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Salla Kaartinen

SPACE USE AND HABITAT SELECTION OF THE WOLF (*CANIS LUPUS*) IN HUMAN-ALTERED ENVIRONMENT IN FINLAND

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SALLA KAARTINEN

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Abstract

The grey wolf is the most widely distributed of all land mammals and is a habitat generalist that inhabits all the vegetation types of the Northern Hemisphere. Wolves also breed well and have the potential to rapidly expand to new areas.

In Finland, the wolf is a game species, and as a result of Finland's membership of the European Union, the wolf population is subject to very limited hunting due to the obligation to protect the species. Mainly for this reason, the wolf population in Finland has increased significantly in recent years. In particular, the birth rate has developed favourably and the number of litters increased from just four in 1996 to 20 in 2005. It also seems at present that the wolf population in Finland is no longer following the fluctuations in wolf numbers in Russian Karelia.

The general aim of this dissertation is to provide applicable knowledge for wolf management and conservation purposes, and especially to examine the effects of human-modified landscapes on wolf population expansion in Finland. Various aspects of habitat selection were investigated in four sub-studies to gain a thorough insight into the space use and habitat needs of wolves. Species data came from a long-term wolf population study that included location information from 85 radio- and GPS-GSM-collared wolves from 1998 onwards, as well as track location data based on about 30 000 annual observations recorded with geographical coordinates by a local network of experts on large carnivores.

I found that adaptability makes it possible for the wolf to live in the multiple-use, semi-wild forests of Finland and that no restrictions are imposed by the landscape on wolf population growth and expansion. In general, the results of my dissertation provide evidence that wolves tend to avoid the presence of human influence when establishing a territory and also when selecting their den site. However, as wolf numbers increase, conflict situations will more frequently occur between wolves and humans, although the risk of depredation events, for example among sheep farms, varies between farms in Finland. That is, there are some environmental and farm level factors that are associated with wolf depredation.

The breeding wolf population in Finland has gradually expanded and the first litters have recently been born in western Finland after an absence of more than 100 years. The geographical distance to the Scandinavian population is shorter from these new western territories than from the population's core area in eastern Finland. This could potentially increase the likelihood of dispersal from Finland to Scandinavia.

Keywords: Canis lupus, den site, dispersal, habitat selection, human influence, large predator, space use, wolf

Kaartinen, Salla, Suden (*Canis lupus*) tilankäyttö ja habitaatinvalinta ihmisen muokkaamassa ympäristössä Suomessa
Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos, PL 3000, 90014 Oulun yliopisto; Riista- ja kalatalouden tutkimuslaitos, Tutkijantie 2 E, 90570 Oulu
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Tiivistelmä

Susi on habitaattigeneralisti, jonka levinneisyys kattaa kaikki pohjoisen pallonpuoliskon kasvillisuustyypit. Sudet myös lisääntyvät hyvin ja voivat näin ollen levittäytyä nopeasti uusille alueille.

Suomessa susi on riistalaji, jonka metsästys on rajoitettua Euroopan unionin jäsenyyden myötä. Lähinnä tästä syystä Suomen susikanta on kasvanut voimakkaasti 1990-luvun ja 2000-luvun alun aikana. Erityisesti syntyvyys on kasvanut: pentueiden määrä lisääntyi neljästä 20:een vuosien 1996 ja 2005 välillä. Näyttäisi siltä, ettei Suomen nykyinen susipopulaatio enää seuraa Venäjän Karjalassa tapahtuvia kannanvaihteluita.

Väitöskirjan tavoitteena on ollut tuottaa susikannan hoidossa ja suojelussa käytettävissä olevaa tietoa ja erityisesti tutkia susikannan levittäytymistä ihmisen muokkaamassa ympäristössä Suomessa. Neljässä osatutkimuksessa on käsitelty suden habitaatinvalintaa eri näkökulmista, jotta saataisiin kokonaiskuva suden tilankäytöstä Suomessa. Tutkimusaineisto rakentui pitkäaikaisesta seuranta-aineistosta, jota on kerätty vuodesta 1989 lähtien. Vuosien 1989 ja 2010 välillä 85 sutta on pannoitettu radio- tai GPS-GSM –pannalla. Tutkimuksessa käytettiin hyväksi myös noin 30 000 vuosittain tehtyä jälkihavaintoa.

Tutkimustulosten perusteella susi selviää hyvin Suomen monikäyttömetsissä, eivätkä maisematyypit itsestään rajoita susipopulaation kasvua ja levittäytymistä. Toisaalta tulokset osoittavat myös sen, että sudet välttelevät ihmistoimintoja valitessaan reviiri- tai pesäpaikkoja. Kuitenkin susien lukumäärän kasvaessa ristiriitatilanteet susien ja ihmisten välillä tulevat lisääntymään, vaikka susivahinkoriskin suuruus vaihteleekin Suomessa huomattavasti. Esimerkiksi lammastilojen susivahinkoriski riippuu sekä ympäristötekijöistä, että tilan sisäisistä tekijöistä.

Kaiken kaikkiaan lisääntyvän susipopulaation esiintymisalue on Suomessa vähitellen kasvanut leviten itärajan tuntumasta kohti länttä. Tämän myötä maantieteellinen etäisyys Skandinavian susipopulaatioon on pienentynyt viimeisten vuosien aikana. Tämä voi edesauttaa susiyksilöiden siirtymistä Suomesta Skandinaviaan.

Asiasanat: Canis lupus, dispersaali, elinympäristön valinta, habitaatti, ihmistoiminnan vaikutus, pesäpaikka, susi, suurpeto, tilankäyttö

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I have been privileged to have the chance to work with a research question and especially with a research animal that has very much intrigued me, both during my PhD project and earlier during my Master's thesis project. Accomplishing this research has been a very interesting but demanding challenge in many ways.

I want to express my gratitude to my supervisor, Doc. Ilpo Kojola, for the interesting research questions he has given me to work with. I am also most indebted to Prof. Miska Luoto for his many useful ideas and thoughtful discussions on the subject of this dissertation. Thanks also to Prof. Alfred Colpaert, who participated in the process of writing the first article for this dissertation.

My PhD research was financially supported by the Finnish Cultural Foundation, the Faculty of Science, the Thule Institute, the Oulu University Scholarship Foundation, Naisten Tiedesäätiö and Suomen Riistanhoito-Säätiö. The Finnish Game and Fisheries Research Institute provided excellent research facilities, including innovative co-workers who have contributed to this work both directly and indirectly. I especially wish to acknowledge Dr Antti Paasivaara and Dr Janne Miettinen for all their ideas and the knowledge they shared with me during the process. I would also like to thank my friends in need, Riikka Holopainen, Laura Virtaluoto, Mari Murtomaa, Marjaana Tahkokorpi and Marja Hyvärinen, who have supported me and spurred me with this work. I am deeply grateful to my hairy companions Natikaiset, Armi and Virna for providing me the always needed stress relief by sharing everyday life with me. I would also like to thank all those friends that sharing my life with dogs has brought about for showing me that there is more to life just academic research. In particular, I want to thank Annina Visuri and Katja Pelkonen.

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Oulu, August 2010 Salla Kaartinen

List of original papers

This dissertation is based on the following papers, which are referred to in the text by their Roman numerals:

- I Kaartinen S, Kojola I & Colpaert A (2005) Finnish wolves avoid roads and settlements. Annales Zoologici Fennici 42: 523–532.
- II Kaartinen S, Luoto M & Kojola I (2010) Selection of den sites by wolves in boreal forests in Finland. Journal of Zoology 281: 99–104.
- III Kaartinen S, Luoto M & Kojola I (2009) Carnivore livestock conflicts: determinants of wolf (*Canis lupus*) depredation on sheep farms in Finland. Biodiversity and Conservation 18: 3503–3517.
- IV Kojola I, Kaartinen S, Hakala A, Heikkinen S & Voipio H-M (2009) Dispersal behavior and the connectivity between wolf populations in Northern Europe. Journal of Wildlife Management 73: 309–313.

The author's contribution: Most of the work in articles I–III was carried out by Salla Kaartinen (SK) and SK participated in the writing and interpretation of the results in IV. All the co-authors of the separate articles have participated in writing by commenting on the text, and thereby improving the manuscripts.

Contents

1 Introduction

1.1 Background

In Finland, the wolf is a game species, and as a result of Finland's membership of the European Union, the wolf population is subject to very limited hunting due to the obligation to protect the species (Ministry of Agriculture and Forestry 2002). The wolf as a top predator is not a habitat specialist, and wolf populations are limited by human-induced mortality, intraspecific conflict, starvation and prey abundance (Mech 1970, 1977, Fuller 1989, Mladenoff *et al.* 1995). Today, human activities affect most of the areas of the globe, and most of the Earth is dominated by a mosaic of agriculture, urbanization, logged forests and degraded land. The consequent habitat change has changed the geographical distributions of numerous species, but whether the effects are positive or negative depends on the species and the scale of the change. Despite this natural habitat fragmentation, some ecological generalists that have a high tolerance of habitat fragmentation can survive and thrive in this new environment if the matrix is friendly (Sunquist & Sunquist 2003). The wolf is not truly a wilderness species, and when public attitudes towards wolves are positive, wolves can colonize a wide variety of habitats (Mech 1995).

Humans have a need to determine where wolves can exist and often influence the ecology and behaviour of wolves in various ways (Mech 1970, Boitani 1995, Hayes & Gunson 1995, Stephenson *et al.* 1995, Thiel & Ream 1995, Bangs & Fritts 1996, Fritts *et al.* 2003). As with most carnivores, wolves also come into conflict with people because of their predatory habits and have been persecuted throughout history. This persecution has often been well-planned, nationally organized and state-funded (Woodroffe 2003). During the past 2000 years, fluctuations in the wolf range have been connected with the persecution efforts of humans (Okarma 1993), and even today humans are a major cause of wolf mortality in most of the current range (Fritts *et al.* 2003). The wolf is irregularly distributed across a variety of diverse settings ranging from ecological to economic and from cultural to political, making the holistic planning of wolf conservation and management difficult under the pressure of local views (Boitani 2003).

1.2 Grey wolf ecology and historical aspects

The grey wolf is the most widely distributed of all land mammals and is a habitat generalist that inhabits all the vegetation types of the Northern Hemisphere (Mech & Boitani 2003). Wolves also breed well and have the potential to rapidly expand to new areas (Ministry of Agriculture and Forestry 2002).

Wolves usually live in packs and the basic social unit of the population is the mated pair. A wolf pack is often a family unit that is made up of a breeding pair and its offspring (Olson 1938, Mech & Boitani 2003). However, wolves can also survive as lone individuals (Mech & Boitani 2003). In favourable circumstances, a breeding pair produces pups every year (Frits & Mech 1981, Mech & Hertel 1983, Peterson *et al.* 1984, Mech & Boitani 2003). Most young individuals remain in their natal pack until about 10–54 months old, but usually all offspring eventually disperse (Gese & Mech 1991, Mech & Boitani 2003).

Almost throughout the entire global range of wolves, ungulates constitute the main natural prey (Okarma 1995, Olsson *et al.* 1997). In northern boreal forests the main prey is usually the moose (*Alces alces*) (Pulliainen 1965, Olsson *et al.* 1997, Gade-Jørgensen & Stagegaard 2000, Kojola *et al.* 2004), but in areas where the wild forest reindeer (*Rangifer tarandus*) co-exists with the moose, it can form an important part of the wolf diet (Kojola *et al.* 2004).

Wolf populations were exterminated from most of their former European range during the 19th and 20th centuries. However, during the last twenty years, wolves have again expanded their range in many countries (Boitani 1995, 2000). The rapid growth of wolf populations together with their adaptability and dispersal ability has allowed them to increasingly colonize developed areas (Mech 1995, Mladenoff & Haight 1997, Boitani 2000). Consequently, wolves are currently living in multiple-use landscapes surrounding human settlements in many parts of Europe (Linnell *et al.* 2001). Within these landscapes there is a high risk of wolves preying on domestic animals (Linnell *et al.* 1999). The conflict with human economies has been the main reason for wolf control, and it is still one of the main causes of wolf mortality (Boitani 2000). Because human tolerance of the wolf largely depends on the behaviour of wolves themselves, landscape features – especially those relating to the impact of humans – can be used to predict suitable wolf habitats (Mladenoff *et al*. 1995, Massolo & Meriggi 1998, Corsi *et al.* 1999). Wolves prefer areas with high forest cover, few roads, and a low human density (Mech *et al.* 1988). Such areas may be the least accessible to humans, and the lack of human presence remains the most important variable predicting wolf viability (Mech 1995).

The wolf population in Finland experienced a major decline during the late 19th century. The distribution shrank to include only the most remote regions in eastern and northern Finland (Pulliainen 1965). However, the number of wolves has recently been increasing in Finland and they have also expanded their range. This in turn has raised a certain degree of concern among people living in the area, and wolves are often perceived as a safety threat to both people and domestic animals (Kojola *et al.* unpubl. data).

The decline of the Finnish wolf population began in the middle of the 19^{th} century when the last wolf was killed on the Åland Archipelago. In mainland Finland, wolves still occurred in all parts in the 1880s, but the decline was rapid and by 1900 the breeding area only included the eastern and northern parts of Finland (Pulliainen 1965). About 400 wolves were killed annually during 20 years around the 1850s and 1960s (Ermala 2003, Kojola 2005), and it is possible that during this period the wolf population totalled more than 1000 individuals (Kojola 2005, Aspi *et al.* 2006).

During most of the 20^{th} century, permanent wolf occupancy was restricted to northern and eastern parts of Finland (Pulliainen 1979, Pulliainen & Rautiainen 1999, Boitani 2003). Fluctuations in wolf numbers in Finland were connected to fluctuations in the wolf population of northwest Russia, especially Russian Karelia, until the late 1990s (Pulliainen 1965, 1979, 1980, 1985, Pulliainen & Rautiainen 2003), and there were some larger than average wolf expansions over the Russian border to Finland during this period (Pulliainen 1985). Reproductions were occasional until the late 1990s, when the wolf population in Finland began to increase as a result of conservation strategies and hunting control (Pulliainen 1965, 1980, Kojola & Määttä 2004, Kojola *et al.* 2006, 2009).

In recent years the wolf population has significantly increased. In particular, the birth rate in Finland has developed favourably and the number of litters has increased from just four in 1996 to 20 in 2005 (Kojola & Määttä 2004, Kojola *et al.* 2006b). It seems that at present the wolf population in Finland is no longer following the fluctuations in wolf numbers in Russian Karelia (Kojola & Määttä 2004).

In much of the current range of the species, humans are still a major cause of wolf mortality (Fritts *et al*. 2003). Although most of the large predator species have some degree of legal protection, legal and illegal persecution continues and contact with human activity still remains a major cause of carnivore mortality, even in protected areas (Woodroffe & Ginsberg 1998, Woodroffe 2003).

1.3 Spatial ecology, habitat use and resource selection

The space use of animals is usually hierarchical and different orders of resource selection can be identified (Johnson 1980). First-order selection is the selection of the physical or geographical range of a species, while second-order selection determines the home range of an individual or social group within that range and third-order selection pertains to the usage made of various habitat components within the home range (Johnson 1980). Fourth-order selection can be identified as the selection of particular elements such as food items within the habitats (general features) (Manly *et al*. 2002). Selection criteria may differ between each order (level) of selection (Johnson 1980, Orians & Wittenberger 1991, Manly *et al.* 2002). The distribution of wildlife populations is determined by the dispersion of habitat elements across space and through time (Morrison *et al.* 2006). Even though animals are able to disperse into unoccupied areas, some individuals select against certain habitats, and animals do not necessarily occupy all their potential range (Krebs 1994). In theory, organisms should prefer environments in which their survival and reproductive success is good (Levins 1974). As an almost universal activity among animals, habitat selection affects nearly all of the subsequent choices of an individual (Orians & Wittenberger 1991). A habitat is a necessary requirement for the survival of the population and species, and is therefore a significant concept in the management and conservation of both populations and species (Otis 1998, Hanski 2005).

As mentioned above, wolves are not as dependent on wilderness areas as they were once assumed to be (Mech 1995), and if they are not killed and have adequate ungulate prey, wolves can occupy a matrix of managed, human-dominated, semi-wild areas (Fuller 1995, Mech 1995, Mladenoff & Haight 1997, Mladenoff *et al.* 1998, Mladenoff *et al.* 1999). For example, in central Italy, the home range of a wolf pack includes several human activity centres (villages, roads, agricultural areas) on the outer parts of the home range. Wolf presence in these human activity centres is minimal and nocturnal (Ciucci *et al.* 1997).

1.4 Outline of this dissertation

This dissertation is based on four research articles that addressed different aspects of the use of space and favourable habitats of wolves in Finland (Fig. 1). The general aim of the dissertation is to provide knowledge applicable for wolf management and conservation purposes, and especially to examine more closely the effects of human modified landscapes on the wolf population expansion in Finland (Table 1). This study addressed four main study questions:

1. How do wolves react to human constructions in an area where the human population density even today remains rather low?
2. Does a human modified landscape affect wolf denning? Where do wolves choose to den?
3. The effects of wolves on reindeer farming in northern Finland can be significant. How about the southern parts of Finland? What threats does the expanding wolf population pose to sheep farming, and where do attacks occur?
4. Kojola *et al.* (2006) found that in Finland wolves disperse randomly in all directions from their natal pack home ranges. Why then do more wolves from the Finnish population not enter the Swedish population? What are the obstacles to wolf dispersion from Finland to Sweden, and are these obstacles natural or human induced?

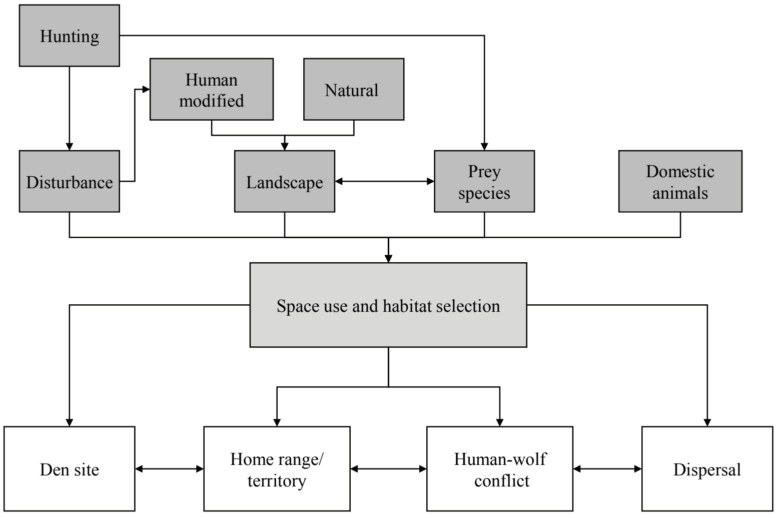

Fig. 1. Factors affecting the space use and habitat selection of wolves in Finland and general study topics of this dissertation.

Table 1. Summary of the study topics and the main background predictions for each study.

Study	Topic	Main predictions based on previous studies
I	Avoidance of human constructions	Although wolves are habitat generalists, some landscape features, especially those relating to human impacts, can be used to predict suitable wolf habitats.
II	Den site selection	Wolves in the present populations may still exhibit a tendency to avoid locating dens near human-influenced areas due to their behavioural adaptation to human persecution
III	Sheep farm depredation risk	The risk of wolf depredation often varies between farms. Landscape features together with characteristics of sheep farms at the farm level predispose certain farms to wolf attacks.
IV	Dispersal to the Scandinavian wolf population	Dispersal distance, behaviour and barriers such as the seas and regions of high exploitation inhibit dispersal from the source population to a smaller population.

2 Material and Methods

2.1 Study area

Studies (I), (II) and (IV) were carried out in eastern Finland in an area comprised of parts of the provinces of Kainuu, Pohjois-Karjala and Pohjois-Savo (Fig. 2). This area belongs to the mildly continental part of the mid-boreal coniferous forest zone (Ahti *et al.* 1968) The topography is flat and elevations (a.s.l.) range from 160 to 307 m. Forests cover about 80% of the land area, but lakes and mires are also common. Commercial forests make up about 93% of the total forested land area, and about half of the mires have been drained for forestry purposes. Young successional mixed forests are common as a result of extensive logging. The dominant tree species in the area are the Scots pine (*Pinus sylvestris*) and the Norway spruce (*Picea abies*). Permanent snow usually appears in mid-November and melts in early May. The snow depth usually exceeds 80 cm and peaks in March.

Eastern Finland is sparsely populated by humans; the mean density of humans in the study area is five people km^{-2}. Population density is low even for Finland, where the mean density of humans is 17 people km^{-2}. Most people in eastern Finland live in densely built-up areas near town centres, but many of them maintain a holiday residence in the countryside.

For study (III), the study area covered southern and central Finland, excluding the Åland archipelago. Most of the area is part of the boreal coniferous zone, and only the southernmost areas of Finland are intermediate between the boreal forests and the temperate forests of Central Europe. Approximately 65% of forests in central and southern Finland are dominated by pine, 23% by spruce and 9% by birch (*Betula* spp.).

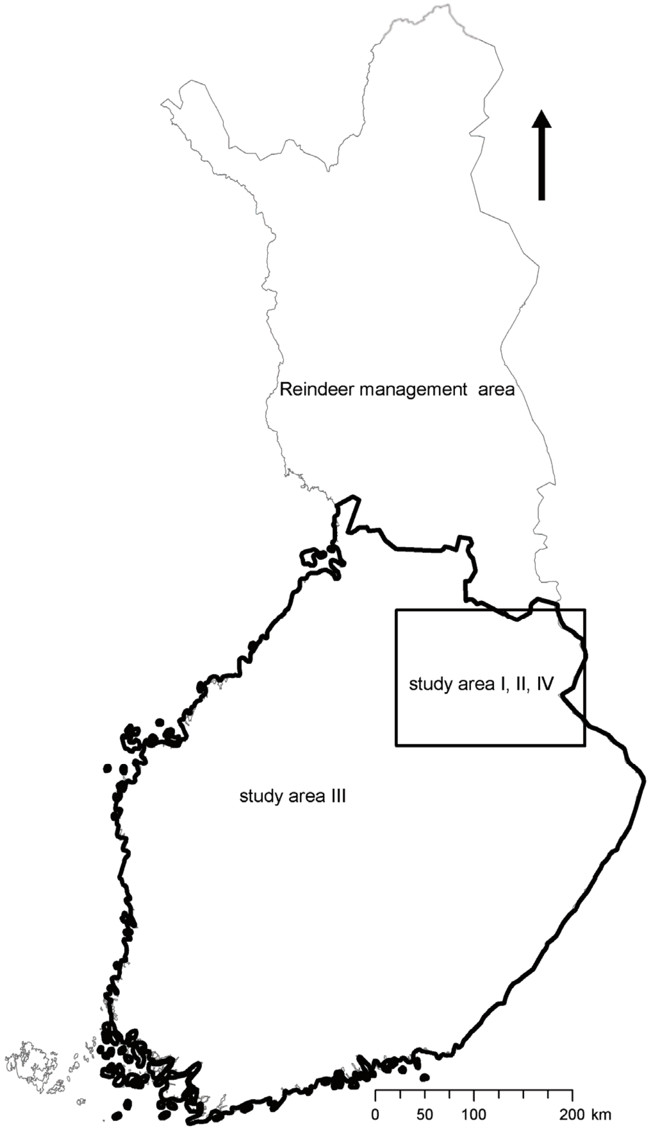

Fig. 2. Study area.

2.2 Collection of the wolf data

The Finnish Game and Fisheries Research Institute fitted 82 wolves with collars between 1998 and 2009. The wolves were captured in February-April using snowmobiles when the snow was soft and over 80 cm deep. Snowmobiles were driven alongside the wolves, which were looped using a neck-hold noose attached to a pole (Kojola *et al.* 2006a, 2009). The drugs and protocol used in immobilization are described in Jalanka and Roeken 1990 and Kojola *et al*. 2006. The capture, handling and anesthetizing of wolves met the permits issued by the Animal Care and Use Committee at the University of Oulu and by the provincial government in Oulu (OYEKT-6-99, OLH-01951/Ym-23).

Wolves were equipped with very high frequency (VHF) radiocollars (Telonics, Mesa, AZ) and transmitters, including Global Positioning System (GPS) and mobile phone component global system for mobile (GSM), i.e. GPS-GSM collars (Televilt, Lindesberg, Sweden and Vectronic Aerospace, Berlin, Germany). VHF-collared animals were radiotracked 2–5 times weekly around the year by vehicle and on foot using receivers and handheld or vehicle-mounted antennae, and the GPS-GSM transmitters were programmed to provide 6 radiolocations daily.

In study (III), the density of wolves was calculated as an index (observations/km^2) that was based on about 30 000 annual observations (sightings, track observations, scats and killings) recorded with geographic coordinates by a national network of circa 1600 experts on large carnivores.

2.3 Research methods

2.3.1 Wolf avoidance of human constructions (I)

The effect of human constructions (roads and buildings) on wolf habitat selection was studied by analysing the habitat selection of 12 breeding wolves from six packs at two scales: territory vs. total study area, and proportional habitat use based on radiolocations vs. home range composition. These correspond to the second and third orders of habitat selection (Johnson 1980). Second-order selection was estimated by comparing the proportion of buffer zones within the home ranges to the proportion of buffer zones available across the study area. Home ranges were calculated as minimum convex polygons (MCP) (Mohr 1947) for each wolf pack for the time period. Third-order selection was estimated by comparing the proportion of buffer zones in location data to the proportion of buffer zones available across the home ranges.

Proximity functions of operations are among the most common spatial analysis tools, and buffering is one of the most commonly used proximity functions. A buffer is a region that is less than or equal to a specified distance from one or more features. They may be determined for point, line or area features, and for raster or vector data. Buffers typically identify areas that are outside a given threshold distance vs. those inside the threshold distance (Bolstad 2003). In this study, a series of distance-from-construction buffers were generated for each type of human construction that created zones around features at a given distance: A (0–100 m), B (100–250 m), C (250–500 m), D (500–1000 m) and E (> 1000 m).

The selection by wolves of different construction buffers was analysed by using log-ratio analysis of compositions, i.e. compositional analysis. Compositional analysis is a MANOVA-based technique used to analyse the statistical significance of differences and the rank order of differences between two sets of data in which variables are presented as proportions (Aebischer *et al.* 1993). As the location data on wolves in a pack were not independent, each breeding pair was treated in the analysis as a statistical unit (Aebischer *et al.* 1993). This was justifiable, as young members usually constitute only a temporary proportion of packs, and the only long-term members are the breeding pair (Mech 1999).

Digital geographic data on human constructions were bought from the National Land Survey of Finland (NLS). The data consisted of vector data of building polygons and road lines. Roads were separated into three classes according to their size and amount of traffic. The first class consisted of primary roads: paved or improved gravel, over five metres wide with two or more lanes. The second class consisted of secondary roads: improved gravel or paved roads that are 3–5 metres wide with one lane. The third class comprised gravel forestry access roads that are less than three metres wide. Buildings were separated into two classes: houses inhabited all year round and holiday residences that are mostly used during the summer.

The selection by wolves of different construction buffers was analysed by using log-ratio analysis of compositions, i.e. compositional analysis (Aebischer *et al.* 1993).

2.3.2 Den site selection (II)

Den site selection was assessed by comparing the land use types of 26 den sites with 26 random points generated by GIS within the wolf territories. Minimum convex polygon (MCP) home ranges were generated to determine the maximum probable home range using all the available location information from each breeding female from one year prior to denning to the year after.

During the study period (1998–2004), 26 dens belonging to 12 packs were found in the study area where at least one individual had been collared as part of a long-term ecological study of wolves. A site was considered to be a den if pups had been born there, regardless of whether the site had been dug or was a surface bed. Only natal dens where pups had been born were included in the analysis. All packs also had rendezvous sites to which the pups were moved from the natal den during the summer.

Dens belonging to the packs with collared wolves were located on the basis of telemetry, and areas of heavy use during May and June were identified as possible denning sites, which we checked after the wolves had permanently moved to another location by walking into the area. Dens were identified on the basis of markings left by wolves, such as tracks, trampled vegetation, scats and hairs. For 8 out of 12 breeding females (67%), the den site could be assessed for more than one season.

Analyses and models included nine explanatory variables (eight land-use types and the roughness of the topography). Landscape data used in the study were extracted from the national Corine database, which has a resolution of 25 m x 25 m in Finland (Luoto *et al.* 2006). For the study, 35 original Corine classes in the study area were reclassified into eight land-use classes: (1) *Yngsuc* comprised forests in young successional stages (plantations and clear cuts), (2) *Conmin* consisted of coniferous forests on mineral soil, (3) *Conpeat* consisted of coniferous forests on peat soil, (4) *Mixmin* and (5) *Mixpeat* included mixed forests of conifers and deciduous trees on mineral and peat soil, respectively, (6) *Hummod* comprised human modified areas (cities, villages, roads and agricultural fields), (7) *Mire* included all the open mires and (8) *Water* consisted of lakes and rivers. The relative proportions of the eight land-use classes were determined around each den and a random reference site within a radius of 50, 100, 200, 400, 800, 1600, 3200 m, with the den or random point as the central point, to determine the scale at which the land-use classes in den site selection were most important.

The effect of different land use types at different distances from the den site on wolf den site selection was examined by using generalised linear mixed effect modelling (lmer). This statistical modelling approach has the advantage of allowing the incorporation of random terms that control for spatial non-independence in the data, arising from grouped observations (Pinheiro and Bates 2000). In this analysis, pack was fitted as a conditioning random term before adding any other variables to the mixed effect model to overcome problems related to the lack of independence in the data (Gillies *et al.* 2006). Models were estimated using the lme4 package (Bates 2007a & b) in the R statistical environment (Crawley 2007).

2.3.3 Wolf-human conflict (III)

To build a predictive model of wolf depredations on sheep farms, 12 explanatory variables were examined for farms with and without depredation at two different scales. These 12 explanatory variables were: four sheep-farm-based variables, the density of wolves, density of moose and six land-cover variables. The four sheep-farm-based variables were the number of sheep, size of the pastures, number of goats and distance from the Russian border. The density of wolves was an index (observations/km^2) based on about 3000 annual observations recorded with geographic coordinates by a local network of experts on large carnivores, and the density of moose an index based on the estimates of hunting clubs for the number of moose left in their hunting districts after the autumn hunting season. Landscape data used in the study were extracted from the national Corine database. Corine classes were reclassified into six classes of land cover: (1) built-up areas mainly comprised areas with fabricated or human-made surface materials (e.g. buildings, roads and green urban areas); (2) agricultural land consisted of cereal and fodder fields and pastures; (3) plantations consisted of clear cuts and plantations with a tree crown cover of less than 30%; (4) forest included all the forest with a tree crown cover of over 30%; (5) wetland comprised mires and other peat bogs; and (6) water included all water bodies (lakes and rivers).

First, all 3016 sheep farms (30 of which were affected) in whole of the study area were used to determine which individual variables were related to farms experiencing depredation events by conducting univariate tests. Since most of these variables were not normally distributed, non-parametric Mann-Whitney U-tests were used to compare farms with and without depredation. The probability of wolf attack on sheep farms was analysed by using general additive models

(GAM) (Venables & Ribley 2002), which were constructed using a backward stepwise procedure to select the relevant explanatory variables and the level of complexity of the response shapes for each variable. Since the response variable represented binary data (the presence or absence of a depredation event), a quasi-binomial distribution of error via a logistic link function was applied (Venables & Ripley 2002). GAMs were fitted using GRASP (generalized regression analysis and spatial prediction) in S-PLUS (Lehmann *et al.* 2002).

Affected (n = 30) and randomly selected nearby unaffected farms (n = 30) were also matched under the assumption that wolves had equal access to both farm groups. These 60 farms were used to determine which land cover classes and farm-based characteristics made some farms in the same area more vulnerable to wolf attack, and by using the matched pair design the aim was to avoid potentially confounding differences in wolf existence and the number of moose. Buffers of 0.5, 1, 2, 4, 8 and 16 km in radius were constructed around the sheep farms to determine the scale at which the land-use classes were most important in predicting wolf depredation. GAMs were then fitted for each buffer radius using land-use classes as predictive variables, and for later models only the most significant buffer radius was used (i.e. the radius with the highest modelling performance).

Because GAMs are sensitive to the selection procedures utilised (Araújo & Luoto 2007), two alternative approaches were used to select the best approximating models to estimate depredation risk: AIC (Akaike's Information Criterion; Akaike 1974) and BIC (Bayesian Information Criterion; Schwartz 1979). Information criteria can be used to determine weights for each model by including a penalty for adding predictor variables to the model. These weights are considered as evidence in favour of each model being the closest to reality when other models are considered. (Rushton *et al.* 2004). The preferred model is the one with the lowest AIC or BIC value. In BIC, the penalty for additional parameters is stronger than that of the AIC (Burnham & Anderson 2002). In addition, receiver operating characteristic plots (ROC) were used to measure the discriminating abilities of the model. This was done by plotting sensitivity (the probability a model will correctly classify positive cases; true positives) and 1 - specificity (the probability a model will incorrectly classify negative cases; false positives) over a range of probability thresholds from 0 to 1. The outcome of this plot, the area under ROC curve (AUC), estimated the ability of the model to correctly distinguish between the two cases. AUC values of 0.5 to 0.7 are usually taken to indicate low accuracy, values of 0.7 to 0.9 to indicate useful applications and values of > 0.9 to indicate high accuracy (Swets 1988).

Based on the results of the analyses on the sheep farms, four predictive maps were generated on which the AIC and BIC indicate how well the models predict the wolf depredation risk for each farm. To make individual farms anonymous, the results were averaged by using inverse distance weighted interpolation to raster using the Geostatistical Analyst extension in the ArcGIS program.

2.3.4 Dispersal (IV)

To assess the potential of wolves to travel from Finnish to Scandinavian wolf populations, the dispersal distances and moving patterns of 26 wolves that dispersed from their home territory during 2000–2006 were analysed in relation to two different dispersal routes. These were a direct route over the ice of the Bothnian Bay and a land route via the reindeer management area in the north (Linnell *et al.* 2005). Dispersal distances were assessed as the straight-line distance between the middle of the capture territory and the middle of the new territory (Merrill & Mech 2000, Linnell *et al.* 2005, Kojola *et al.* 2006a). Based on performance and tooth wear (Ballard *et al.* 1995, Kojola *et al.* 2006a), all dispersing wolves were assumed to be 10 to 24 months old and to have been born in the territory where they were captured. A wolf was assessed to have established a new territory if it spent at least eight months in a new home range (Kojola *et al.* 2006). If a wolf died or a transmitter stopped working before the new territory was established, the minimum distance was calculated as the distance between the middle of the home territory and the last radiolocation. For those wolves that were fitted with a GPS transmitter, the length of the dispersal route was determined as a sum of the distances between consecutive radiolocations and the duration of the dispersal was determined as the number of days between the day of departure and the day of arrival in the area where the wolf settled down. A wolf was considered to be dispersed from the natal territory when it moved consistently outside the territory boundaries (Boyd & Pletscher 1999). The length of the dispersal route and the duration of the dispersal were only assessed for the GPS-collared wolves, because the VHF-collared wolves could not be air-tracked comprehensively to assess the day of arrival in the new home range.

To evaluate the potential of crossing the Bothnian Bay, the timing of dispersal was related to the melting and thawing of the sea ice. Data on the duration of the ice cover were provided by the Finnish Institute of Marine Research.

3 Results and Discussion

3.1 Human construction avoidance (I)

The results of this study provided evidence that wolves avoided human settlements and roads in the study area. There are several potential explanations as to why wolves did not use residential areas. Livestock, especially sheep farms, could act as an attraction for wolves, but there were only a few in the study area. At the same time, the abundance of the primary prey (moose) in the area was moderate. The mean numerical ratio was approximately 50 moose per one wolf within the wolf pack territories, calculated from the observed moose density (0.35 moose km^{-2}; V. Ruusila, unpubl. data based on helicopter surveys in March 2003 and 2004), the mean maximum pack size in midwinter (7.0, range from 3 to 12; I. Kojola *et al.*, unpubl.) and the mean home range size. This is fairly close to the similarly high prey density area in Quebec, Canada (calculated from Messier 1985). The moderate number of pups (on average 4 -5 pups born per pack) produced every year also indicated that the amount of nutrition acquired by wolf packs was adequate.

It seems that in the Finnish wolf population there are individuals that actively seek domestic dogs (*Canis familiaris*), and during the study there were 21 wolf attacks on dogs within wolf territories. Most confirmed attacks (76%) were in one territory, and 70% of attacks made by this pack took place in house yards (Kojola *et al.* 2004). Overall, 44% of wolf attacks on dogs occur in house yards (Kojola & Kuittinen 2002). However, the radio-tracking data suggest that wolves in the area still avoided human residential areas most of the time and did not spend time near human settlements.

Road density has frequently been used as a landscape feature to predict suitable wolf habitats (Mech *et al.* 1988, Mech 1989, Mladenoff *et al.* 1995, Corsi *et al.* 1999, Wydeven *et al.* 2001). Road systems are primarily transport corridors imposed on the environment by humans to allow the movement of people and the goods required by human society (Bennett 1991). The combined density of primary and secondary roads in study area, at 0.4 km/km^2, was substantially lower than the threshold value in North American forests, which was assessed at 0.6 km/km^2 (Wydeven *et al.* 2001). Although road density did not have a critical effect on the viability of the wolf population, wolves in the study area did avoid larger roads. Roads are likely to be avoided for two potential reasons: the risk of traffic accidents and being shot by humans using the road. In areas where public access is restricted, road density does not act as a good indicator of wolf presence (Merrill 2000), suggesting that wolves may avoid the threat induced by humans rather than roads (Musiani & Paquet 2004). Roads have, for example, been found to increase mortality among grizzly bears (*Ursus arctos*) by providing easier access to the bears for hunters and poachers (McLellan & Shackleton 1988). Some studies indicate that wolves may use roads and other linear corridors as easy travel routes in areas with limited human activity (Thurber *et al.* 1994). Thus, roads and other linear corridors may allow wolves to travel more quickly through their environment (James & Stuart-Smith 2000).

On average, 9.5% of the estimated wolf population was legally harvested in Finland during 1994–2004 (I. Kojola, unpubl.). In Finland, fladders are regularly used in wolf hunting. Fladders consist of a tether that is several kilometres long and has flags stitched to it at regular distances. Hunted wolves are driven into a loop formed out of the fladders, where gunmen are waiting. Since the fladders retain a human scent for several days, wolves tend to stay within the encircled area. Fladders are usually placed near small forest roads (M. Suominen, pers. comm.). Moving on roads, especially in the daytime, increases the risk of being shot illegally, and this may also shape the behaviour of wolves.

Traffic noise is apparently more important than visual disturbance in the avoidance of roads by various animals (Forman & Alexander 1998). This could explain why the largest, most heavily used roads in the study area had the largest impact on wolf avoidance. On the other hand, it is possible that the avoidance is caused by the absence of prey from areas near roads. Various large mammals tend to have lower population densities within 100–200 m of roads, and these road-effect zones generally exhibit lower breeding densities and reduced numbers of species compared to control sites (Forman & Alexander 1998). No studies have been carried out on the avoidance of roads by moose in Finland. Rolley and Keith (1980) found that moose in North America tended to avoid agricultural clearings. In their study, the avoidance of disturbances such as roads and settlements was dependent on the time of the year and the mean distance from dwellings, roads, and clearings, and decreased as moose moved to winter ranges (Rolley & Keith 1980). On the other hand, in Sweden, damage to pine trees in winter caused by moose browsing is heaviest within 3 km of roads. Roads may act as a partial barrier for moose and make their migration more difficult, which increases their density near roads. Moose may also be attracted by road salt (Ball & Dahlberg 2002).

Wolf avoidance patterns in relation to human constructions may be influenced by the impact of prey behaviour (Mladenoff & Sickley 1998), but little can be inferred before more information is collected on the behaviour of prey in relation to human constructions.

3.2 Den site selection (II)

The results of this study suggest that the most important factor in wolf den site selection in Finland is human influence. Selection against the human-influenced land use class already happens at long distances, so that the effect of the class is greatest within the largest buffer areas. This avoidance of human influence has also been reported in a study conducted in the Bialowieza Forest in eastern Poland, where wolves tended to locate dens further away from forest edges, villages and intensively used roads than random sites (Theuerkauf *et al.* 2003a). Protected areas in the study area were small and therefore not likely to be selected by wolves (Theuerkauf *et al.* 2003b).

The main component of increases in wolf numbers is reproduction, and especially pup survival (Fuller 1989, Mech & Cochrane 2003). Den site selection and other events at the den site affect the reproductive success of the pack, since the greatest pup mortality occurs within the first six months (Van Ballenberghe & Mech 1975, Harrington & Mech 1982). The selection of den sites has probably historically influenced wolf pup survival, because humans have in the past actively sought out dens in order to kill the pups (Ermala 2003). Although today wolves are fully protected during their denning season in several European countries, including Finland, wolves in Russia, for instance, have never been protected and there are no restrictions on hunting methods (Bogolov *et al.* 2002). The wolf is still a controversial species and persecution, including the extermination of active dens, may still occur, even in areas with legal protection. This is especially so in Europe, where wolves usually live in multiple-use landscapes surrounding human settlements (Salvatori & Linnell 2005). Wolves in the present populations may still exhibit a tendency to avoid locating dens near human influenced areas due to their behavioural adaptation to human persecution (Theuerkauf *et al*. 2003a).

There have been several studies focusing on wolf reproduction and denning (e.g. Ballard & Dau 1983, Mech & Merrill 1998, Thiel *et al.* 1998, Ciucci & Mech 1992, Heard & Williams 1992, Norris *et al.* 2002, Theuerkauf *et al.* 2003a, Trapp 2004). However, analyses concentrating particularly on wolf den site selection in boreal environments have hitherto received only limited attention. Many wolf populations have established in forested regions similar to North European boreal forests, where intensive forestry practices, hunting and development take place. It is therefore important to assess landscape-level habitat use by wolves in multiple-use forest ecosystems (Mladenoff *et al.* 1995, Norris *et al.* 2002).

A direct relationship exists between wolf productivity and nutritional status (Boertje & Stephenson 1992). In Finland, the average number of pups per pack surviving to the next winter during 1999 to 2004 was 4.3 pups (3.4, S.D = 0.8 for the first litter of the breeding female (11 packs) and 5.25 S.D = 1.49 for the second litter (8 packs)). The mean number of pups in packs in the winter (4.3) was relatively high (see Fuller *et al.*, (2003) for a review). Thus, it seems that the abundance of prey in the study area is high enough to support wolf pup productivity. Den site selection by wolves is probably to some extent dependent on the habitat selection of prey animals. In Finland, moose habitat selection is directed by younger successional stages of forests, especially in pine-dominated habitats, and when the proportion of these younger successional stages is high enough at the home range level, the mixture of other habitat types becomes important in habitat selection within the home range (Nikula *et al.* 2004). The results of this study demonstrate a tendency of wolves towards selecting den sites in areas where younger successional stages, such as clear cuts and plantations, dominate the landscape. When forests in later successional stages are considered, wolf den site selection seems not to be dependent on the availability of certain forest types. In this study, wolves did not prefer pine forests, as many previous studies have proposed (Ballard & Dau 1983, Norris *et al.* 2002), even though this forest type has well-drained sandy soil that is easy to dig into and less undergrowth. Wolves in this study seemed not to have any preferences for the land soil type, and mineral and peat lands were equally used. Instead, wolves preferred den sites with good cover for hiding, and used surface beds under spruces, boulders and fallen trees for denning, which are easily found in all types of forests. Most den sites found (21 out of 26) were surface beds. Hiding cover is greatest in young successional forests, which are common in the study area and in Finland in general. For example, in the Kainuu area, 64% of the forest land is comprised of advanced seedling stands or young thinning stands. Furthermore, 43.7% of the forests contain a large amount of undergrowth (Finnish Statistical Yearbook of Forestry 2004).

Wolves in this study selected for major water bodies only at 800 metres radius around the dens. Norris *et al.* (2002) found in Ontario, Alaska, that wolves avoided major water bodies in areas immediately surrounding the dens. In the present study area there was no significant relationship between wolf den site selection and the existence of lakes and rivers close to dens. Dens are often found near water, which is probably due to the increased need for hydration by lactating females (Mech 1970, Norris *et al.* 2002, Trapp 2004). Within a 2.01 km^2 area around dens (800 metres radius), there are likely to be several small water bodies, such as streams flowing to larger water bodies, offering easy access to a water source for females.

In this study, 25 of the 26 (96.2%) dens that were found during the study period were new denning sites and only one (3.8%) was used over two consecutive years. This is a small number compared to previous studies. In Minnesota, 85.7% of dens were reused (Ciucci & Mech 1992) and in Alaska at least 26% of the dens had been used for three seasons and 26% at least twice (Ballard & Dau 1983). This difference may be due to past differences in the level of risk of the litter being exterminated by humans in North America and Europe. Killing of pups from dens was common in Finland during the 19th century (Ermala 2003). Excavated dens were not even used twice, although making this type of den demands much more effort from wolves than surface beds. This may be because of the knowledge that a wolf den existed in the area increased the number of people visiting the site. Most dens had not been excavated at all and consisted of surface beds under the branches of large Norway spruces. This type of den requires little effort from the pack and can easily be replaced if it is disturbed.

In conclusion, in forested regions where intensive forestry practices, hunting and development take place, the distribution of human disturbance together with the prey habitat are the main factors determining the den site selection of wolves. The forest type and other habitat characteristics have a secondary role.

3.3 Sheep farm depredation (III)

Wolf depredation on sheep farms in Finland is still a very small problem when compared to most other countries in Europe with wolves. The overall loss of sheep, goats and cattle to carnivores in regions such as Finland, where they are kept in herds in fenced pastures, is generally low (Kaczensky 1996). The total proportion of sheep farms in Finland that suffered verified wolf depredation was only 1% during a six-year study period. Nevertheless, for those farmers losing their livestock, the emotional toll of wolf depredation is large and the threat of depredation creates stress for livestock producers (Fritts *et al.* 2003). The expanding wolf population may increase the number of depredation events. The number of compensation claims for wolf depredation increased from 2 to 17 between 2000 and 2003; and at the same time, the reported number of sheep killed by wolves increased from 23 to 135.

Individually assessing factors that may predispose livestock to predation by large carnivores is difficult because of the interdependence between livestock husbandry, environmental factors and the behavioural ecology of predators (Stahl *et al.* 2002). Nevertheless, some farmers seem to have recurring predation problems, whereas other farms nearby do not experience losses or do so only occasionally. In Finland, there were 46 reported cases of wolf attacks on 34 sheep farms between 1998 and 2004. Most affected farms (82%) were depredated only once during this period, five of the farms (15%) had two depredation incidents in two consecutive years and one farm (3%) was attacked in three different years. A recent study suggests that depredated farms have a higher risk for a repeat predation event within 12 months compared to other farms in the same area (Karlsson and Johansson 2010). Detailed analyses of the livestock losses have usually revealed pronounced differences between livestock farms (Nass *et al.* 1984, Cossa *et al.* 1996, Stahl *et al.* 2002). The risk of a depredation event also varies among sheep farms in Finland. According to this study, some environmental and farm-level factors are associated with wolf depredation.

Wolf distribution in Finland is not even and the population is concentrated in the eastern part of the country, near the Russian border. Suitable habitat with a high prey abundance also exists further west, but the human pressure is greater there. This has slowed the expansion of wolves to the west and south of Finland (Aspi *et al.* 2006). However, the wolf population in Finland has increased and expanded to the west: the wolf distribution increased from a little less than 20 000 km^2 in 1996 to over 100 000 km^2 in 2004 (Kojola *et al.* 2005). According to the spatial model, the risk of wolf depredation was highest for farms in the areas where wolves were most abundant. Probably for this same reason, the risk of wolf attack diminished with the distance of the farm from the Russian border.

Factors related to ranch size differentiate ranches with depredations from those without (Mech *et al.* 2000, Treves *et al.* 2004). Bradley and Pletscher (2005) observed that pastures that were larger, had more cattle and were located far from residences were most likely to experience depredation. These factors are often correlated with each other (Mech *et al.* 2000, Bradley & Pletcher 2005). There are three different kinds of grazing systems. In the first system, the livestock are entirely free-ranging and unattended within a natural carnivore habitat, while in the second the livestock are kept in open fields, constantly herded or confined at night (Linnell *et al.* 1999, 1996). In the third system falling between the two previous systems, sheep are fenced in, unevenly distributed but not herded or protected from carnivore predation (Stahl *et al.* 2002). In Finland, the third system is the prevailing one. Sheep are usually not constantly herded but their condition has to be checked daily. Flocks are usually kept in fenced fields where there is cover from the weather conditions, either with tree cover or built shelters. Pastures are mainly fenced by board or wire-netting fences. Some farms have some level of protection against wolf attacks, such as wolf-proof electric fences, but these are not common. Some farmers also keep their flocks in a sheep house during the night.

At the farm level, the most important factor defining the wolf depredation risk in Finland is the size of the sheep flock. Large herds of livestock may serve as greater attraction to wolves, or have a higher probability that the herd contains highly vulnerable individuals (Bradley & Pletcher 2005). In Finland, most sheep farms are relatively small: of all the farms in our study, 91.3% had 100 or less and only 8 farms had more than 500 sheep. The risk of a wolf attack on the farm is greater on those farms with a larger flock. Small farms may not have enough animals to attract attention from wolves. The smallest sheep flocks may also be situated nearer to farm buildings, especially those with very few individuals that are often considered as household pets. This is in contrast to Mech *et al.* (2000), who were sceptical that grazing cattle farther from residences increased the risk of depredation, since in the United States wolves often kill livestock near houses. Data on the exact locations of depredation events are necessary in further analysis.

The results also provided some evidence that in Finland pasture size affects the depredation risk, but the relationship between the risk of wolf attack and pasture size was not conclusive. The depredation risk appears to be highest in rather small pastures and decreases very slightly as the pasture size grows. This may be because most of the large sheep farms with large pastures are situated in south-western Finland, where wolf densities are very low, the land is mostly in agricultural use and human density is higher than in the east.

Wolf predation on livestock may be affected by human-imposed changes in the abundance of wild ungulates (Sidorovich *et al.* 2003). Meriggi *et al.* (1996) also suggested that in the areas where only one wild ungulate species is present, even at a high density, wolves may be obliged to prey upon livestock. The diet breadth of wolves increases when large prey are scarce, for instance if the presence of ungulates has for some reason decreased (Meriggi & Lovari 1996). Wolves are then forced to prey on a variety of other food resources, such as small and medium-sized mammals and livestock (Meriggi & Lovari 1996, Sidorovich *et al*. 2003). In the north western United States of America, wolves were attracted to areas with large numbers of elk (*Cervus canadensis*), and the presence of elk in the pastures was found to be the factor most strongly associated with depredation (Bradley & Pletscher 2005). Sheep pasture sizes in Finland are usually small and it is therefore probable that they do not extensively attract moose. In Finland, moose density may have an effect on wolf depredation on sheep farms, but the evidence for this in the study was not conclusive. Nevertheless, there seems to be a negative correlation between moose density and depredation events that may be explained by the fact that south of the reindeer husbandry areas of Finland, wolves mainly prey on moose, since the distribution range of wild forest reindeer (*Rangifer tarandus fennicus*) covers only some parts of eastern Finland and a small area of central Finland (Gade-Jörgensen & Stategaard 2000, Kojola *et al.* 2004). The diet breadth of wolves in Finland is therefore rather narrow.

Results from study III demonstrated that in Finland, wolf attacks on sheep farms are most likely to occur in the mosaic of forest, small wetland, clear cuts and plantations. Wolves seem to avoid areas with a large proportion of agricultural and built-up landscapes. Pasturing in areas with dense vegetative cover has been identified as a factor predisposing livestock to attacks by wolves and other carnivores in other studies (Mech *et al.* 2000, Bangs & Shivik 2001, Stahl *et al.* 2001). A negative association has also been reported between carnivore predation on livestock and the density of roads and human settlements (Robel *et al.* 1981, Stahl *et al.* 2001).

3.4 Scandinavian dispersal (IV)

The breeding wolf population in Finland has gradually expanded, and the first litters were recently born in western Finland after an absence of more than 100 years (Kojola *et al.* 2006). The geographical distance to the Scandinavian population is shorter from these new western territories than from the population's core area in eastern Finland. This potentially increases the chances of dispersal from Finland to Scandinavia. On the other hand, the population increase in western Finland may shorten the dispersal time and at the same time the dispersal distance, because at present wolves probably find a mate sooner than in the recent past, when there were only very few wolves roaming in the area (c.f. Pulliainen 1980).

Despite this recent expansion of the Finnish wolf population, it is unlikely that the Finnish population can provide numerous immigrants to the Scandinavian population (study IV). Even now that the two separate populations have become closer to each other, the direct distance between them over the ice of the Bothnian Bay is about 700 km, and the land route via the reindeer management area adds an extra 100 km to the distance. Because of the large distance, only a few of the dispersing wolves can be expected to immigrate to the Scandinavian population (Linnell *et al.* 2005), regardless of the ability of the wolf to disperse over long distances across human modified habitats, even in the absence of suitable corridors (Aspi *et al.* 2009). Both genetic (Aspi *et al.* 2006) and telemetry (Kojola *et al.* 2006) approaches have shown that the average dispersal distance of Finnish wolves is less than 100 km. About half of the studied, GPS-collared wolves (15/26) moved more than 800 km during their natal dispersal (study IV). This would be enough for a wolf moving along the shortest routes to reach the Scandinavian population, but although dispersal distance (straight line) and the distance of the dispersal route were correlated, most wolves moving towards new regions established a new territory less than 200 km (straight line) from their natal home range. Irregular patterns of movement resulted in the dispersal distances being too short for successful dispersal to the Scandinavian population.

The land route from the Finnish to the Swedish wolf population passes through a reindeer management area where the wolf controls are more liberal due to the wolf predation on reindeer (Ministry of Agriculture and Forestry 2005, Kojola *et al.* 2006). Free-ranging, semi-domesticated reindeer are an easy prey for wolves and their densities are higher than those of wild ungulates. Wolf depredation on reindeer causes considerable losses to the herds (Nordberg & Nieminen 2007). Wolf depredation of livestock usually occurs in peripheral ranges where human-caused deaths reduce the dispersal between core ranges (Musiani & Paquet 2004). Because of the depredation risk, the wolf exploitation rate in the area is so high that wolves can only occasionally reach the Scandinavian territory without being harvested. Wolves dispersing to the reindeer management area usually settle down near their home territory in the southern boundary of the reindeer management area (Kojola *et al.* 2006). Mortality of wolves is also high in northern Sweden. During 2002–2005, four wolves were found in Sweden that had come from the Finnish wolf population, but only one of them was still alive in 2005 (Seddon *et al.* 2005).

Although the Bothnian Bay can be seen as a travel route between the Finnish and Scandinavian populations, it actually acts as a barrier for wolf migration because the dispersing wolves arrive at the shore of the Bay when the ice has already melted. Wolf dispersal in Finland is unimodal, and most wolves depart from their home territories in the spring (Kojola *et al.* 2006). There is also a spring peak in several other wolf populations (Fritts & Mech 1981, Ballard *et al.* 1987, Fuller 1989), but seasonality may vary even between geographically close wolf populations (Fuller 1989, Gese & Mech 1991).

Recent findings suggest that the gene flow between separate wolf populations can be restricted, for example, due to prey and habitat specialization (Pilot *et al.* 2006) and human built obstacles (Aspi *et al.* 2009), despite the wolf appearing to be an incredible disperser (see Linnell *et al.* 2005 for review).

4 Main conclusions and management implications

My central finding in the studies forming this dissertation was that adaptability makes it possible for the wolf to live in the multiple-use, semi-wild forests of Finland, and no restrictions are imposed by the landscape on wolf population growth and expansion. In general, wolves tend to avoid the presence of human influence (I, II). They try to establish home ranges in areas where human disturbance is minimal, and inside these home ranges they tend to choose areas away from human influence. Den sites have also been selected away from human modified areas. However, as wolf numbers have recently started to increase in Finland, conflict situations between wolves and humans nowadays occur more frequently than, for instance, in the 1980s when reproducing packs were absent (III). These conflicts strongly influence peoples' attitudes towards wolves and often lead to the extermination of some of the wolves. In many cases, these measures are justified, although this is not always so. Functional bridges between populations are crucial for the long-term viability of small populations. Thus, we should find a way to increase the number of immigrants entering the Scandinavian breeding wolf population from the Finnish population (IV). For all these reasons, it is important to find solutions to ease the problems occurring between wolves and humans.

4.1 Wolf-human conflict

The increase in the Finnish wolf population during the last 15 years has been a result of the strict wolf policies brought along with Finland's membership of the EU. The attitudes of people living in wolf areas have not become any more positive than they were before the wolf expansion. In the southern and western parts of Finland there are large areas where the wolf has been absent for the past 100 years. People in the areas where wolf populations have returned after the long absence often feel that the presence of wolves forces them to change their way of life, and adaptation to this new situation may be difficult (Skogen & Krange 2003, Skogen *et al.* 2008, Bisi 2010). The long-term absence of any organism from a region can cause the "shifting baseline" syndrome (Pauly 1995), where over the generations the memory of people living in the area of a particular organism diminishes and the expectations of what are good ecological conditions become gradually lower (Pauly 1995, Miller 2005). This can be a major barrier to restoration (Manning *et al.* 2006).

Furthermore, human persecution has been a dominant factor in the extirpation of the wolf from its historical range. The objective of the persecution has usually been the need to reduce wolf predation on domestic animals (Boitani 2003). The presence of wolves can cause increasing conflicts with humans and their economic interests through competition over livestock (Treves & Karanth 2003, Berger 2006). This is a natural side-effect of wolf population expansion in Europe, where the home ranges of carnivores and livestock husbandry overlap (Linnell *et al.* 2001). Livestock depredation is one of the reasons for the deep-rooted abhorrence of carnivores throughout the world, and is one reason why a change in attitudes towards wolves has not necessarily taken place among people living near them. The potential for conflict between wolves and humans particularly exists in rural areas, where livestock production is a socially and culturally important activity. Researchers and wildlife managers are increasingly engaged in efforts to maintain populations of carnivores in coexistence with people (Mech *et al.* 2000, Musiani *et al.* 2003, Sillero-Zubiri & Laurenson 2003, Treves & Karanth 2003, Berger 2006). Often, the local need to remove problem animals has extended to the extermination of wolves over large areas (Boitani 2003).

Expectations regarding the quality of ecosystems and the way of life of people living in areas where wolves are regarded as newcomers after their long absence, as well as the fact that an increasing wolf population will cause conflicts in the form of lost livestock and pets, work against the positive attitudes towards the return of the wolf in Finland. This may lead to at least local extirpations of wolf packs and may be one reason why the wolf population actually decreased during 2009. Determining the risk factors that predispose farms to wolf depredation is one way to enable more effective defence against wolf attacks. Knowing the risks and having some way to protect one’s livelihood from wolf depredation may reduce the need for lethal control methods. The results of my research have shown the risk factors that predispose some farms to wolf depredation in Finland (II). These findings could be used to more effectively direct the preventive methods to certain farms and risk areas.

4.2 Expansion and dispersal in the future

There are both natural and human-induced obstacles to wolf dispersal from Finland to Sweden (IV). The largest of the natural obstacles is of course the Baltic Sea. Dispersing wolves move onto the shore of the sea in the spring when the ice is already melting. Global warming may shorten the season when wolves can move over the Baltic Sea by ice even further (Kojola & Heikkinen 2007). This makes the northern land route through the reindeer management area a more likely route for dispersal between Finnish and Scandinavian wolf populations. On the other hand, the mortality rate of wolves is high in the northern parts of Finland and Sweden, as due to economic interests the wolf protection measures in the Finnish reindeer management area are not as strict as in other parts of Finland. Even so, the growing wolf population in Finland may increase the probability of successful dispersal incidents as the number of travelling wolves increases (IV). Previous research has demonstrated that young dispersing wolves in Finland leave their home territory rather evenly in all directions and that dispersal to the reindeer management area is common (Kojola *et al.* 2006). The population viability of small wolf populations separated from the source population by distance, barriers or human exploitation can be promoted by limiting the harvest in the peripheral areas or by introducing wolves from the source population (Fuller 1989, Fritts & Carbyn 1995, Haight *et al.* 1998). More detailed study of wolf travel routes between Finnish and Scandinavian wolf populations could help in finding solutions to enhance the survival of the dispersing wolves.

4.3 Future research questions

Many studies carried out before this dissertation have come to the conclusion that wolves can adapt to live close to human activities as long as they are not disturbed (Boitani 2000). The survival tactics of wolves in areas where the environment has been altered by human activity may involve a process of finely-tuned adaptation to local conditions. The home-range location and configuration, habitat use, activity and movements are highly integrated to make the best functional compromise between the necessity to exploit the main food resources available and the need to avoid any direct form of disturbance by humans (Ciucci *et al.* 1997). There are aspects of space use and habitat selection by Finnish wolves that need to be studied in the future. In this dissertation I have not discussed the spatiotemporal selection of different habitats in relation to human influence. The relationship between the main prey species and wolves also remains to be explored, hopefully in the near future.

The value of wolves to ecosystems cannot be observed on an individual and economic scale of time (Sharpe *et al.* 2001). As Leopold (1949) states in his essay "Thinking like a Mountain": "Only a mountain has lived long enough to listen objectively to the howl of a wolf." Wolves and other top predators play an important role in natural ecosystems (Mladenoff *et al.* 1997), and wolves set the constraints against which other species compete (Sharpe *et al.* 2001). There is evidence that large carnivores such as wolves have a significant effect on spatial patterns and processes structuring the natural characteristics of forests by impacting large mammalian herbivores (Manning *et al.* 2009). The recovery of wolves has an impact on human society and other aspects of forest biodiversity besides wolves (Mladenoff *et al.* 1997). In Finland, only a few studies have been performed on wolf predation and in general they have mainly discussed the food composition of wolves (Kojola *et al.* 2004, Gade-Jørgensen & Stategaard 2000). In the future, there is also a need to more closely examine predator-prey interactions between the wolf and the moose, wild forest reindeer and also the semi-domesticated reindeer. As the populations of these prey species are constantly managed by humans, there is a need to evaluate the impact of wolves on the population dynamics and habitat selection of the prey species. With the increasing wolf numbers, will a different kind of "landscape of fear" (see Manning *et al.* 2009 for example) evolve in Finnish forests? The answer to this question will probably also shed more light on the use of space by wolves in Finland.

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