differences between species. In order to compare activity in spruce stands to other stand types, I made an index for density of tracks per species for each forest type: Each species' number of tracks per forest type (spruce vs. non-spruce) was recorded in every triangle and corrected for number of days since last snowfall and the relative availability of the forest type in question. Species-specific track indices were analysed as a function of forest type using linear mixed effects models (Pinheiro et al. 2007) in R, version 2.6.0 (R Development Core Team 2007, function `lme{nlme}`). Triangle was considered a random effect, while forest type and species were set as fixed factors, being the explanatory variables of interest. The response variable (the track index) was transformed by the natural logarithm, to obtain an adequate distribution of the residuals. In order to estimate the difference among species, a model with the interaction between forest type and species was initially fitted the data. Model selection (which explanatory variables and interactions to include in the model) was performed by Akaike's Information Criterion (AIC) (Anderson et al. 2001). When the difference in AIC values between two models was small (<1) the simplest model was chosen.

2.4.2 Landscape level

The density of tracks at the level of triangles (here termed landscape level) was estimated in almost the same way as density of tracks at forest stand level. Abundance of tracks per triangular route for each species was divided by number of track nights (days since last snowfall) and kilometers of the triangle (ranging from 2.93 to 3.25 km) in order to compare use of different areas. Species-specific track indices (as the response variable) were analysed with respect to the percentage of spruce in the triangle and the degree of fragmentation. The degree of fragmentation was given by the number of edges per kilometer for each triangle. The most complex model included a two-way interaction between species and the two continuous landscape variables. Triangle was once again considered a random effect. All other variables, i.e. percentage of spruce, species and number of edges per kilometer, were taken as

fixed factors. The distribution of residuals improved considerably when transforming the response variable (the track index) by the natural logarithm, so this was applied. The most appropriate model was selected by means of AIC-values. The analysis was conducted using linear mixed effects models (Pinheiro et al. 2007) in R, version 2.6.0 (R Development Core Team 2007, function `lme{nlme}`).

2.4.3 Regional level

Possible spatial correlation between species track indices at triangle level was tested in R (R Development Core Team 2007) by computing spearman rank correlation coefficients. This analysis was conducted to elucidate if different species tended to show the same spatial distribution among landscapes (i.e. triangles) within the region. To what extent the separate species show a spatially clustered distribution (i.e. spatial autocorrelation) at the level of the study region was evaluated by Mantel's test (Mantel 1967), as implemented by the `mantel.rtest{ade4}` function in R.

3. Results

1736 animal tracks were counted during March and April 2003. 1618 of these belonged to the four most numerous species groups, i.e. mountain hare (n=815), red fox (n=430), small mustelids (n=228), and moose (n=145). All other species had track numbers below 100.

3.1 Responses at the tree stand level

3.1.1 Interspecific differences in edge response

The species-specific 95% confidence intervals of mean track distances relative to edge of spruce stand were overlapping (Figure 2). Consequently, there was no evidence for interspecific differences in response to spruce plantation edges.

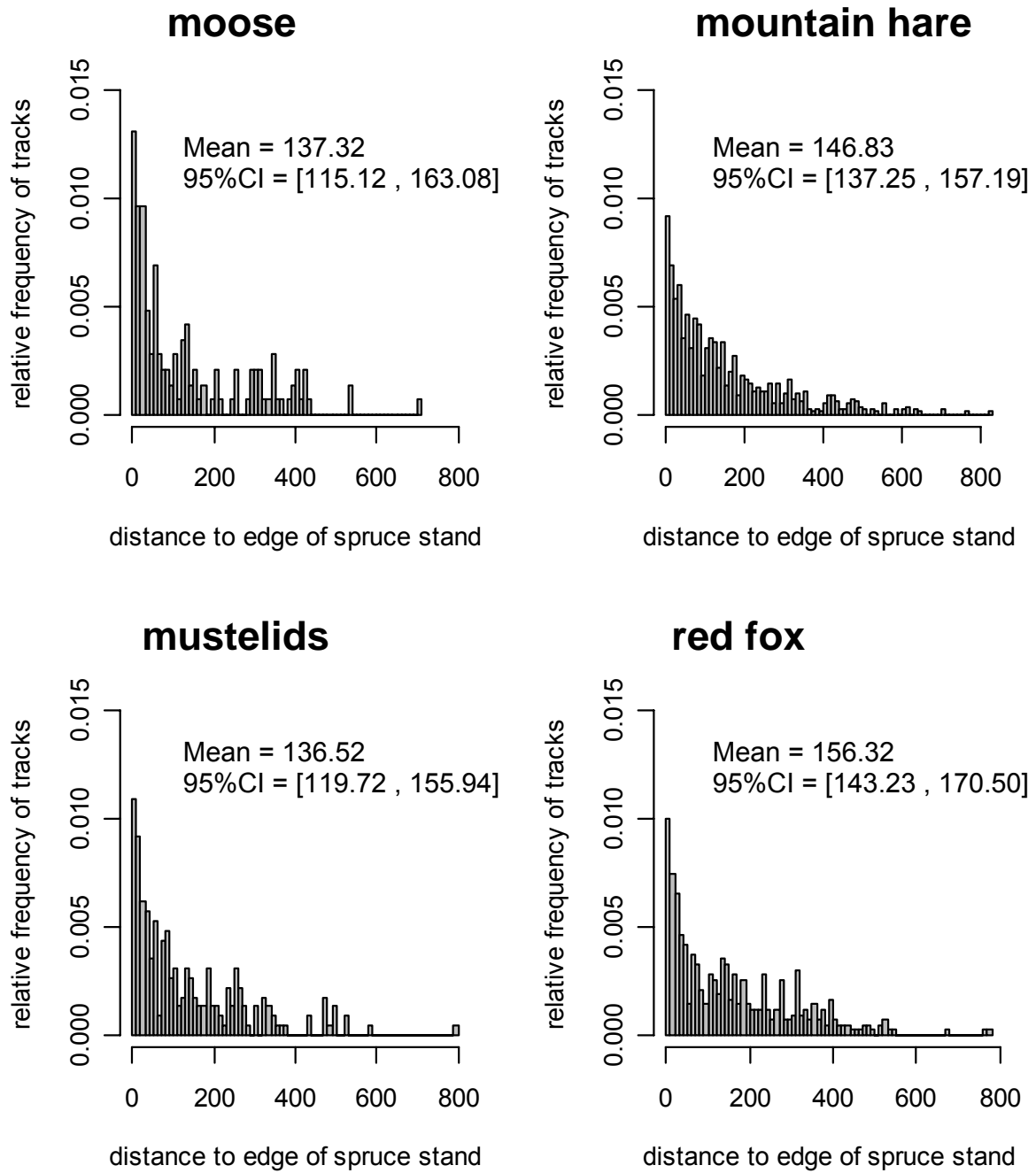


Figure 2. Frequency of track distances (in meters) relative to edge of a spruce stand in four species (groups). The values for the mean and its bootstrap 95% confidence intervals are inserted.

3.1.2 Forest stand type response

The density of tracks at the stand level was best described (according to AIC; Appendix 2A) by a model only including species, and there was no evidence for any selection or avoidance of spruce plantations for any of the species (Figure 3).

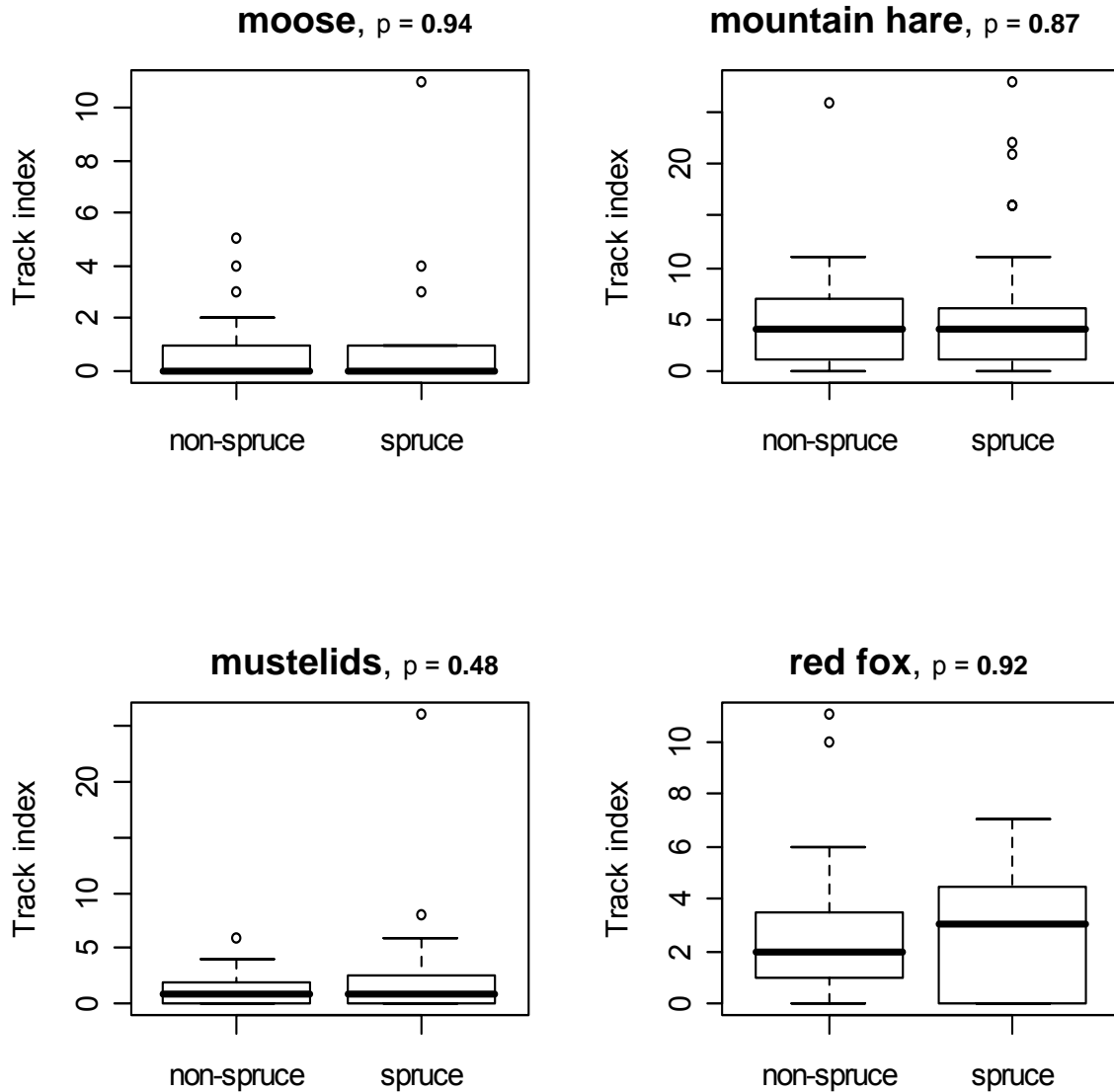


Figure 3. Track indices of spruce and non-spruce (i.e. other forest types as a group) at stand level in four species (groups) shown as boxplots. The inserted p-values are from tests of the parameters estimating the species-specific difference in occurrence in spruce vs. non-spruce (Appendix 3 A), obtained from the most complex model in Appendix 2 A.

3.2 Responses at the landscape level

The density of tracks at the level of sampling triangles was best described by a model that included an interaction between percentage spruce and species (Appendix 2 B). Thus, the percentage of spruce appeared to influence the abundance of the different species (groups) to a different extent. However, inspecting the parameters of the selected linear model gave no indications that there were statistical significant effects of percentage spruce within the different species (Appendix 3 B), although the slope was positive for all species (Figure 4). The number of spruce edges per kilometer was not correlated to the density of tracks, as this variable was excluded in the model selection (Appendix 2 B).

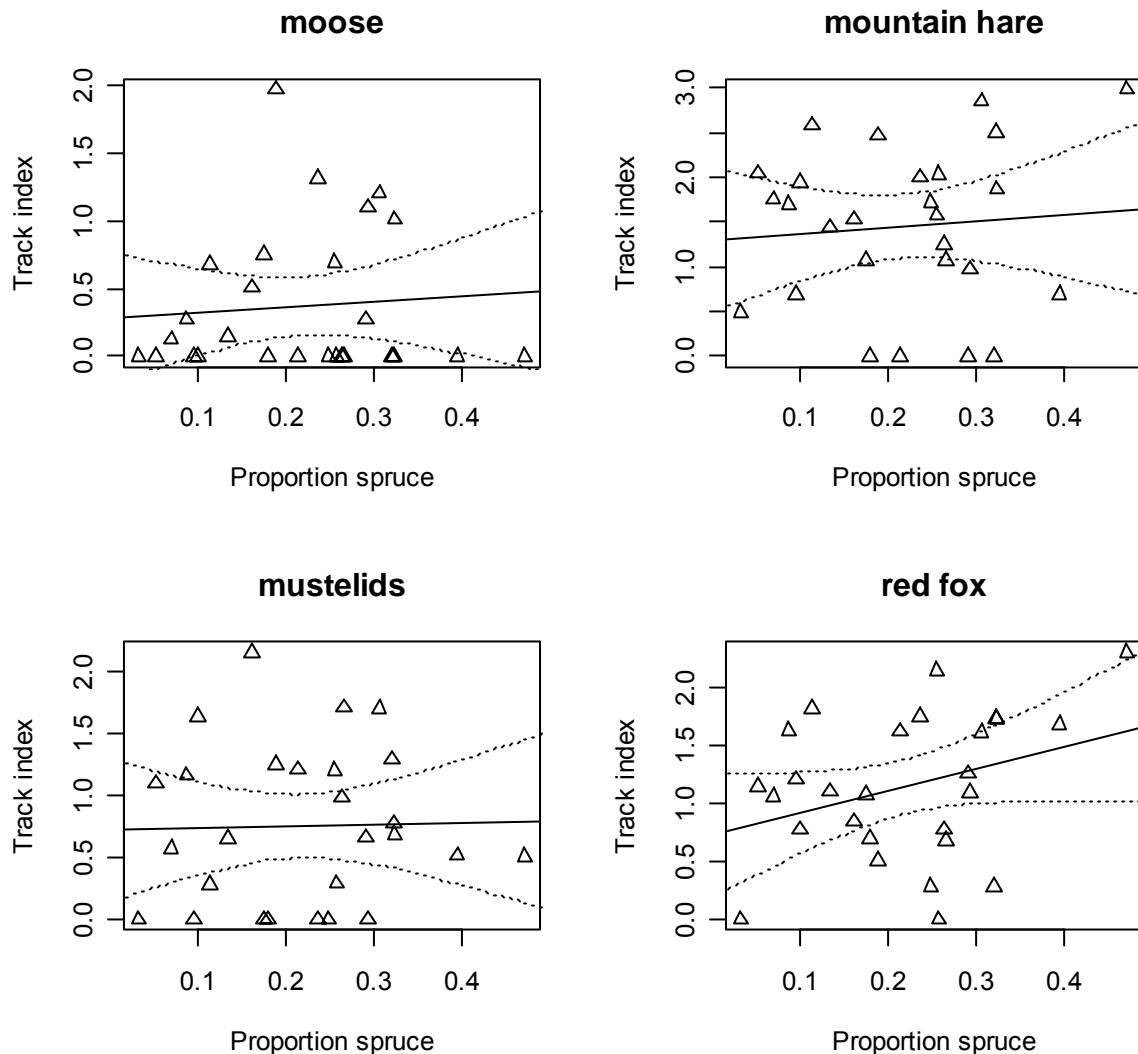


Figure 4. Density of tracks as a function of spruce percentage for four species (groups). The scatterplots and linear regression lines with 95% confidence intervals show the natural logarithm of track indices as a function of spruce percentage. Each triangle represents data from each of the tracking triangles.

3.3 Regional level distributions

There was a rather clear indication of a positive spatial association between red fox and mountain hare, as revealed by correlation analysis of track indices among the sampling triangles (Table 3). A weaker positive spatial association was indicated between mountain hares and moose. Spatial autocorrelation as evaluated by Mantel test indicated a spatial aggregation of mountain hare and a weaker for moose within the general study area (Figure 5).

Table 3 Spearman correlation coefficients between pair of species (below the diagonal) and their corresponding p-values (above). The significant spatial association is indicated in **bold**.

	moose	mountain.hare	red.fox	mustelids
moose		0.0861	0.8597	0.6921
mountain.hare	0.3366		0.0069	0.6048
red.fox	0.0357	0.5074		0.6461
mustelids	0.0799	0.1043	-0.0926	

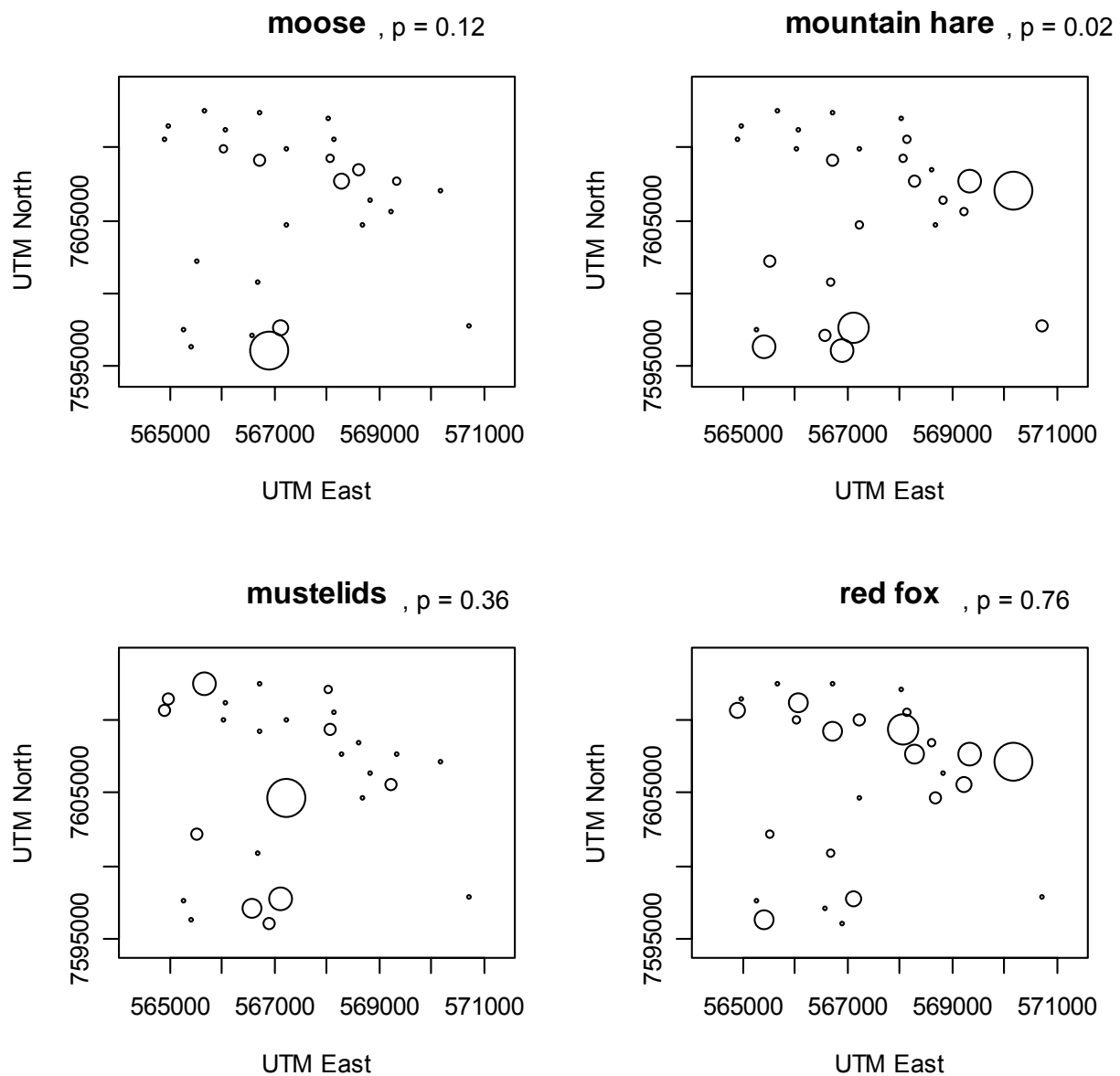


Figure 5. The spatial distribution of tracks for the different species (groups) within the general study area. Each circle represents the track index from one triangle, its size being proportional to the density of tracks. P-values from a Mantel test of spatial autocorrelation are inserted.

4. Discussion

Loss of habitat, fragmentation and introduction of exotic species are the main threats to biological diversity today (Andrén 1997, Chapin et al. 2000, Richardson 1998) and introduction of spruce in northern Norway can represent all three of these. Still, the present study found no responses to spruce at stand level or landscape level for the species studied. Trends in spatial distribution of tracks were only significant at the regional level, and this was not related to spruce.

4.1 Tree stand level

4.1.1 *Lack of interspecific differences in edge response*

The distance of tracks relative to the edge of spruce stands did not vary between species, meaning that all species responded in the same way to spruce edge. Although not tested explicitly, the lack of species differences (and the lack of preferences or avoidance of spruce stands) indicates that the species did not avoid or select such edge habitats. Habitat edges are one of the most extensively researched landscape elements in ecology, often associated with a change in abundance, activity or diversity of species (Yahner 1988, Ries et al. 2004), although results vary tremendously. The lack of edge effects in the present study is consistent with the majority of studies on birds and mammals (Lahti 2001, Ries et al. 2004). Edges are generally defined as boundaries between distinct habitat patches (Ries et al. 2004), and my focus here (as in Wiens 1976) is what a mammal will define as a distinct habitat patch. Generally, a stand of spruce was expected to represent a much denser structure than its surrounding vegetation, especially in the winter when deciduous trees lack leaves. Instead, the greatest differences in forest density are probably to find within the chosen categories, according to my observations in the field. There are still only a few small patches of mature spruce stands in the general study area. Most plantations are presently in an early succession stage, spread throughout the landscape and mixed with birch trees (Hausner et al. 2002). The plantation edges in this landscape are often more like a slow gradient than a sharp change in structure. Einarsen et al. (2007) worked in the same study area, comparing predation rate between spruce edges that differed in respect of their sharpness. Still, they found no effects of spruce edges on predation on artificial ground nests (Einarsen et al. 2007). I have all

reason to believe that the mammal species included in the present study do not perceive the spruce edge, sharp or gradual, as a distinct habitat change, or that they do discern a difference, but without acting upon that information. This can be explained in terms of a fine-grained response of the forest (Wiens 1976), for instance, due to large homeranges relative to the size of spruce stands (Appendix 1).

4.1.2 Lack of response to forest stand type

The density of tracks in spruce did not differ from track densities in other stand types, meaning that spruce stands were utilized in direct proportion to their frequency of occurrence, i.e. in a random fashion. As mentioned for edge effects, this can mean that the species do not perceptually differentiate spruce from other stand types or that they discern a difference but do not act upon that information, in accordance with a fine-grained response (Wiens 1976). In boreal coniferous forests, mountain hares were found to prefer medium aged spruce (Lindlöf et al. 1974, Hulbert et al. 1996), and the same was reported for snowshoe hares in North America (Wolff 1980). However, spruce was not a food source for the hares (in accordance with Pulliainen & Tunkkari 1987), the preference for spruce was mainly explained by the well developed over and understory providing shelter in these areas. Essentially, shelter reduces wind speed, thereby lowering the rate of convective heat loss to the surrounding air, as well as reducing the detectability by predators (Thirgood & Hewson 1987). Spruce plantations >2 meters tall in my study area may serve a good canopy cover and hereby protection from avian predators, but the ground vegetation is generally suffering from increased shading, acidification and a reduced microbial activity (Fremstad 1997, Saetre 1999). This is in line with my observations in the field; there was a general lack of understory in spruce plantations >2 meters tall. Accordingly, the spruce plantations in my study are not likely to shelter mountain hares from mammalian predators or wind. This can contribute to the mountain hares' lack of preference to spruce. Red fox is generally described as a habitat generalist; its path is given by the search for prey (Carr & MacDonald 1986), e.g. mountain hares (Marcström et al. 1988, Lindström et al. 1994). This is consistent with the present results of red fox not responding to spruce at stand level. The absence of large predators in the study area suggests that moose in northern Norway generally do not seek shelter to avoid predators (Saeter et al. 1996). However, several studies have documented how cervids like the moose selectively use cover to reduce heat loss by wind in cold periods (Belovsky 1981, Schwab and Pitt 1991, Demarchi and Bunnell 1995). My study was conducted in a period of

unusually high temperatures and this could have reduced the need of shelter for moose. Stoat and weasel are small opportunistic mustelids, considered to be rodent specialists (King 1983, Sheffield & King 1994) although their diets also consist of lagomorphs (rabbits), birds and birds eggs (McDonald et al. 2000). Little research has been conducted on mustelids' response to habitat structure, but both seem to prefer productive areas where the abundance of preferred *Microtus* prey is the highest (Aunapuu & Oksanen 2003, Hellstedt & Henttonen 2006). Spruce planting in northern Norway has reported a negative effect on density of rodents at stand level (Sigurdson 2000), related to conditions in ground vegetation (Fremstad 1997). One may assume that mustelids would avoid spruce at stand level, but this effect is not seen in the present study.

4.2 Landscape level

Percentage of spruce at the level of sampling triangles appeared to influence the abundance of the different species to a various extent and in a positive manner for all species. However, these effects were weak and none of the species showed statistically significant responses to spruce. The density of tracks did not respond to number of spruce edges in the landscape either.

Fragmentation and loss of natural habitat at the landscape level are major threats to biological diversity (Wilcove et al. 1986). Bender et al. (1998) reviewed 25 published studies that tested for a relationship between patch size and population density and found that predators differed from prey and migratory from residential species in their responses to increasing fragmentation. My lack of responses to number of spruce edges can indicate that the species do not perceive the spruce planting as a fragmentation of their landscape, or if they do, that the magnitude of planting in the general study area is below the threshold for changes in the spatial activity of the selected species (Andrén 1997).

An abundance or lack of animal tracks in a particular area may not necessarily reflect habitat quality. Track densities may be due to local temporal variability in food items, predator populations or abiotic factors rather than long term habitat quality (Forsey & Baggs 2001). One should also be aware that areas used according to availability or avoided could be areas essential to a species, even though little time is spent in those areas. My indicated interspecific differences in response to spruce may be understood in terms of spruce

plantations serving different functions for the different species, as pointed out by McIntyre & Wiens (1999). Still, the lack of significant effects weakens this hypothesis. The structures in the landscape that serve functions for the mammals included in the present study might be on a much larger scale (Wiens 1976).

4.3 Regional level

The spatial association between red fox and mountain hare was rather clear. Mountain hares and moose did also show some spatial association, although to a less extent. Spatial autocorrelation at the regional level indicated a spatial aggregation of mountain hares and a weaker for moose within the general study area.

The spatial association between red fox and mountain hare can be explained by the fact that red fox seek and predate on mountain hares (Lindström et al. 1994). Mountain hares and moose are most probably seeking the same areas because they feed on the same type of vegetation, preferably deciduous trees (Lindlöf et al. 1974, Pulliainen & Tunkkari 1987, Cederlund et al. 1980). The spatial autocorrelation for mountain hare and moose show that there are some large scale regional factors affecting the spatial distributions of the species. I cannot single out any of these factors or value their relative contribution on track densities, but I know that this effect is not related to spruce. The detection of regional trends, combined with a lack of response to spruce plantations at smaller scales, is in accordance with what Einarsen et al. (2007) found on predation rates on artificial ground nests in the same study area. The coastal deciduous forest is naturally fragmented on a large scale by mountains, fjords and marshes. Mountain hare and moose may be aggregated and correlated due to a possible same scale aggregation of the deciduous tree species they both prefer.

4.4 Conclusion

Niemelä (1999) ranks forestry as the main disturbance in the Fennoscandian boreal forest. Still, my results suggest that nearly a century of spruce planting have not affected the way that the four most common mammals move in the landscape. The only trends in spatial distribution of tracks are found at the regional level, possibly related to the distribution of preferred food plants. However, statistical analysis on ecological interactions must be interpreted with caution. Small sample size could have a profound effect on the outcome of

a test. This study is related to structural differences in vegetation, but only at the tree level. The mammals in the present study may not be influenced by the structural differences between trees, considering their ecology. Mountain hares browse trees in winter but switch to eating grass in the summer (Hulbert et al. 1996). Moose appear in forested valleys during the winter, but the summer behavior is quite different; moving long distances in the mountains to feed (Cederlund et al. 1987). Mustelids and red fox are also well known inhabitants in the mountains, above the tree line (King 1983, Hersteinsson & MacDonald 1992, Sheffield & King 1994). The extensive use of areas above the treeline contributes to the idea that structural variation in trees may not be so important for these mammals' perception of the landscape. Communities of birds have shown a response to spruce plantations in Norway (Hausner et al. 2002, Gjerde & Saetersdal 1997, Gjerde et al. 2005), but the present study found no such effects on mammals. As a result, I know that responses to spruce plantations in Norway may differ greatly among vertebrates. There is still a general lack of empirical data on birch forests and its species (Hausner 2001, Einarsen et al. 2007), and further research is needed to predict the effects of spruce planting in this ecosystem.

References

- Anderson, D. R., W. A. Link, et al. 2001. Suggestions for presenting the results of data analyses. *Journal of Wildlife Management* **65**: 373-378.
- Andrén, H. 1997. Habitat fragmentation and changes in biodiversity. Boreal ecosystems and landscapes: structures, processes and conservation of biodiversity. L. e. Hansson. Dublin, Ireland, *Ecological Bulletins*. **46**: 171-181.
- Aronson, Å. and P. Eriksson 1992. Dyrespor og kunsten å spore. Cappelen, Oslo in Norwegian.
- Aunapuu, M. and T. Oksanen 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology*. **17**: 371-392.
- Beckel, L. 1995. Satellite remote sensing forest atlas of Europe. Justus Perthes Verlag.
- Belovsky, G. E. 1981. Optimal activity times and habitat choice of moose. *Oecologia* **48**: 22-30.
- Bender, D. J., T. A. Contreras, et al. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **72**: 517-533.
- Carr, G. M. and D. W. Macdonald 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* **34**: 1540-1549.
- Cederlund, G., H. Ljungqvist, et al. 1980. Foods of moose and roe-deer at Grimso in central Sweden: results of rumen content analyses. *Swedish Wildlife Research* **11**: 169-247.
- Cederlund, G. and H. Sand 1994. Home-Range Size in Relation to Age and Sex in Moose. *Journal of Mammalogy* **75**: 1005.
- Cederlund, G., F. Sandegren, et al. 1987. Summer movements of female moose and dispersal of their offspring. *Journal of Wildlife Management* **51**: 342-352.
- Chapin III, F. S., E. S. Zavaleta, et al. 2000. Consequences of changing biodiversity. *Nature* **405**: 234-242.
- D'Eon, R. G. 2001. Using snow-track surveys to determine deer winter distribution and habitat. *Wildlife Society Bulletin* **29**: 897-887.
- Demarchi, M. W. and F. L. Bunnell 1995. Forest cover selection and activity of cow moose in summer. *Acta Theriologica* **40**: 23-36.
- Efron, B. and R. Tibshirani 1991. Statistical data analysis in the computer age. *Science* **253**: 390-395.
- Einarsen, G., V. H. Hausner, et al. 2007. Predation on artificial ground nests in birch forests fragmented by spruce plantations. *Ecoscience*, in press.
- Esseen, P.-A., B. Ehnström, et al. 1997. Boreal forests. Boreal ecosystems and landscapes: structures, processes and conservation of biodiversity. L. Hansson. Dublin, Ireland, *Ecological Bulletins*. **46**: 16-47.
- Forsey, E. S. and E. M. Baggs 2001. Winter activity of mammals in riparian zones and adjacent forests prior to and following clear-cutting at Copper Lake, Newfoundland, Canada. *Forest Ecology and Management* **145**: 163-171.
- Frafjord, K. 2004. Winter range of a red fox *Vulpes vulpes* group in a northern birch forest. *Mammalian Biology - Zeitschrift fur Saugetierkunde* **69**: 342-348.

- Fremstad, E. 1997. Vegetasjonstyper i Norge. NINA Temahefte **12**: 1-279.
- Fremstad, E. and Ø. Norman 1982. Registration of localities with rich deciduous forests in Troms, Northern Norway. Inventing av rik løvskog i Troms. In Norwegian with English summary. University of Tromsø, Tromsø Naturvitenskap **34**.
- Gjerde, I. and M. Saetersdal 1997. Effects on avian diversity of introducing spruce *Picea* spp. plantations in the native pine *Pinus sylvestris* forests of western Norway. *Biological Conservation* **79**: 241-250.
- Gjerde, I., M. Saetersdal, et al. 2005. Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. *Biodiversity and Conservation* **14**: 377-393.
- Gustavson, M. 1974. Berggrunnskart Narvik 1:250 000, Norges Geologiske undersøkelser, Trondheim.
- Hausner, V. H. 2001. Scenarios for managing biodiversity in coastal birch forests fragmented by spruce plantations. PhD thesis, Department of Biology, Faculty of Science, University of Tromsø, Tromsø.
- Hausner, V. H., N. G. Yoccoz, et al. 2002. Changes in bird communities by planting non-native spruce in coastal birch forests of northern Norway. *Ecoscience* **9**: 470-481.
- Helle, E., H. Pekka, et al. 1996. Wildlife populations in Finland during 1990-1995, based on wildlife triangle data. *Finnish Game Research* **49**: 12-17.
- Hellstedt, P. and H. Henttonen 2006. Home range, habitat choice and activity of stoats *Mustela erminea* in a subarctic area. *Journal of Zoology* **269**: 205-212.
- Hersteinsson, P. and D. W. MacDonald 1992. Interspecific Competition and the Geographical Distribution of Red and Arctic Foxes *Vulpes Vulpes* and *Alopex lagopus*. *Oikos* **64**: 505-515.
- Hewson, R. and M. D. C. Hinge 1990. Characteristics of the Home Range of Mountain Hares *Lepus timidus*. *The Journal of Applied Ecology* **27**: 651-666.
- Högmander, H. and A. Penttinen 1996. Some statistical aspects of Finnish wildlife triangles. *Finnish Game Research* **49**: 37-43.
- Hulbert, I. A. R., G. R. Iason, et al. 1996. Home-range sizes in a stratified upland landscape of two lagomorphs with different feeding strategies. *The Journal of Applied Ecology* **33**: 1479-1488.
- Jedrzejewski, W., B. Jedrzejewska, et al. 1995. Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. *Ecology* **76**: 179-185.
- King, C. M. 1983. *Mustela erminea*. *Mammalian Species* **195**: 1-8.
- Kurkki, S., A. Nikula, et al. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *Journal of Animal Ecology* **67**: 874-886.
- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biological Conservation* **99**: 365-374.
- Lindén, H., E. Helle, et al. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research* **49**: 4-11.
- Lindlöf, B., E. Lindström, et al. 1974. On activity, habitat selection and diet of the mountain hare *Lepus timidus* L. in winter. *Viltrevy* **9**: 27-43.

- Lindström, E. R., H. Andren, et al. 1994. Disease Reveals the Predator: Sarcoptic Mange, Red Fox Predation, and Prey Populations. *Ecology* **75**: 1042-1049.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**: 209-220.
- Marcström, V., L. B. Keith, et al. 1989. Demographic responses of arctic hares *Lepus timidus* to experimental reductions of red fox *Vulpes vulpes* and martens *Martes martes*. *Canadian Journal of Zoology* **67**: 658-668.
- McDonald, A. R., C. Webbon, et al. 2000. The diets of stoats *Mustela erminea* and weasels *Mustela nivalis* in Great Britain. *Journal of Zoology (London)* **252**: 363-371.
- McIntyre, N. E. and J. A. Wiens 1999. Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* **14**: 437-447.
- Moen, A. 1998. National atlas of Norway: Vegetation, Norwegian Mapping Authority, Hønefoss.
- Mysterud, A. and E. Østbye 1999. Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography. *Wildlife Society Bulletin* **27**: 385-394.
- Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology and Management* **115**: 127-134.
- Nilsen, K. W. 2007. Variation in epiphytic vegetation in spruce plantations and adjacent native birch forests in North Norway. MSc Thesis, Department of biology, Faculty of science, University of Tromsø, Tromsø.
- Nilssen, E. and K. D. Vorren 1990. Skogens innvandringshistorie. Skogbruk i Nord-Norge. A. Sveli, Nord-Norges Skogmannsforbund.
- Pedersen, H. C., T. Bretten, et al. 1995. Moulting, predation and winter ecology in mountain hare *Draktskifte, predasjon og vinterøkologi hos hare*. NINA Oppdragsmelding **339**: 1-18.
- Pinheiro, J., D. Bates, et al. 2007. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-85.
- Pulliamin, E. and P. S. Tunkkari 1987. Winter diet, habitat selection and fluctuation of a mountain hare *Lepus timidus* population in Finnish forest Lapland. *Holarctic Ecology* **10**: 261-267.
- R Development Core Team 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, D. M. 1998. Forestry trees as invasive aliens. *Conservation Biology* **12**: 18-26.
- Ries, L., R. J. J. Fletcher, et al. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Reviews of Ecology, Evolution and Systematics* **35**: 491-522.
- Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: Conceptual issues and the evidence. *Biological journal of the Linnean Society*. **42**: 149.
- Saether, B.-E., R. Andersen, et al. 1996. Ecological Correlates of Regional Variation in Life History of the Moose *Alces Alces*. *Ecology* **77**: 1493-1500.
- Saetra, H. 1971. Samanhengen mellom plantesamfunn og granbonitetar i Nord-Troms. Cand.real.thesis, Department of biology, Faculty of science, University of Bergen, Bergen.

- Saetre, P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. *Ecography* **22**: 183-192.
- Schwab, F. E. and M. D. Pitt 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Canadian Journal of Zoology* **69**: 3071-3077.
- Sheffield, S. R. and C. M. King 1994. *Mustela nivalis*. *Mammalian Species* **454**: 1-10.
- Sigurdson, T. 2000. Treslagskifte fra bjørk *Betula pubescens* til gran *Picea abies* i Nord-Norge: effekter på økologiske prosesser i subarktiske bjørkeskoger. MSc Thesis, Department of biology, Faculty of science, University of Tromsø and Norwegian institute of nature research, Tromsø.
- Telfer, E. S. 1970. Winter Habitat Selection by Moose and White-Tailed Deer. *The Journal of Wildlife Management* **34**: 553-559.
- Tenow, O. 1996. Hazards to a mountain birch forest - Abisko in perspective. *Ecological Bulletins* **45**: 104-114.
- Thirgood, S. J. and R. Hewson 1987. Shelter Characteristics of Mountain Hare Resting Sites. *Holarctic Ecology* **10**: 294-298.
- Thompson, I. D., I. J. Davidson, et al. 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. *Canadian Journal of Zoology* **67**: 1816-1823.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Reviews of Ecology, Evolution and Systematics* **7**: 81-120.
- Wilcove, D. S., C. H. McLellan, et al. 1986. Habitat fragmentation in the temperate zone. *Conservation biology: the science of scarcity and diversity*. M. E. Soulé, Sinauer, Sunderland, Massachusetts, USA.
- Wolff, J. O. 1980. The Role of Habitat Patchiness in the Population Dynamics of Snowshoe Hares. *Ecological Monographs* **50**: 111-130.
- Yahner, R. H. 1988. Changes in Wildlife Communities Near Edges. *Conservation Biology* **2**: 333-339.

Appendix 1

Species registered in the snow track survey, home range and study scale**.*

Group	Species* registered in the snow track survey	Homerange (km ²)	Study scale**
Predator specialists	Stoat <i>Mustela erminea</i>	1.49-1.66 (breeding – nonbreeding season, ♂) 0.35-0.66 (breeding – nonbreeding season, ♀) (Hellstedt & Henttonen 2006)	X
	Weasel <i>Mustela nivalis</i>	0.051-0.242 (summer-autum, ♂) 0.425-1.666 (spring-summer, ♂) (Jedrzejewski et al. 1995)	X
Predator generalists	Red fox <i>Vulpes vulpes</i>	1.58-5.82 (Frafjord 2004)	X
Herbivores (prey)	Mountain Hare <i>Lepus timidus</i>	0.06-1.13 (Hewson & Hinge 1990, Pedersen et al.1995, Hulbert 1996)	X
	Moose <i>Alces alces</i>	13.7 ± 2.2 SE (adult ♀) 25.9 ± 3.3 SE (adult ♂) (Cederlund & Sand 1994)	X

* Other species in the study area are predators e.g. black-billed magpie *Pica pica*, common raven *Corvus corax*, goshawk *Accipiter gentiles*, hooded crow *Corvus corone*, jay *Garrulus glandarius*, lynx *Felis lynx*, mink *Mustela vison*, pine marten *Martes martes*, tengmalm's owl *Aegolius funereus* and herbivores e.g. black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus*, common shrew *Sorex araneus*, field vole *Microtus agrestis*, red vole *Myodes rutilus*, roe deer *Capreolus capreolus* and squirrel *Sciurus vulgaris*. All of these were registered in too few numbers ($n < 100$) to be included in the statistical analysis.

** X = homerange larger than the present spruce plantations. Most plantations are relatively young and mixed with birch trees, while elderly plantations are more homogeneous. The old plantations are small in size, ranging from 0.008 km² to 0.170 km², averaging at 0.057 km² (Hausner et al. 2002).

Appendix 2

A) Tree stand level

AIC values for different set of variables explaining the density of tracks at tree stand level. Track indices are transformed by the natural logarithm in the model. The best model is indicated in **bold**.

Species	Forest type	Species * Forest type	AIC
x	x	x	521.6687
x	x		513.2538
X			508.6786
	x		562.4472

B) Landscape level

The table show AIC values for different models explaining the distribution of tracks (as indices and transformed by the natural logarithm) at landscape level. The selected model is indicated in **bold**.

Sprucepercentage	Species	Sprucepercentage * species	Edges per km	Edges per km * species	AIC
x	x	x	x	x	250.5233
x	x	x	x		237.7126
X	X	X			232.1954
x	x				235.1839
x					262.0141
	x		x	x	256.8122
	x		x		242.0264
	x				235.5757
			x		268.8566

Appendix 3

A) Tree stand level

Results from a linear mixed effects model for the natural logarithm of track indices as a function of an interaction between forest type and species. The p-values of interest are indicated in **bold**.

Parameters	Value	Std.Error	DF	t-value	p-value
a) fixed effects					
Intercept*	0.35	0.15	182	2.26	0.03
Mountain hare	1.07	0.19	182	5.57	0.00
Mustelids	0.27	0.19	182	1.39	0.17
Red fox	0.71	0.19	182	3.71	0.00
Moose ** index change from "other" to spruce	-0.02	0.19	182	-0.08	0.94
Mountain hare index change from "other" to spruce	0.05	0.27	182	0.17	0.87
Mustelids index change from "other" to spruce	0.19	0.27	182	0.71	0.48
Red fox index change from "other" to spruce	0.03	0.27	182	0.10	0.92
b) random effects					
~1 triangle					
St. Deviation intercept	0.37				
Residual	0.70				
* The intercept indicates the moose track index in "other" forest types. "Hare", "Mustelids" and "Fox" indicate these species track indices difference from moose in forest type "other".					
** This indicates how the track index of moose changes (the slope) when going from foresttype "other" to "spruce". Values of other animals index change indicate difference from moose in slope inclination					
Number of observations = 216 (4 species * 2 forest types * 27 triangles)					
Number of groups = 27 (27 triangles)					

B) Landscape level

Results from a linear mixed effects model for the natural logarithm of track indices as a function of percentage of spruce at a landscape level. The p-values of interest are indicated in **bold**.

Parameters	Value	Std.Error	DF	t-value	p-value
a) fixed effects					
Intercept*	0.28	0.30	75	0.95	0.34
Mountain hare	1.01	0.38	75	2.66	0.01
Mustelids	0.43	0.38	75	1.14	0.26
Red fox	0.44	0.38	75	1.15	0.25
Moose** index change for increasing levels of spruce	0.40	1.24	25	0.32	0.75
Mountain Hare index change for increasing levels of spruce	0.33	1.57	75	0.21	0.83
Mustelids index change for increasing levels of spruce	-0.24	1.57	75	-0.15	0.88
Red fox index change for increasing levels of spruce	1.52	1.57	75	0.97	0.34
b) random effects					
~1 triangle					
St. Deviation intercept	1.14				
Residual	2.67				
<p>* The intercept indicates the moose track index at zero percentage of spruce. "Hare", "Mustelids" and "Fox" indicate how much these animals track indices are different from moose at zero percentage of spruce</p> <p>** This indicates how the track index of moose changes when the share of spruce in an area increase by 1.00 (100%). Values for other animals indicate difference from moose in slope inclination.</p> <p>Number of observations = 108 (4 species * 27 triangles)</p> <p>Number of groups = 27 (27 triangles)</p>					

