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To: [Kevin Doherty](#)
Subject: Fwd: Effective Population Size FYI
Date: Monday, May 15, 2017 12:25:19 PM
Attachments: [Koskela 2013 Dissertation.pdf](#)

Need to talk to you about this today.

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Here was what I sent in March. I attached Koskela's Dissertation.

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From: **Grizzle, Betty** <betty_grizzle@fws.gov>
Date: Wed, Mar 8, 2017 at 11:23 AM
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In preparation for the call on Friday re genetics, I read through Anni Koskela's 2013 dissertation (Finland), who developed estimates of effective population size for two wolverine subpopulations in that country.

Background/context: In the April 2016 court ruling, the judge specifically ruled in favor of the Plaintiffs that the Service's "unlawfully ignored best available science" regarding threats posed to wolverine by small population size and lack of genetic diversity, and remanded this to the Service (for further consideration).

I am sharing with you the following excerpts so you can see the level of effort that this type of analysis can entail, and also to contrast Koskela's methods with the methods that were used in the reference we cited in the previous proposed rule to conclude that wolverine effective population sizes are very low (Feb 4, 2013; 78 FR 7884). Highlights/notes added.

From Schwartz et al. (2009):

(from Methods section)

Effective population size

Using only those samples from the main part of the Rocky Mountains (i.e., eliminating samples from the Crazy and Belt Mountains, as Cegelski et al. 2003 suggested they form a different subpopulation), we estimated the effective population size and 95% credible limits of the estimate via summary statistics and approximate Bayesian computation methods using ONeSAMP (Tallmon et al. 2008). To determine the temporal stability of the wolverine population, we subdivided the samples into three time frames and used ONeSAMP to estimate effective population size in each frame. [I'm not sure how many samples they used for this analysis; somewhere between 142 and 210]

(from Results section)

Effective population size, calculated using ONeSAMP....was 35 (credible limits = 28–52) and was found not to change over time (N_e 1989–1994 = 33, credible limits 27–43; N_e 1995–2000 = 35, credible limits 28–57; N_e 2001–2006 = 38, credible limits 33–59). [Note credible limits of N_e exceed 50 in two of their subdivided samples. They separated these samples into 3 time periods in order to determine "temporal stability" - would be interesting to see the N_e estimate if they were kept together]

From Koskela Dissertation (2013):

To study the population genetics of wolverines in Finland, 406 scat samples, ten muscle tissue samples and two oral mucosa swabs as sources of DNA were collected during 2004–2011, mainly in northern and eastern Finland.

From Methods (pp. 32-34): The program DIYABC 1.0.4.46 (Cornuet *et al.* 2010) was used in order to infer the time at which population clusters had split from an ancestral population, as well as to infer the effective population sizes (N_e) of the assumed populations. The program makes inferences about population divergences, admixtures and changes in population size using approximate Bayesian computation. The program BOTTLENECK 1.2.02 (Cornuet & Luikart 1996) was used to detect recent reductions in effective population size. The program detects an excess of heterozygotes, as would be expected under a scenario of recent population bottlenecks, by using different tests: a sign test, a standardized differences test and a Wilcoxon rank test. The effective population size (N_e) was estimated using LD N_e 1.31 (Waples & Do 2008). The program estimates contemporary effective population sizes using a biased correction for the Hill method (Hill 1981, Waples 2006) based on linkage disequilibrium data. Three estimates of N_e are given based on the lowest allele frequency used (0.01, 0.02 and 0.05).

From Results: N_e = 14-17 in this study.

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WOLVERINE HABITAT SELECTION, DIET AND CONSERVATION GENETICS

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ACTA UNIVERSITATIS OULUENSIS
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ANNI KOSKELA

**WOLVERINE HABITAT SELECTION,
DIET AND CONSERVATION
GENETICS**

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Abstract

Rare and elusive species are difficult to study, because they are usually secretive, solitary, occur at low densities and have large home ranges. Wolverines (*Gulo gulo*) can both hunt and scavenge for food. In Fennoscandia, wolverines co-exist with either wild or semi-domesticated reindeer, which constitute their most important winter food. Approximately half of the 180–220 Finnish wolverines are found in northern Finland within the reindeer management area. However, the other half of the population is distributed in eastern and central Finland, and the ecology of wolverines especially in this area is poorly known. This research examined the habitat selection, diet and population genetics of wolverines in northern and eastern Finland. The results suggest that wolf presence is one of the most important variables influencing the habitat selection of wolverines. This finding supports the speculative idea that wolverines might benefit from being sympatric with wolves through increased scavenging opportunities. Furthermore, both the reproductive status of wolverines and the availability of different prey items were found to affect the wolverine diet. In northern Finland, semi-domesticated reindeer and mountain hare were the most frequently utilized prey species for breeding female wolverines. In eastern Finland, the most important food source for breeding females was moose carrion, whereas males and non-breeding females heavily utilized mountain hares. These results support the predictions of the optimal foraging theory, suggesting that wolverines opportunistically utilize the food source that is most energy-efficiently available. In areas with a low density of medium-sized ungulates, scavenging of wolf- and human-killed carrion plays an essential role in food acquisition by wolverines. According to the results of a population genetics investigation, two wolverine subpopulations exist in Finland: a northern and an eastern one. The overall genetic variability was found to be low, and signs of a recent population bottleneck were detected in both populations. It is likely that the wolverine populations in Finland would benefit from improved connectivity between them, but also with neighbouring populations in Scandinavia and north-eastern Russia.

Keywords: carnivore guild, diet, habitat selection, population genetics, predation, scavenging, wolf, wolverine

Koskela, Anni, Ahman habitaatinvalinta, ravinto ja populaatiogenetiikka.

Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos

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Tiivistelmä

Ahma (*Gulo gulo*) tunnetaan sekä haaskansyöjänä että keskikokoisia hirvieläimiä ja pienriistaa saalistavana petona. Fennoskandian alueella peuran kesy tai villi muoto on ahman merkittävän saalislaji. Noin puolet Suomen 180–220 ahmasta elää Pohjois-Suomessa poronhoitoalueella, ja loput Itä- ja Keski-Suomessa. Poronhoitoalueen ulkopuolella elävien ahmojen ekologiaa on tutkittu erityisen vähän. Väitöstyössäni tarkastelin ahman habitaatinvalintaa, ruokavaliota ja populaatiogenetiikkaa pääasiassa Pohjois- ja Itä-Suomen alueilla. Tutkimukseni tulokset osoittivat, että suden läheisyys oli yksi tärkeimmistä ahman habitaatinvalintaan vaikuttavista tekijöistä. Tämä havainto tukee hypoteesia, jonka mukaan ahma saattaisi hyötyä susien läheisyydestä suuremman haaskatiheyden ansiosta. Todennäköisesti ahmat elävät mielellään samoilla seuduilla susien kanssa, mutta kaihtavat läheistä kanssakäymistä välttääkseen killansisäisen saalistuksen. Tutkimusteni perusteella sekä ahman lisääntymistila että alueen saaliseläinten saatavuus vaikuttivat ahman ruokavalioon. Poro ja metsäjänis olivat lisääntyvien ahmanaraiden tärkein ravintokohde Pohjois-Suomessa. Itä-Suomessa merkittävin lisääntyvien naaraiden ravintokohde oli hirvi, jota ahmat hyödyntävät lähinnä haaskojen muodossa, mutta urokset ja ei-lisääntyvät naaraat sen sijaan saalistivat eniten metsäjänistä. Ahmat siis näyttävät hyödyntävän opportunistisesti sitä ravintokohdetta, joka kullakin alueella on energiatehokkainta saavuttaa. Susien ja ihmisten jälkeensä jättämät haaskat ovat merkittävä ravintolähde ahmoille alueilla, joilla keskikokoisten hirvieläinten tiheydet ovat alhaisia. Ahman populaatiogeneettinen tutkimus osoitti, että Suomen ahmat ovat geneettisesti jakautuneet kahteen alapopulaatioon, pohjoiseen ja itäiseen. Ahmakannan geneettinen monimuotoisuus oli pientä, ja molemmissa alapopulaatiossa oli nähtävissä merkkejä äskettäisestä pullonkaulailmiöstä. Populaatioiden välisen geenivirran määrän tulisi olla nykyistä korkeampi, jotta ahmakannan elinvoimaisuuden voisi katsoa olevan turvattu tulevaisuudessa.

Asiasanat: ahma, haaskansyönti, habitaatinvalinta, petokilta, populaatiogenetiikka, ravinto, saalistus, susi

To my parents

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A final tribute to those wolverines who "cooperated" in this project and whose tracks led me to fascinating sights, new experiences and unforgettable memories in nature: Eeki, Seita, Tahvo and many other intriguing wolverine individuals in the boreal forests of Finland.

List of original articles

- I Koskela A, Kaartinen S, Aspi J, Kojola I, Helle P & Rytkönen S (2013) Does grey wolf presence affect the habitat selection on wolverines? *Annales Zoologici Fennici* 50: 216–224.
- II Koskela A, Kojola I, Aspi J & Hyvärinen M (2013) The diet of breeding female wolverines (*Gulo gulo*) in two areas of Finland. *Acta Theriologica* 58: 199–204.
- III Koskela A, Kojola I, Aspi J & Hyvärinen M (2013) Effect of reproductive status on the diet composition of wolverines (*Gulo gulo*) in boreal forests of eastern Finland. *Annales Zoologici Fennici* 50: 100–106.
- IV Esparza-Salas R, Joensuu M, Koskela A, Ollila T & Aspi J Population genetic structure and genetic diversity of the wolverine (*Gulo gulo*) in Finland. (Manuscript)

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1 Introduction

1.1 Large carnivores in changing environment

People and large carnivores have been in conflict throughout their common history (Woodroffe 2000, Linnell *et al.* 2001, Distefano 2005). Virtually all of the large mammalian carnivores have suffered range collapses during the last two centuries, mainly due to persecution, deforestation and habitat fragmentation (Mech 1995, Treves & Karanth 2003). The grey wolf (*Canis lupus*), brown bear (*Ursus arctos*) and Eurasian lynx (*Lynx lynx*) existed almost throughout Europe, but during the last century they disappeared from their southernmost distribution area (Boitani 2000, Breitenmoser *et al.* 2000, Swenson *et al.* 2000). The wolverine (*Gulo gulo*) also once occupied areas as far south as the southern parts of Scandinavia, Estonia, Lithuania, and north-east Poland, but has been restricted to a more reduced range (Landa *et al.* 2000).

Small populations are vulnerable to extinction through random fluctuations and the loss of genetic diversity (Lande 1993, Foley 1994). Extinction rates are commonly greatest among large species (Jablonski & Raup 1995, MacFadden 2000). Therefore, small populations of large carnivores should be especially extinction-prone because of their trophic positions, which constrain them to ranging widely at low population densities. Colinvaux (1979) explained the rarity of large carnivores to be the natural result of Eltonian pyramids. Food webs can support only a few apex predators due to inefficiencies of converting energy produced by plants (Hutchinson 1959). However, human-induced mortality contributes more to the extinction of populations of large carnivores isolated in small reserves than do stochastic processes (Woodroffe & Ginsberg 1998). Nowadays, direct and indirect negative interactions with humans limit the abundance of carnivores. Linnell *et al.* (2001) found that populations of large carnivores increased after favourable legislation was introduced, despite an increase in human densities. Therefore, large carnivore persistence is probably more adequately explained by management policy than by human population density. Reduced hunting and increased ungulate populations might also explain the recolonization by large carnivores of their former ranges in North America and Europe (Massolo & Meriggi 1998, Oakleaf *et al.* 2006).

Nowadays, the grey wolf, brown bear, Eurasian lynx and wolverine are globally considered as “least concern” species according to the criteria of the

International Union for Conservation of Nature (IUCN 2012). Globally, populations remain large, but locally there are many small, isolated populations. Large carnivores still face threats such as over-exploitation through legal and illegal hunting, small population risks such as inbreeding, and the fragmentation of habitats, with resulting areas becoming too small to ensure the long-term viability of populations. However, the European Mammal Assessment determined that the European wolverine is considered as “vulnerable”; thus, the least concern listing is driven by the estimation that some large populations remain in North Asia and North America. In Finland, brown bear and Eurasian lynx populations are considered as “vulnerable”, the grey wolf as “endangered” and the wolverine as “critically endangered” (for classification and criteria, see Rassi *et al.* 2010).

1.2 The role of large predators in ecosystems

Large carnivores have the potential to place extraordinary pressures on their prey population, which in turn may lead to a variety of effects on the structure and function of ecosystems (Berger *et al.* 2001, Soulé *et al.* 2003, Estes *et al.* 2011). The structure of a community may be controlled by bottom-up or top-down forces. The bottom-up model postulates that it is mainly nutrients that limit the community by controlling plant numbers, which control herbivore numbers, in turn controlling predator numbers (Lindeman 1942). In contrast, according to the top-down model, consumers at higher trophic levels limit the abundance of lower trophic levels (Power 1992), and it is mainly predation that controls the community. Top carnivores are limiting consumers at lower trophic levels and create ripple effects throughout the food web. Such trophic cascades result from the top-down control of consumers over their prey (Paine 1980). Hairston *et al.* (1960) argued that since the world looks green, it is not overgrazed by herbivores (green world hypothesis). They concluded that carnivores and producers are controlled by density-dependent processes, but density-independent processes (e.g. predation) regulate the herbivores in the middle.

Large carnivores typically have low population densities, large habitat area requirements and a position at the top of the food chain, and are thus often chosen as target species of conservation efforts (Ray 2005). Although the role of top predators in ecosystems is still not well understood, they are increasingly recognized as keystone species. Keystone species are single species that greatly affect communities but constitute only a small proportion of the community biomass (Paine 1966, 1969, Power *et al.* 1996). Most examples of keystone

predators are from either marine or freshwater aquatic ecosystems (Ray 2005), such as the sea otters (*Enhydra lutris*; Power *et al.* 1996), large predatory snails (Castilla & Duran 1985) or freshwater bass (Power *et al.* 1996). Terrestrial predator-prey interactions may be more difficult to study because they play out over much larger areas and over a much longer period of time (Ray 2005).

The effects of terrestrial carnivores as keystone species can become evident when they are reintroduced to isolated ecosystems such as islands or national parks. The reintroduction of wolves into the Yellowstone National Park (Wyoming, USA) is a good example of top-down trophic cascades. During a period of 70 years without wolves in the park, notable changes in wildlife were the colonization of moose (*Alces alces*; Tyers 2003), elimination of beavers (*Castor canadensis*) and white-tailed deer (*Odocoileus virginianus*), reduction of aspen (*Populus tremuloides*), cottonwood (*Populus deltoides*) and willow (*Salix* sp.), and reduction of song birds (Hansen & Rotella 2002). Since their reintroduction within the park in 1995, wolves have mediated many effects throughout the food chain. The population size of moose has declined due to wolf predation, and coyote (*Canis latrans*) densities have diminished because of spatial avoidance and intraguild predation. At least 16 vertebrates have been shown to be affected in ecologically important ways by wolf predation (Ray 2005). Wolves have also facilitated the availability of carrion for at least 12 vertebrate scavengers, such as grizzly bears (*Ursus arctor horribilis*), golden eagles (*Aquila chrysaetos*) and ravens (*Corvus corax*). McLaren & Petersen (1994) also found that the density of wolves in Isle Royale National Park (Michigan, Canada) controls the abundance of moose, which in turn controls the abundance of the island's balsam fir (*Abies balsamea*).

In addition, the concept of umbrella species has been related to some large carnivores. Umbrella species are defined as species with large area requirements, which if given a sufficient protected area will bring many other species under protection (Noss 1990). An umbrella species needs large expanses of habitats and can therefore be used as a surrogate for many other biodiversity components that have similar but less extensive spatial requirements. Because of their large habitat area requirements, large carnivores are often seen as good umbrella species in conservation strategies. However, the ability of large carnivores to thrive in industrial forests means that the many species that are sensitive to modern forestry will not fall under the umbrella of areas managed for large carnivores (Linnell *et al.* 2000).

1.3 Intraguild interactions in large carnivore guilds

An ecological guild is defined as a group of species that exploit the same resources in a similar way (Root 1967). On each continent, a guild of large carnivores has evolved, including members of the bear, dog, cat, hyena and mustelid families. However, predator pressure is often dominated by one species: the tiger (*Panthera tigris*) in Asia, the grey wolf in North America, and the lion (*Panthera leo*) in Africa. In Finland, the members of large carnivore guild are brown bear, grey wolf, Eurasian lynx and wolverine. Mesopredators (e.g. red fox, *Vulpes vulpes*; pine marten, *Martes martes*; golden eagle) also affect the overall predation pressure. Interactions between carnivores are usually categorized as competition (Peterson 1995, Creel & Creel 1996, Fedriani *et al.* 1999), predation (Palomares & Caro 1999, Linnell & Strand 2000) and mutualism or commensalism (DeVault *et al.* 2003, Selva 2004).

Competition can occur and becomes important when two or more species strive for something that is not in adequate supply for both of them. The competition exclusion principle states that two species so similar that they compete for the same limiting resources cannot coexist in the same place (Gause 1934, Hardin 1960). Either the less competitive species will be driven to local extinction, or one of the species will evolve enough through natural selection to use a different set of resources. Interspecies competition has been recognized to be of two types, exploitation competition and interference competition. Exploitation competition is indirect and occurs through a common limiting resource. Competition for food is a form of exploitation competition in which carnivores interact with one another to access a shared prey species. Two large carnivore species in Finland, grey wolf and Eurasian lynx, are obligate predators, but they do not compete for the same prey species, as there are marked differences in their prey assortment (Pulliainen *et al.* 1995, Kojola *et al.* 2004). Two other species, the brown bear and wolverine, are seen as opportunistic predators and scavengers that can switch between food sources if one becomes rare.

Interference competition occurs directly between individuals via aggressive behaviour and interspecific killing. Interspecific killing, or intraguild predation, is common among mammalian carnivores (Palomares & Caro 1999). Age, size and patterns of grouping play a significant role in the outcome of interactions between mammalian carnivores. Smaller species may kill cubs, young or subadult individuals of the larger species, but in general, larger species usually kill both

adult and juvenile individuals of the smaller species. For example, in North America, eight of the fourteen documented wolf–wolverine interactions resulted in death for the wolverines (Ballard *et al.* 2003). The reasons why wolves sometimes kill wolverines might include interspecific competition, hunger, territoriality or curiosity.

Interference competition might result in avoidance behaviour and spatial segregation between carnivore species. May *et al.* (2008) found that wolverines differed in their habitat use compared to the three forest-dwelling carnivore species, as wolverines selected rugged terrain at higher elevations. This result fits well with the perception that susceptibility to fragmentation and human influence, and the avoidance of other carnivores affect wolverine habitat selection. In Finland, the elevational variation is low, and the availability of spatial refuges at higher elevations is therefore also low, especially in the eastern parts of the country. In addition, due to the scarcity of middle-sized ungulates in some areas, Finnish wolverines might greatly depend on moose carcasses in their diet, which may increase sympatry between wolverines and other large carnivores.

Carnivores do not necessarily only have negative influences on each other, as intraguild interactions might even be beneficial for one (commensalism) or for both species (mutualism). Scavenging is a common form of foraging behaviour in the carnivore guild (DeVault *et al.* 2003, Selva 2004). Carcasses are considered as an ephemeral, rare and unpredictable resource in terms of their spatio-temporal availability (e.g. Heinrich 1988, Wilmers *et al.* 2003, Wilmers & Post 2006, Baglione & Canestrari 2009, DeVault *et al.* 2011). One foraging strategy that scavengers can employ to discover unpredictable food sources is to associate with other predators that provide food (Stahler *et al.* 2002). Carrion provided from the kills of predators and hunters may be much more predictable, especially for those scavenger species associating with large predators (Stahler *et al.* 2002, Wilmers *et al.* 2003, Selva *et al.* 2005). Other advantages of this type of a strategy include a reduced searching time, decreased energy expenditure and access to large, high quality food items (Brockmann & Barnard 1979, Heinrich 1988). On the other hand, predators can be a threat for scavengers (White *et al.* 2002, Ballard *et al.* 2003). The benefits gained from scavenging possibly compensate for the associated risk of being killed by a predator (Paquet 1992, van Dijk *et al.* 2008a, Gorini *et al.* 2012).

The interactions between the members of Finnish large carnivore guild have been poorly studied and are probably not very strong because of the low population densities. Competition could occur between all species, as their diets

partly overlap. The largest species, the brown bear and grey wolf, might also exhibit occasional intraguild predation towards smaller guild members. Scavenger species, the brown bear and wolverine, display commensal behaviour by feeding on carrion killed by more efficient predators (Fig. 1).

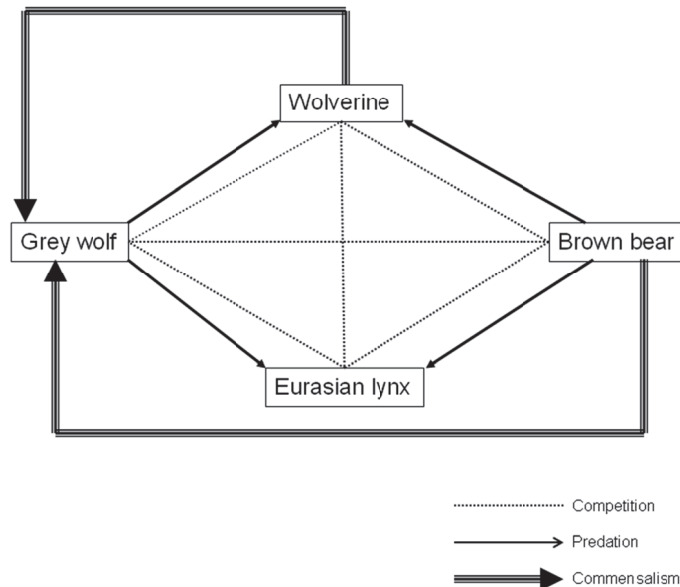


Fig. 1. Possible interactions among large carnivores in Finland.

1.4 Study species

Within their holarctic distribution range, wolverines occupy a variety of habitats ranging across tundra, alpine and taiga biomes. The wolverine is often viewed as being a high alpine dweller for which anthropogenic factors, probably due to persecution (Persson *et al.* 2009), are more important in the selection of the home range than habitat factors (May *et al.* 2006). Factors such as the density of prey and landscapes where they could find a suitable denning habitat are also important (Landa *et al.* 2000, May *et al.* 2010, May *et al.* 2012).

At the end of the 16th century, the distribution range of wolverines covered almost the whole Finland (Pohja-Mykrä & Kurki 2008). The population size

started to decrease because of increased hunting pressure, and at the end of the 19th century the wolverine was common in northern Finland, but rare in other parts of the country (Ermala 2003). The estimated minimum population level, 50–80 individuals, was probably reached before wolverines received protection in 1982. In 1979–1998, 16 wolverines were translocated from northern Finland to central parts of the country as an attempt to reduce reindeer (*Rangifer tarandus tarandus*) predation by wolverines and to expand the distribution area of wolverines to south (Pohja-Mykrä & Kurki 2008).

Nowadays, approximately half of the estimated 180–220 Finnish wolverines are found in northern Finland within the reindeer management area, this subpopulation consisting of 80–90 individuals (Heikkinen & Kojola, in press). The other half of the population is distributed south of the reindeer management area, in eastern and central Finland. The subpopulation in eastern Finland consists of 50–60 individuals, whereas the estimated population size in central Finland is only 20–30 individuals (Heikkinen & Kojola, in press). Ungulate and carnivore densities differ considerably between the areas of the three subpopulations, which may be reflected in the foraging behaviour of wolverines.

The eastern wolverine population has one unique feature: the population is located outside the reindeer management area in a forested habitat, where the density of medium-sized ungulates is low. This type of pattern can also be found in Sweden, where two isolated sub-populations have established in areas characterized by boreal forests with active forestry (Hedmark & Ellegren 2007). The minimum number of individuals in these populations was found to be 5 and 17, with one subpopulation showing increasing numbers and the other decreasing. The viability of these subpopulations in lowland forests is still unknown (Hedmark & Ellegren 2007). In Finland, about 80 wolverines are estimated to be living in boreal forests outside the reindeer management area, and even though the population is small, it has been stable during the last ten years (Heikkinen & Kojola, in press). This indicates that the wolverine is also capable of surviving in a habitat with a low number of medium-sized ungulates.

The wolverine diet is varied and shows seasonal changes (Magoun 1987, Landa *et al.* 1997, Lofroth *et al.* 2007, van Dijk *et al.* 2008b, Dalerum *et al.* 2009). In North America and Scandinavia, the main food sources during the snow-free months are grouse species, mountain hares (*Lepus timidus*), small rodents and bird eggs. In winter, wolverines hunt reindeer and caribou and scavenge on ungulate carrion. The hunting success in winter is largely determined by the texture of the snow: if the snowpack is sufficiently hard to bear the weight of the

wolverine but not of the reindeer, the latter is an easy prey. Wolverines cache any surplus food and these reserves are important for their survival during periods when hunting is not possible or successful (Samelius *et al.* 2002, Wright & Ernst 2004).

Species richness in most groups of organisms generally decreases towards the poles (Planka 1966, Currie & Paquin 1987, Kaufman 1995, Qian 1998), and a similar trend can also be found in Finland, with greater species diversity in southern Finland than in northern parts of the country. This may be reflected in differentiated foraging behaviour in wolverines, as there are more mesopredators and herbivores in eastern Finland than in the northernmost parts of the country.

Wolverines have large home ranges, they occur at low densities and prey upon larger prey such as semi-domesticated reindeer. This predatory behaviour causes a conflict between wolverines and human interests. In northern Finland, the wolverine was responsible for most (51%) of the adult (<1 year old) reindeer predator-caused mortality between 2003–2008 (Norberg *et al.* 2010). Wolverine predation on semi-domesticated reindeer seems to be concentrated in the northernmost municipalities of northern Finland, and predation is heaviest during the late winter to early spring (Pohja-Mykrä & Kurki 2008). Reindeer depredation by large carnivores has been increasing during the last decade (Nordberg *et al.* 2010). On the contrary, in eastern Finland, predation by wolverines on domestic livestock is seldom reported. Between 2000–2006, the wolverine was responsible only on four reported cases of livestock losses outside the reindeer management area in Finland (Pohja-Mykrä & Kurki 2008).

Wolverines have larger home ranges than other similar-sized carnivores. In North America and Europe, males and non-breeding females usually utilize the largest home ranges (200–1500 km²), whereas the area used by females with cubs ranges from 40 to 100 km² (Whitman *et al.* 1986, Banci & Harestad 1990, Landa *et al.* 1998, Landa *et al.* 2000). Male wolverines roam within the ranges of several females. The wolverine is a polygamous species, and mating occurs from May to August (Wright & Rausch 1955, Rausch & Pearson 1972, Magoun & Valkenburg 1983, Mead *et al.* 1991). Wolverines exhibit delayed implantation (Wright & Rausch 1955), whereby the blastocyst does not immediately implant in the uterus but is maintained in a state of dormancy. Implantation usually occurs in November, with an effective gestation period of 30–50 days (Rausch & Pearson 1972). Most females give birth before late March in snow caves, and the average litter size is 2–3 cubs (Pulliainen 1968, Banci & Harestad 1988, Blomqvist 1995, Magoun & Copeland 1998, Persson *et al.* 2006). Young are weaned at 9–10

weeks and begin to travel with their mothers by late April. Mörner *et al.* (2005) found that the most common cause of death of wolverines in Sweden was traumatic injuries caused by other predators or wolverines, and human-caused mortality (killed by hunters in self-defence or suspected to be illegally shot). In North America, human-caused mortality accounted for 46% of deaths, and starvation was the most common natural mortality source (Krebs *et al.* 2004). The causes of wolverine mortality in Finland have not been studied.

1.5 Genetic population structure of wolverines

The wolverine has small remnant populations in northern Europe, which are vulnerable due to persecution and conflict with human activities. It is unclear whether these populations are distinct from each other or whether they are connected to each other by migration. The isolation resulting from habitat fragmentation and the lack of connectivity can result in a decline in genetic variability and an increase in inbreeding. Reduced genetic variability can affect the reproductive potential and survival, which in turn can increase the extinction risk of a population (Frankham *et al.* 2002, Höglund 2009, Allendorf *et al.* 2013). The loss of genetic diversity can also be caused by a sudden or continuous reduction in population size, also known as a population bottleneck. Depending on the severity and duration of a bottleneck, rare alleles can be permanently lost in a population, even if it recovers from the bottleneck, and its evolutionary potential may consequently be reduced (Frankham *et al.* 2002, Höglund 2009). The low reproductive rate of the wolverine makes the species very sensitive to changes in survival rates. The deleterious effects of population reductions can be counteracted by increased migration. Immigrants from neighbouring populations can add new genetic variation to a population, preventing the extinction of small populations. Such a rescue effect has been observed, for example, in the Scandinavian wolf population (Vila *et al.* 2003).

Wolverines exist in four countries in Europe (Norway, Sweden, Finland and Russia) and have two population strongholds: a “Scandinavian population”, which includes the areas of Norway, Sweden and far northern Finland, and a “Karelian population” including areas of eastern Finland and neighbouring parts of north-eastern Russia. It is likely that both populations are connected to each other, as wolverines are known to sporadically occur in areas between the two populations (Kaczensky *et al.* 2013). The combined population of wolverines for Norway, Sweden and Finland is estimated at approximately 1 250 individuals.

Census data from the Russian part of the Karelian population are not available (Kaczensky *et al.* 2013).

The genetic population structure of wolverines in Scandinavia has previously been studied (Walker *et al.* 2001, Flagstad *et al.* 2004, Hedmark & Ellegren 2007), although the connection with the Karelian population has not been addressed. Extant Scandinavian populations appear to be subdivided and genetic variability was found to be lower than reported for other mustelid species (Walker *et al.* 2001). In North America, wolverine populations from southernmost regions, in which anthropogenic factors are strongest, were revealed to be more genetically structured than northern populations (Kyle & Strobeck 2001).

Wolverines are highly mobile with the ability to disperse up to 300 km in one year (Gardner 1985, Magoun 1985, Gardner *et al.* 1986, Vangen *et al.* 2001, Cegelski *et al.* 2003). However, if the wolverine population in central Finland is isolated, it is likely that a population this small will face serious inbreeding problems. No information is available on genetic exchange between the central Finnish population and the Finnish-eastern Russian population.

1.6 Aims of the study

The wolverine is one of Finland's rarest mammals and least-studied large carnivores, with only few previous studies conducted in northern Finland (Pulliainen 1968, 1975). Even though the wolverine has been researched in North America and Scandinavia during recent years, knowledge of its ecology, population dynamics and genetics has remained limited. This thesis research focused on wolverine habitat selection (paper I), diet (papers II and III) and population genetics (paper IV).

Wolverines, like other scavengers and opportunistic carnivores, can benefit from being sympatric with a more efficient predator (van Dijk *et al.* 2008b). One objective of this study was to investigate the relationship between wolverines and wolves. Understanding and predicting the interactions between the members of a large carnivore guild is crucial when trying to understand the ecology of species and manage their populations.

In paper I, the aim was to investigate which factors affect the habitat selection of wolverines. Wolverine habitat selection is known to be negatively affected by human activity, including roads, infrastructure and backcountry recreation (Caroll *et al.* 2001, Rowland *et al.* 2003, May *et al.* 2006, Krebs *et al.* 2007). In this study, the possible effect of wolf presence on wolverine habitat selection was of

particular interest. Moreover, the effects of settlements and forest types on the habitat selection of wolverines were examined. Wolverines were predicted to prefer wolf presence and avoid settlements.

In paper II, the diet of breeding female wolverines was investigated in two areas differing in the availability of prey. Wolverines were predicted to utilize the most available ungulate species, which are semi-domesticated reindeer in northern Finland and moose (carrion) in eastern Finland. Furthermore, a high density of medium-sized ungulates (semi-domesticated reindeer) in the northern Finland study area was expected to reduce the dietary niche breadth of wolverines.

Paper III concentrates on possible sex differences in wolverine foraging ecology. The hypothesis was that breeding female wolverines, probably due to their smaller home ranges and higher energy demands (because of gestation and lactation), are forced to rely more on food caches and carrion than other wolverines.

In paper IV, the aim was to investigate the genetic population structure, gene flow and genetic diversity of wolverines in remnant populations in Finland by examining microsatellite loci variation in DNA obtained by non-invasive sampling. One goal was to look for evidence of a population bottleneck in the Finnish wolverine populations and estimate the level of gene flow between the populations. Due to the small population size of wolverines in Finland, evidence of low genetic diversity and possible bottlenecks was predicted.

Overall, this thesis research aimed to provide a better understanding of the ecology and genetics of Finnish wolverines. In this study, the unique ecology of wolverines living in eastern Finland outside the reindeer management area in forested habitat was of special interest. The results will provide a lot of practical information needed in securing the viability of small wolverine populations and preparing a management plan for Finnish wolverines.

2 Material and methods

2.1 Study areas

The thesis is mainly based on data collected from two areas: within the reindeer management area in northern Finland and outside this area in eastern Finland (Fig. 2). The study area in northern Finland (Inari: 68°54'N, 27°01'E) belongs to the north-boreal coniferous forest zone (Ahti *et al.* 1968) and is composed of mountain plateaus with peaks of up to 600 m, consisting of bare rock and alpine tundra with heath and lichen vegetation. Lower elevation forests are dominated by mountain birch (*Betula pubescens*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The landscape in eastern Finland (Kajaani: 64°13'N, 27°43'E) belongs to the mid-boreal coniferous forest zone (Ahti *et al.* 1968) and is mainly composed of boreal forests, lakes and mires, the dominant tree species being the Scots pine and Norway spruce. Permanent snow usually appears in October/November and melts in May/June in northern Finland. In eastern Finland, the snow-cover period lasts from November/December to April. The elevation ranges from 100 to 600 m a.s.l. in northern Finland and from 100 to 300 m in eastern Finland. Temperatures vary from a minimum of -35 °C in winter to as high as 30 °C in summer. The annual precipitation ranges from 600 to 700 mm, with most of this falling during July and August.

Both study areas are sparsely populated by humans; the mean density of humans is 0.4 people/km² in the northern study area and 3.9 people/km² in the eastern study area. Settlements and infrastructure are constrained near town centres, but many people maintain a holiday residence in the countryside. Extensive forest harvesting has occurred in both study areas, and the density of forestry roads is high.

The study areas differ considerably in their ungulate and carnivore densities (Lavsund *et al.* 2003, Kojola *et al.* 2004, Wikman 2010, Nieminen *et al.* 2011). Free-ranging semi-domesticated reindeer dominate the ungulate population in the northern study area with a density of 2 animals/km². The density of moose is 0.1 animals/km². Other large carnivores are present at low densities (wolf and lynx: < 0.001 animals/km², golden eagle: 72 breeding pairs). In the eastern study area, the density of wild forest reindeer (*Rangifer tarandus fennicus*) is 0.1–0.2 animals/km² and that of moose 0.3–0.5 animals/km². Densities of wolves and lynx are higher than in the northern study area (wolf 0.004 animals/km², lynx 0.02

animals/km²). In both study areas, mountain hares, grouse and small rodents form other possible food sources for the wolverine.

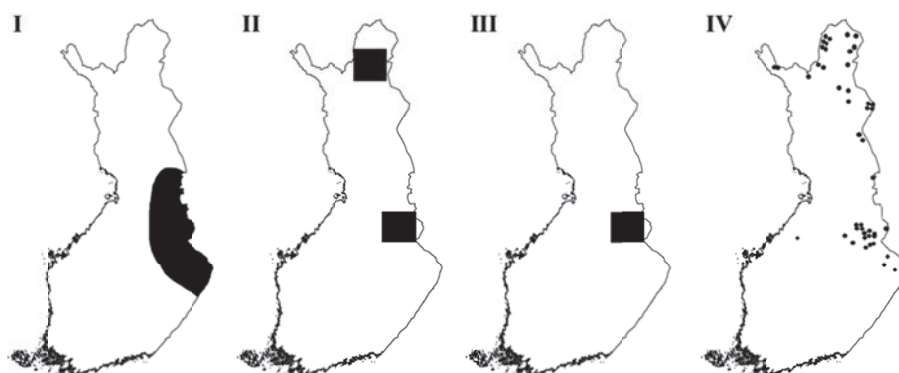


Fig. 2. Study areas. The wildlife triangle data (paper I) were collected from eastern Finland, from the provinces of Kainuu, Northern Karelia and Northern Savonia. Scat samples for the dietary studies were collected from northern and eastern Finland (paper II) and eastern Finland (paper III). Most of the genotyped individuals (paper IV) were from northern and eastern Finland, but in addition two individuals from northwestern Russia and one individual from the reintroduced western Finnish population were genotyped. The samples from Russia were from the Pinega Strict Nature Reserve, Arkhangelsk region (not shown on the map).

2.2 Research methods

2.2.1 Habitat selection (I)

The habitat selection of wolverines was studied by using wildlife triangle snow-track data and the landscape data that were from the CORINE Land Cover 2000 database. Wildlife triangles are equilateral triangles with a perimeter of 12 km, scattered throughout Finland. During the census, the tracks of mammals crossing the triangle line are counted, and a track index and density can be calculated. All geographic coordinates of crossings of wolverines and wolves were selected in the wildlife triangle data (original field forms) from our study area in eastern Finland (Fig. 2) in 2005–2008. As control plots, an equal number of random crossings were generated from existing wildlife triangles in our study area in

order to determine whether wolverines seek areas closer to wolves rather than having a random proximity.

Six landscape variables representing both infrastructural features and the main habitat types in Finland were selected to determine the factors behind wolverine habitat selection. The variables comprised six classes of land cover variables: (1) settlements, (2) mixed forests, (3) coniferous forests, (4) deciduous forests, (5) young forests and (6) mires. The seventh variable that was included in the analysis was the distance to the closest wolf crossing. Settlements were entered in the models as the distance of a given crossing or control plot from the nearest settlement. Other landscape variables were measured as the proportion of each habitat type around the crossing or control plot within a given radius. To determine the scale at which the landscape variables were most important in predicting wolverine occurrence, buffers of 75, 150, 300, 600, 1200, 2400 and 4800 m in radius around the wolverine and control plots were constructed. Generalized linear models were then fitted for each buffer radius using landscape variables as predictive variables. For later models, only the most significant buffer radius was used.

Before any modelling, Spearman's pairwise correlation analysis was conducted between the explanatory variables to identify possible multicollinearities. As there were no variables with a strong correlation ($|r| > 0.6$), they were all included in the models (Green 1979, Fielding & Haworth 1995, Sawyer *et al.* 2006, Klar *et al.* 2008).

A set of 128 candidate models of the occurrence of wolverines and wolves were designed based on the two following general hypotheses: 1) wolverines seek areas in proximity to wolves (May *et al.* 2008, van Dijk *et al.* 2008a, van Dijk *et al.* 2008b); and 2) wolverines and wolves avoid the proximity of settlements where human presence is continuous (May *et al.* 2006, Krebs *et al.* 2007, Kaartinen *et al.* 2010).

Logistic regression was used together with Akaike's Information Criterion corrected for small sample sizes (AICc) to model the important habitats for wolverines and wolves in the study area. Selection of the best approximating models was based on the ΔAICc values, which were calculated as the differences between the current and minimum observed values of the model AICc (Burnham & Anderson 2002). The Akaike weights (w_i) were also calculated for all models. The Akaike weight is a measure of the likelihood of the model for the given data (Johnson & Omland 2004), so that models with a larger w_i better approximate the

data (see Burnham & Anderson 2002). The primary objective in model fitting was to assess the relative importance of the seven variables included.

Akaike weights were summed across all the models in which individual variables occurred to obtain the relative importance of the variables. The larger the sum of the Akaike weights, the more important a variable is relative to the other variables considered. Model averaging was used to produce the best model, including aspects of a number of models (Greaves *et al.* 2006). In the set of best approximating models, parameter estimates were examined to assess the reliability of each variable as a predictor of the occurrence of a wolverine or wolf. Due to the uncertainty in model selection, the model-averaged slopes (β -values) of the variables and their standard errors were calculated using equations 4.1 and 4.9 in Burnham & Anderson (2002); models with $\Delta AICc < 4$ were included. Statistical analyses were carried out using the free software R 2.12.1 (R Development Core Team 2010) with the package MuMIn (Barton Kamil 2010).

2.2.2 Foraging ecology (II, III)

The diet of wolverines was investigated by analysing scats collected from wolverine denning sites (papers II and III) and by snow-tracking wolverines (paper III). In paper II, the dietary composition of breeding female wolverines in the reindeer management area (northern Finland) was compared with that of wolverines breeding outside this area (eastern Finland). Altogether, 421 scats collected from six active dens in northern Finland and four dens in eastern Finland during 2004–2006 were analysed (Fig. 2). In paper III, the dietary habits of wolverines in eastern Finland were examined by comparing the diet composition of breeding females with that of males and non-breeding females. Scats representing the winter diet of breeding females ($n = 168$) were collected from four wolverine den sites located in eastern Finland during 2004–2006. Scats representing the diet of males and non-breeding females ($n = 64$) were collected by tracking six wolverine individuals in eastern Finland during 2009–2011.

Scats from den sites were collected after the denning period (from February/March to April/May), when the female wolverines and cubs had left their dens, and the scats thus represented the diet of the reproducing females during the denning period. Scats of males and non-breeding females were from the winter season, and by tracking these animals for long enough it was possible to determine that these scats did not belong to breeding females.

Collected scats were frozen and analysed at the University of Oulu. Each scat sample was washed in a 0.5-mm sieve under running water. The remains (hairs, feathers, bones, plant material, non-food items) were oven-dried at 80 °C for 24 hours. Hairs and feathers were identified to the species level using macroscopic and microscopic characteristics (Debrot *et al.* 1982, Teerink 1991, De Marinis & Asprea 2006) and a reference collection. The percentage occurrences of the prey species in scats were then calculated (van Dijk *et al.* 2007).

In paper II, the occurrence of prey species in the diet was assessed using logistic mixed-effects models with the study area as a fixed covariate and the den as a random factor. In paper III, the reproductive status entered the model as a fixed covariate and the individual as a random factor. To measure how specialized or generalized wolverines are in their foraging behaviour, the diet breadth was calculated using the standardized Smith's measure of niche breadth, FT, following equation 1:

$$FT = \sum (\sqrt{p_j a_j}) , \quad (1)$$

where

FT = Smith's measure of niche breadth

p_j = proportion of individuals found in resource state j ($\sum p_j = 1.0$)

a_j = proportion of resource j is of the total resources ($\sum a_j = 1.0$)
(Smith 1982).

The 95% confidence interval was calculated using equation 2:

$$\sin[\arcsin(FT) \pm 1.96/(2\sqrt{N})] , \quad (2)$$

where

FT = Smith's measure of niche breadth

N = total number of individuals studied.

All statistical analyses were performed with SYSTAT version 13 (SYSTAT, Inc, Evanston, Illinois) and Microsoft Excel, version 2003.

2.2.3 Population genetics (IV)

To study the population genetics of wolverines in Finland, 406 scat samples, ten muscle tissue samples and two oral mucosa swabs as sources of DNA were collected during 2004–2011, mainly in northern and eastern Finland (Fig. 2). The PSP Spin Stool DNA Plus Kit (Invitex) was used to collect and extract DNA from

the scat samples following the manufacturer's instructions. DNA from the tissue samples was isolated using the DNeasy tissue kit (Qiagen) protocol for the purification of total DNA from animal tissues. To test whether the extracts had sufficient DNA quality and quantity, the extracts were amplified using the microsatellite marker Ggu 14 (Walker *et al.* 2001, Hedmark *et al.* 2004, Hedmark & Ellegren 2006). A total of twenty microsatellite loci were amplified from the samples that had a sufficient amount of DNA using a two-step multiplex polymerase chain reaction method. Primers DBY3Ggu and DBY7Ggu (Hedmark *et al.* 2004) designed from intron sequences of a Y-linked DBY gene were used as markers for sex identification. The ten microsatellite loci from multiplex groups 1 and 2 were used for the preliminary identification of individual wolverines using the Individual Identification analysis implemented in the program Cervus 3.0 (Kalinowski *et al.* 2007). The program uses a likelihood-based statistical method for parentage analysis and identity analysis for co-dominant genetic markers.

The presence of null alleles, as well as of scoring errors in the microsatellite genotypes caused by stuttering, large allele dropout or typing mistakes was tested using the program MICRO-CHECKER 2.2.3 (van Oosterhout *et al.* 2004). The program identifies various genotyping and typographic errors by estimating the frequency of null alleles at a locus using a series of algorithms.

The software STRUCTURE 2.3.4 (Pritchard *et al.* 2000, Falush *et al.* 2003, 2007, Hubisz *et al.* 2009) was used to infer the most likely number of populations (K) in the dataset. The program assigns individuals probabilistically to one of several assumed populations, characterised by their allele frequencies, using a Bayesian clustering method. The Bayesian spatial explicit model of population structure implemented in the program GENELAND 3.2.4 was used to detect possible areas of genetic discontinuity (Guillot *et al.* 2005). The program estimates the number of populations in a dataset as well as their spatial organisation based on allele frequency variation, using models that implement both geographic and genetic information. A graphical representation of the correspondence between allele scores and individual scores was produced with factorial correspondence analysis (FCA) as implemented in the program GENETIX 4.05 (Belkhir *et al.* 2004).

The program DIYABC 1.0.4.46 (Cornuet *et al.* 2010) was used in order to infer the time at which population clusters had split from an ancestral population, as well as to infer the effective population sizes (N_e) of the assumed populations. The program makes inferences about population divergences, admixtures and changes in population size using approximate Bayesian computation.

An analysis of molecular variance (AMOVA) using Arlequin 3.5.1.3 (Excoffier *et al.* 2005, Excoffier & Lischer 2010) was performed to test the scenario of population subdivision and to calculate the contribution of the different population hierarchy levels to the observed level of genetic variation. The number of permutations used in the AMOVA analysis was 10 000. For this analysis, the scenario of two wolverine populations was tested: one in northern Finland and one in eastern Finland. Wright's F-statistics were calculated for the analysis between populations, for the whole dataset and separately for each gender using the program FSTAT 2.9.3.2 (Goudet 2001) based on 10 000 permutations, and 95% confidence intervals were obtained by bootstrapping over loci.

Expected heterozygosities and deviations from Hardy-Weinberg expectations were estimated using Genepop 1.4.10 (Raymond & Rousset 1995, Rousset 2008). Moreover, FSTAT was used to estimate allelic richness (A_R) and inbreeding coefficient (F_{IS}). The program estimates gene diversity per locus and sample using Nei's (1987) unbiased estimator. Genetic diversity parameters and F_{IS} were calculated for each locus in each population.

The program BOTTLENECK 1.2.02 (Cornuet & Luikart 1996) was used to detect recent reductions in effective population size. The program detects an excess of heterozygotes, as would be expected under a scenario of recent population bottlenecks, by using different tests: a sign test, a standardized differences test and a Wilcoxon rank test.

A spatial analysis of genetic diversity was performed with the program SPAGeDi 1.3 (Hardy & Vekemans 2002) to detect correlations between the kinship coefficient (Loiselle *et al.* 1995) and logarithmic geographical distance classes. The correlation was tested for the complete dataset, as well as individually for each gender. A difference between the slopes of the regression for each gender was tested using ANCOVA.

The program GeneClass (Piry *et al.* 2004) was used to detect first-generation migrants. The ratio of the likelihood computed from the population from which the individual was sampled (L_{home}) over the highest likelihood value among all population samples, including the population from which the individual was sampled (L_{home}/L_{max}) (Paetkau *et al.* 2004), was chosen for likelihood computation. A Bayesian-based model from Rannala & Mountain (1997) was chosen for the criteria for computation. The probability that an individual is a resident was estimated with a resampling algorithm from Paetkau *et al.* (2004) by simulating 10 000 individuals. Long-term migration rates were estimated using

BayesAss 3 (Wilson & Rannala 2003). The program uses a Bayesian method relying on Markov chain Monte Carlo sampling to estimate immigration over the last several generations. Delta values of 0.15 were set for allele frequency, migration rate and inbreeding.

The effective population size (N_e) was estimated using LDNe 1.31 (Waples & Do 2008). The program estimates contemporary effective population sizes using a biased correction for the Hill method (Hill 1981, Waples 2006) based on linkage disequilibrium data. Three estimates of N_e are given based on the lowest allele frequency used (0.01, 0.02 and 0.05).

3 Results and discussion

According to the results, wolf presence was one of the most important variables influencing the habitat selection of wolverines (I). In eastern Finland, wolverines heavily utilized moose carrion provided by wolves and hunters, whereas semi-domesticated reindeer were the most important food source in northern Finland (II). Breeding female wolverines opportunistically utilized carrion and hunted less on small prey than males and non-breeding females (III). According to the results of a population genetics investigation, two wolverine subpopulations exist in Finland, migration between the populations was quite low, and genetic diversity and effective population sizes were low (IV). A brief summary of the predictions, observations and conclusions is presented in Table 1.

Table 1. Summary of predictions, results and conclusions concerning the four substudies.

Study	Prediction	Observations	Conclusions
I	Wolverines favour wolf presence.	Yes	Remote forest areas and the presence of wolves are important to wolverines in their habitat selection.
	Wolverines and wolves avoid settlements.	Yes	
II	Wolverines opportunistically use the (ungulate) food source that is most energy-efficiently available.	Yes	Ungulates have an important role in the diet of breeding female wolverines. Alternative, smaller prey and carcasses may replace ungulates in the wolverine diet in areas with a low density of mid-size ungulates.
	Wolverines in northern Finland have a smaller niche breadth than those living in eastern Finland.	No	
III	Breeding females rely more on food caches and carrion than males and non-breeding females.	Yes	Breeding female wolverines use carrion opportunistically and hunt less on small prey than males. The larger home ranges and greater mobility of male wolverines probably enable them to more frequently come into contact with smaller prey than females.
	Breeding female wolverines have a smaller niche breadth than males and non-breeding females.	No	
IV	Wolverines are suffering from low genetic diversity.	Yes	There are two wolverine subpopulations in Finland: northern and eastern ones. Signs of a recent population bottleneck were detected in both populations.
	Wolverine populations have experienced population bottlenecks.	Yes	

3.1 Effect of wolf presence on wolverine habitat selection (I)

The main result was that wolverines favoured wolf presence, coniferous forests, mixed forests and mires and avoided settlements, young forests and deciduous forests in their habitat selection. The model best explaining wolverine habitat selection included the presence of wolves, deciduous forests and distance from settlements as explanatory variables. These findings support the preliminary idea that wolverines might benefit from being sympatric with wolves through increased scavenging opportunities. Wolverines are known to utilize carcasses left by wolves (van Dijk *et al.* 2008a, 2008b) and lynx (Mattisson *et al.* 2011). On the other hand, van Dijk *et al.* (2008a) observed that wolverines do not use the tracks of other carnivores to locate carcasses. Accordingly, wolverines might occupy the same regions as wolves because of greater carrion availability, but not live in very close proximity to them in order to avoid intra-guild predation. Although the data did not distinguish the behavioural mechanisms behind the preferential association of wolverines with wolves, it is likely that both innate and learned behavioural responses towards wolves are involved.

Wolves and wolverines generally selected the same type of habitat: they favoured coniferous and mixed forests and avoided settlements, young forests and deciduous forests. However, the relative importance of variables differed between the species. For wolverines, the most important variables predicting habitat selection were the presence of wolves, deciduous forests and distance from settlements (Table 2). The model best explaining wolf habitat selection consisted of settlements, coniferous forests and mixed forests.

Table 2. The relative importance of variables in the wolverine habitat selection model.

Variable	Relative variable importance
Wolf	1.00
Deciduous forests	1.00
Settlements	0.68
Mixed forests	0.40
Coniferous forests	0.19
Mires	0.18
Young forests	0.15

Our results indicate that both wolverines and wolves in eastern Finland avoid settlements. The selection of remote forest areas is consistent with previous studies on habitat selection and home range use by wolverines (May *et al.* 2006, Krebs *et al.* 2007) and wolves (Theuerkauf *et al.* 2003, Kaartinen *et al.* 2010).

Human activities have expanded and left less living space for wolverines, which appear to be very sensitive to human disturbance and also to habitat fragmentation (Carroll *et al.* 2001, Rowland *et al.* 2003). The disadvantageous effects of human activity on wolverines not only result from habitat loss, but also from the loss of prey species and other carnivore species that provide carrion (Landa *et al.* 2000). Poaching is one of the main causes of adult mortality for both species (Boitani 2000, Landa *et al.* 2000, Krebs *et al.* 2004, Mörner *et al.* 2005, Lovari *et al.* 2006, Persson *et al.* 2009), and the selected habitats in this study correspond to areas providing safety from human disturbance. The main distribution areas of wolverines in Finland are located in areas with a low human population density. In the future, wolverines might expand to new areas in the south, following the recolonizing wolves. Observations that people and predators can co-exist even at high human densities (Woodroffe 2000) suggest that the possible expansion of wolverines from north to south might be successful.

Both study species selected forest types in a similar way: they favoured coniferous and mixed forests and avoided young and deciduous forests. According to LANDSAT satellite data, the majority (66%) of Finnish forests are mixed, with lower relative proportions of pure spruce (15%), pure pine (11%) and pure deciduous forests (8%) (Lindfors & Laurila 2000). Thus, the selected habitats might reflect the proportions of different forest types in Finland. Even though there were no variables with a strong correlation in the analysis, deciduous and young forests might be located closer to settlements than random, which might explain the avoidance of these forest types by both study species. The avoidance of young forests by wolves was, however, unexpected, because previous studies have demonstrated a tendency of wolves to select similar habitats to moose, their most important prey species (James *et al.* 2004).

Global warming is expected to have profound effects on northern habitats. Concern over the decline of alpine habitats and associated species in climate change scenarios could have implications for wolverine conservation in the future. The wolverine is one of the 25 terrestrial mammal species in Canada whose northern distributions are bounded by the Arctic Ocean (Forsyth 1985). These species are not able to migrate further north because of the Arctic Ocean barrier (Kerr & Packer 1998). Wolverines, due to their widespread distribution and habitats in taiga forests, are not likely to become extinct or even rare with substantial climate change, but they are nevertheless likely to undergo significant losses of habitat, and may eventually require management intervention.

Snow is seen as an important part of the wolverine's seasonal habitat requirement (Magoun & Copeland 1998, Aubry *et al.* 2007). Copeland *et al.* (2010) studied the hypothesis that the occurrence of wolverines is constrained by their obligate association with spring snow cover that persists throughout the denning period from February–May to April–March. They collected spatial information for 562 wolverine reproductive den sites in North America, Finland, Sweden and Norway, and found that 97.9% of the den sites occurred in areas that were snow-covered in at least 1 of 7 years. Scandinavian wolverines preferred den sites that were snow-covered in 6–7 of 7 years. All dens reported in Finland (n = 10) were determined to be snow dens, but 8 of them were located outside the satellite-based spring snow coverage area. According to the results, the wolverine's southern range extends slightly beyond the spring snow coverage range, especially in areas with low topographic relief. It is possible that snow coverage is limiting the breeding success of wolverines in central Finland.

3.2 Effects of prey availability and reproductive status on the wolverine diet (II, III)

Both the reproductive status of wolverines and prey availability in the area affected the wolverine diet. In northern Finland, the semi-domesticated reindeer and mountain hare were the most utilized prey species for breeding female wolverines. In eastern Finland, the most important food source of breeding females was moose, whereas males and non-breeding females heavily utilized mountain hares. A brief summary of the results concerning the diet of wolverines in Finland is presented in Table 3.

Table 3. Percentage occurrence of different prey species found in wolverine scats. The final rows give the Smith's measure of niche breadth and confidence intervals (95%).

Food source	Northern Finland	Eastern Finland	
	Breeding females	Breeding females	Males and non-breeding females
Moose	3.7	55.2	22.0
Semi-domestic reindeer	65.9	0	0
Wild forest reindeer	0	0	3.3
Domestic pig	0	13.4	0
Mountain hare	15.6	12.7	51.9
Grouse	7.4	11.0	14.8
Beaver	0	1.4	0
Raccoon dog	0	1.4	3.1
Pine marten	0	1.3	0
Red fox	0	0	3.1
Rodents	6.3	2.3	0
Other	1.2	1.4	1.7
Number of scats	253	168	64
Number of wolverines	6	4	6
Niche breadth	0.640	0.763	0.680
CI%	0.29–0.89	0.37–0.98	0.40–0.88

Ungulates were an important part of the wolverine diet in all three groups (breeding females in northern Finland, breeding females in eastern Finland, and males and non-breeding females in eastern Finland). Ungulates (moose + semi-domesticated reindeer) formed 70% of the wolverine diet in northern Finland. In eastern Finland, ungulate (moose + wild forest reindeer) remains occurred in 55% of the scats of breeding females. Males and non-breeding females in eastern Finland also utilized ungulates (25%). The occurrence of moose did not differ between the groups in eastern Finland. The proportion of moose in the diet of breeding females was statistically significantly higher in eastern Finland and that of reindeer was higher in northern Finland.

The wolverine appears to use different foraging strategies depending on the area and prey availability. In northern Finland, wolverines utilize semi-domesticated reindeer mainly by predation, as the densities of other carnivores are low in the area, and reindeer carrion is therefore only occasionally available. In eastern Finland, as moose are very seldom killed by wolverines, they scavenge from moose carrion killed by wolves and hunters. Prey caching is a common

foraging strategy of mustelids (Oksanen 1983, Oksanen *et al.* 1985, Wright & Ernst 2004), and wolverines may also benefit from food caches during periods of food scarcity (Vander Wall 1990, Pasitschniak-Arts & Larivière 1995). Persson (2005) suggested that carrion cached in late fall or early winter is an important determinant of the condition of female wolverines at the time of pregnancy and lactation and determines their reproductive success. As moose are harvested in autumn and early winter, it is evident that wolverines benefit from moose hunting by humans primarily before the breeding season, while wolf-killed moose is available for wolverines during all seasons. However, wolverines may also benefit from human-killed moose during the winter in the form of food caches.

Although wild forest reindeers were present in small numbers in the eastern study area, there was no indication of wild forest reindeers being an important part of the wolverine diet. Only 3% of the diet of males and non-breeding females consisted of wild forest reindeers, and breeding females did not utilize them at all. When comparing semi-domesticated and wild forest reindeer, the latter might be a more elusive and challenging prey species for wolverines. However, there have been some observations of wolverines utilizing the carcasses of wild forest reindeer in eastern Finland, although the cause of mortality of reindeer in these cases is unknown (A. Koskela, unpublished data). The main wintering grounds of wild forests reindeer are located north of the eastern study area, and this might also explain the lack of the species in the diet of wolverines in our study. Nevertheless, as wolverines inhabit both of the main distribution areas of wild forest reindeer in Finland, in eastern and central Finland, it is reasonable to assume that wolverines also utilize wild forest reindeer at least in areas where the availability of other prey species or carrion is low.

The presence of domestic pigs (*Sus scrofa domesticus*) in the diet of two breeding female wolverines in the eastern study area was most probably a consequence of wolverines visiting feeding sites at which pig carcasses had been placed to attract large carnivores for photographic purposes. Domestic pig constituted a notable proportion (52%) of the diet of one of the female wolverines. The distance between the den and the closest feeding site was 2.5 km. Persson (2005) found that the reproduction of wolverines is influenced by food availability in the winter, as reproduction was higher for food-supplemented females than for non-supplemented females. The feeding of large carnivores for photographic and recreational purposes is a common and increasing practice in eastern Finland, and this carrion supply might have a notable effect on the breeding success of wolverines.

The most frequently utilized food species for males and non-breeding females based on scat samples was the mountain hare, and mountain hare remains were also the most common carrion that was observed when tracking these wolverines. The diet of males and non-breeding females included more mountain hare than that of breeding females. These results support the predictions of the optimal foraging theory, suggesting that wolverines opportunistically utilize the food source that is most energy-efficiently available. Hunting ungulates or smaller prey such as mountain hare or grouse might incur greater energetic costs than scavenging, but searching for wolf- or human-killed carcasses takes more time. The larger home ranges and greater mobility of male wolverines probably enable them to more frequently come into contact with smaller prey than breeding females.

In southern Norway, the main factor influencing the number of wolverine cubs surviving was the abundance of small rodents (Landa *et al.* 1997). Van Dijk *et al.* (2008b) also observed that small rodents formed 12% of the wolverine diet in forest habitats. However, our results demonstrated that small rodents were of negligible importance in the diet of breeding female wolverines (6% in northern Finland and 2% in eastern Finland). The proportion of small rodents in the wolverine diet was significantly higher in northern Finland than in the eastern study area. Small rodent remains were not found from the scats of males or non-breeding females. Voles in northern Europe have been shown to exhibit cyclic population dynamics. The length of the vole population cycle is reported to be 3–5 years, with generally synchronous fluctuations in different vole species (Hansson and Henttonen 1985, 1988). During 2004–2006, when the scats of breeding females were collected for this study, vole densities were very low in eastern Finland (Huitu *et al.* 2009). In northern Finland, vole population densities were very high in 2005, but in 2004 and 2006 the densities of small rodents were low (Huitu *et al.* 2009). Vole population cycles might therefore explain the small proportion of rodents in the diet of breeding female wolverines in our study.

The niche breadth was highest in the diet of breeding females in eastern Finland (0.76) and lowest in the diet of breeding females in northern Finland (0.64) (Table 2). However, because the confidence intervals overlapped, the niche breadth did not differ significantly between the groups. Nevertheless, the diet of wolverines in eastern Finland contained more prey species than that of wolverines in northern Finland, indicating that wolverines in northern Finland are more specialized in hunting semi-domesticated reindeers and are not opportunistic scavengers to the same extent as wolverines in eastern Finland.

In Finland, the wolf population has been declining for the last five years. Although the wolverine population size in Finland has remained stable during recent years, decreasing wolf numbers might have a negative effect in the long term. At the same time, other sources that provide carrion to wolverines might compensate the effects of the declining wolf population. Wolverines might also utilize brown bear kills outside the hibernation season. In Sweden, wolverines have been found to benefit from being sympatric with lynx through increased scavenging opportunities (Mattisson *et al.* 2011, Rauset 2013). The lynx population has been strongly increasing in Finland during the last decade. Moose and other carcasses also become available for wolverines through hunter harvesting, ecotourism, vehicle collisions and natural death.

The survival rate of adult females is generally one of the most important parameters for the population growth of long-lived animals (Nelson & Peek 1982). These results demonstrated the great importance of carrion, especially to breeding female wolverines during the breeding season. Therefore, if the goal is to facilitate the colonization of wolverines from northern Finland to eastern and southern parts of the country, the highest priority should be given to ensuring the carrion supply by maintaining the wolf population size at a viable level in the wolverine distribution area.

3.3 Population genetics of wolverines (IV)

Altogether, DNA was extracted from 406 scat samples, from which 211 DNA isolates amplified well enough to be visible in agarose gels, giving a success rate of 52%. After the individual analysis of all available genotypes, we were able to identify a total of 67 individuals. We were able to correctly assign the gender to 61 individuals.

The likelihood values obtained with STRUCTURE were highest for four populations, although the *delta K* values suggest the most likely number of populations is two. The individuals largely split into two groups, with one population including the northern Finland individuals and one western Finland individual (hereafter “northern population”) and another population that included samples from eastern Finland (hereafter “eastern population”). The two individuals from Pinega, Russia were grouped together with the northern population. The Bayesian spatially explicit analysis of Geneland supported a scenario of two populations, with a rather clear boundary between them. The results for the analysis of molecular variance suggest that most of the observed

variation could be explained by differences within the populations (96%), and to a lesser extent by differences between the northern and eastern populations (4%). The fixation index (F_{ST}) value of 0.042 was highly significant, which indicates a significant differentiation between the two populations.

It is unlikely that such a population structure is an artefact of strong isolation by distance with non-sampled individuals (Frantz *et al.* 2006), as has been found in other carnivores (Aspi *et al.* 2006, Kopatz *et al.* 2012), since this study included samples covering much of the latitudinal distribution in the area. The observed population structure in such a relatively small area could be explained by post-glacial colonization, which is characteristic of a number of species in Fennoscandia (Pamilo & Savolainen 1999), whereby some genotypes originated from glacial refuges in central or eastern Europe and arrived through eastern Finland, whereas others originated in western or central Europe and arrived via past land bridges connecting the Jutland and Scandinavian peninsulas.

The sample from Western Finland was also assigned to the northern population and was not genetically differentiated enough to cluster on its own, suggesting that the western Finnish wolverines have not differentiated enough from the northern population (from which they originate due to translocations) to form a genetically distinct population. However, these results are not reliable due to the small sample size, although they offer an interesting topic for future research.

The F-statistics (Weir & Cockerham 1984) across all loci were estimated with the program FSTAT. The analysis gave an F_{IT} value of 0.025, a pairwise F_{ST} value of 0.046 and an F_{IS} value of -0.022. The F-statistics were estimated separately for both sexes using the program FSTAT. The program gave males an F_{IS} value of -0.088 and an F_{ST} value of 0.066. For females, the F_{IS} value was 0.023 and the F_{ST} value 0.048. The p-value for the F_{ST} test was 0.714, suggesting that there is no male-biased dispersal according to these data. The fixation index F_{ST} between the Finnish populations was the same magnitude as the global F_{ST} reported between wolverine populations in Scandinavia (Walker *et al.* 2001), and within the confidence intervals of those estimated more recently between a main population and two recently founded populations in Scandinavia (Hedmark & Ellegren 2007). The F_{ST} was more similar to that recorded between fragmented populations in North America than to that of more continuously connected populations within Alaska (Kyle & Strobeck 2001).

The observed and expected heterozygosities, as well as allelic richness were found to be similar in both populations, although the observed heterozygosity was

slightly higher. The mean inbreeding coefficients were slightly negative and not significantly different from zero in either population. The expected heterozygosities appeared to be relatively low and similar to those reported in Scandinavian populations (Flagstad *et al.* 2004, Hedmark & Ellegren 2007), although generally lower than in larger North American populations (Kyle & Strobeck 2001). Heterozygosities were lower than those found in other large carnivores in the same areas in Finland (Aspi *et al.* 2006, Kopatz *et al.* 2012).

The observed differentiation between populations could be due to the effects of drift in small populations, which can be particularly intense in populations that have experienced severe population bottlenecks (Barton & Charlesworth 1984). Evidence of recent population bottlenecks was found in both populations, with the assumption of 70% stepwise mutation in all three tests. Under the assumption of 90% stepwise mutation, we found significant values for both populations using the Wilcoxon test, but not using the sign test or the standardized differences test, although some of the results were somewhat close to significance.

The program GeneClass detected one immigrant (female) from the eastern to the northern population and two migrants (one female and one individual of unknown sex) from the northern to the eastern population. The position of these first-generation migrants was evident in the factorial correspondence analysis. Long-term migration estimated using the Bayesian approach detected global non-migration rates of 0.833% and migration rates of 0.166%. Between-population migration estimates were estimated at around 0.30 in either direction, and were not significantly different from each other. Global and between-population migration rates were significantly different from zero, as indicated by the 95% confidence intervals, which implies a low to moderate level of migration.

There was some evidence of gene flow between the two populations, as indicated by the migration results and the presence of individuals in either population that appeared to have an ancestry from another population. This indicates that the populations are not completely isolated from one another, although the gene flow has not been large enough to homogenize the allele frequencies in both populations.

The effective population size was 14.2–16.8 in the eastern population and 14.4–17 in the northern population depending on the lowest allele frequency used. The values were low and similar in both populations. The estimated effective population sizes were considerably lower than the census population size, and lower than the N_e value of 50, which has been suggested as the minimum size to

avoid serious loss of genetic variation in the short term (Soulé & Kohm 1989, Allendorf & Ryman 2002).

The results of this study demonstrate that the extant wolverine populations in Finland suffer from relatively low genetic diversity, potentially resulting from a recent population bottleneck. It is likely that the wolverine populations in Finland would benefit from improved connectivity between them, but also with neighbouring populations in Scandinavia and north-eastern Russia. There appears to be an increasing trend locally in the European wolverine populations, but the low effective population sizes and the evidence of population bottlenecks suggest that these populations have a larger extinction risk and are vulnerable to population reductions caused by humans or by stochastic events.

4 Conclusions and recommendations for future research

The results presented in this thesis suggest that a multitude of factors influence the foraging behaviour of wolverines. Both the reproductive status of wolverines and the prey availability in the area, as well as the amount of carrion, affected the wolverine diet. The foraging ecology of wolverines markedly differed between northern and eastern Finland. Wolverines preyed heavily on semi-domesticated reindeer in northern parts of the country, whereas in eastern Finland wolverines tended to be mainly scavengers. Outside the reindeer management area, breeding females utilized moose carrion, whereas males and non-breeding females hunted small prey species.

There is considerable interest in understanding the role of scavengers on the community level. Scavengers might cause predators to kill more, by stealing food remains, and strengthen the top-down effect on vegetation through the control of ungulate populations. Furthermore, wolverines should be seen not only as scavengers utilizing carrion left by other carnivores, but also as predators offering carcasses to smaller carnivores. In the rugged habitats of arctic, sub-arctic and boreal forest zones, where the number of large carnivore species is low, the impacts of wolverines on the ecosystem require further study.

In addition to reproduction status and prey availability, the presence of another large carnivore, the grey wolf, affected the wolverine diet. The present results revealed that wolf presence was one of the most important variables influencing the habitat selection of wolverines. It appeared that wolverines occupied the same regions as wolves because of greater carrion availability, and that the benefits of scavenging for wolverines were worth the risk of aggression from wolves. The importance of scavenging in the foraging behaviour of wolverines indicates that maintaining a wolverine population in the presence of wolves is ecologically feasible. Keeping the wolf and wolverine populations viable is a management challenge that will test wildlife managers in Finland. The presence of the grey wolf was an important factor influencing the wolverine diet, but it is reasonable to assume that wolverines also benefit other carnivore species, such as the brown bear, Eurasian lynx, red fox and raptors. Therefore, the nature of wolverine interactions with other large carnivores requires further study.

The overall genetic variability was low in both wolverine populations in Finland according to the heterozygosity values when compared with other wolverine, Mustelidae and carnivore populations. Estimates of the effective

population size were also low in both populations and below the suggested threshold value for populations to avoid the loss of genetic variation in the short term. One of the future management goals should be to increase the effective population sizes and genetic variability of the Finnish wolverine populations to ensure their viability. Furthermore, the level of connectivity with other extant population clusters in northern Europe needs to be resolved in order to propose management decisions that are relevant to the whole region.

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Original articles

- I Koskela A, Kaartinen S, Aspi J, Kojola I, Helle P & Rytönen S (2013) Does grey wolf presence affect the habitat selection on wolverines? *Annales Zoologici Fennici* 50: 216–224.
- II Koskela A, Kojola I, Aspi J & Hyvärinen M (2013) The diet of breeding female wolverines (*Gulo gulo*) in two areas of Finland. *Acta Theriologica* 58: 199–204.
- III Koskela A, Kojola I, Aspi J & Hyvärinen M (2013) Effect of reproductive status on the diet composition of wolverines (*Gulo gulo*) in boreal forests of eastern Finland. *Annales Zoologici Fennici* 50: 100–106.
- IV Esparza-Salas R, Joensuu M, Koskela A, Ollila T & Aspi J Population genetic structure and genetic diversity of the wolverine (*Gulo gulo*) in Finland. (Manuscript)

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