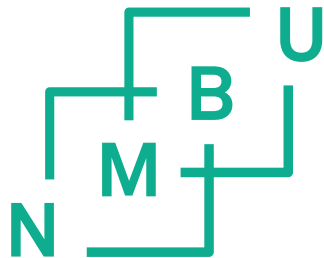# Assessing territoriality in wolverines (*Gulo gulo*) using non-invasive genetic sampling

Territorialitet hos jerv (*Gulo gulo*) undersøkt
med ikke-invasiv genetisk analyse

Master Thesis in Ecology

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Preface

This master thesis is the final product for my Master of Science in general ecology at the department of ecology and natural resource management, Norwegian University of Life Sciences. In collaboration with the Norwegian Institute for Nature Research (NINA), I have assessed territorial behaviour in wolverine and what happens to a territory after the owner´s death. This work started in the summer/fall of 2013 and was completed in late spring 2014.

Working on this thesis has helped me learn about spatial ecology, territoriality, monitoring strategies, and wildlife management. I have gotten to know the wolverine, and I find this a fascinating species to study. I have learnt how to work with data and the use of statistical analysis. This thesis has further increased my interest in ecology, and has motivated me to continue my studies.

I want to thank both my advisors Richard Bischof (NMBU), and Øystein Flagstad (NINA). Thanks to Øystein for giving me this topic, supplying me with monitoring data on wolverine, and for proof reading. A big thanks to Richard for helping me with the analytical and statistical part, writing and proof reading, and for always being patient when I came for help.

Best regards,
Ås, May 13th 2014

Espen Rise Gregersen

Abstract

Monitoring rare and elusive animals, such as large carnivores, is difficult and expensive. Non-invasive genetic sampling (NGS) has become a popular monitoring method, since it allows for spatial and genetic studies of rare and elusive species. The main objective of my research is to assess the home ranges, territoriality and potential turnover in wolverines.

The main study area for my thesis is located within the wolverine's distribution range in Southern Norway. Altogether, 2250 noninvasively scat samples were collected, which were attributable to 288 individual wolverines. NGS with GPS derived home ranges were compared to assess NGS reliability. For 32 individuals, I estimate multiple-year home ranges using NGS scat samples. Using approaches similar to resource selection function (RSF), I assessed territory exclusion (and avoidance) of conspecifics and tested for diminished or eliminated exclusion after a territory owner died.

I show a consistency between NGS and GPS derived home ranges with a high degree of overlap. Patterns in spatial arrangement of wolverine scats suggested that wolverine exclude conspecifics from their home range. General linear mixed models (GLMM) revealed that scats from male wolverines were less likely to be located inside another male's home range, and the effect is also detected for the female:female case. I did not find evidence of exclusion between the two sexes, suggesting that there is intersexual tolerance in wolverines. GLMM strongly indicate that there is diminished exclusion of conspecifics of the same sex after the territory owner dies.

A comparison with telemetry data (GPS) showed that that NGS can be a reliable method for evaluating spatial patterns in wolverine. My results are indicative of intrasexual territoriality in wolverines. Wolverines were found to begin using vacant territories after the territory owner´s death, meeting a requirement for eventual territory turnover and suggesting that wolverines are able to quickly fill gaps in the species distribution range. It is noteworthy that patterns of territoriality were pronounced enough to be detected using scat-based NGS data. This suggest that NGS is a sensitive and useful method for monitoring of elusive and rare animals.

Sammendrag

Overvåkning av sjeldne og unnvikende dyr (*e.g.* store rovdyr) med lav populasjons tetthet, store hjemmeområder og som lever på ufremkommelige steder er utfordrende og kostbart. Ikke-invasiv genetisk prøvetaking (Non-invasive genetic sampling; NGS) er en attraktiv overvåknings metode, siden metoden tillater demografiske og genetiske studier av frittgående dyr som jerven. Målet med oppgaven er å undersøke hjemmeområder, territorial adferd og potensiell utskifting av territorieholdere hos jerv.

Studieområdet for oppgaven var begrenset til fylkene Oppland og Hedmark, disse fylkene utgjør en betydelig del av jervens utbredelse i Sør-Norge. Det ble samlet inn 2250 møkk-prøver fra jerv fra 2000 – 2012, disse prøvene ble DNA-analysert og deretter genotypes til 288 unike individer av jerv. Jeg sammenligner hjemmeområder estimert både med NGS og GPS, for å teste påliteligheten til NGS estimerte hjemmeområder. For 32 individer ble det estimere flerårige hjemmeområder. Ved å bruke liknende fremgangsmåte som resurs seleksjons funksjoner (resource selection function; RSF), undersøker jeg om jerven ekskluderer individer av samme kjønn, og hva som skjer med eksklusjon etter territorieholderen dør.

Jeg fant at hjemmeområder estimert fra NGS og GPS overlappet hverandre i stor grad og overlappet var konsekvent for alle individer. Jeg identifiserte at jerv ekskluderer individer av samme kjønn fra territoriet. GLMM avdekket at møkk fra hanner hadde mindre sannsynlighet for å være lokalisert inne i en annen hanns hjemmeområde, denne effekten var også avslørt for hunn:hunn. GLMM indikerer at det er mindre eksklusjon av individer av samme kjønn etter territorieholderen er død, dette tyder på at jerven har muligheten til å fylle gap i artens utbredelse.

I denne oppgaven konkluderer jeg med at hjemmeområder basert på NGS data er pålitelige når det kommer å undersøke territorier hos jerv. Resultatene indikerer en klar eksklusjon av individer av samme kjønn, og ser en forminsket eksklusjon etter territorieholderen døde. Dette indikerer at jerven fyller gap i artens distribusjon. Det er verdt merke seg at disse territorialitet var tydelige nok til å bli oppdaget av møkk-basert NGS data. Dette indikerer at NGS er en sensitiv og nyttig metode for overvåkning av sjelden og unnvikende dyr.

Definition of select terms

Home range – "A home ranges is the area in which an animal normally lives, exclusive of migrations, emigrations and unusual erratic wanderings. Home ranges are defined and estimated without reference to the presence or absence of particular types of behaviour (e.g. defence or advertisement) or of other individuals (e.g. exclusive areas), only the presence of the animal is necessary" (Brown & Orians 1970).

Territory – "A territory has 3 essential characteristics; 1. it is a fixed area (may change slightly over a period of time), 2. acts of territorial defence by the possessor which evoke escape and avoidance in rivals so that 3. the area becomes an exclusive area with respect to rivals" (Brown & Orians 1970).

Minimum Convex Polygon (MCP) – "A MCP is a polygon with all internal angles not exceeding 180 degrees. The polygon is called minimum because it is the smallest area convex polygon that contains all location points." (Worton 1987)

Utilization distribution – "The utilization distribution is defined as the two-dimensional relative frequency distribution for the points of location of an animal over a period of time" (Van Winkle 1975)

Non-invasive genetic sampling (NGS) – "DNA analysis and genotyping of noninvasively collected DNA samples. Non-invasive sampling should be restricted to situations in which the DNA is left by behind by the animal and can be collected without disturbing the animal" (Taberlet et al. 1999).

Resource selection functions (RSF) – "Resource selection functions are defined as any function that is proportional to the probability of use by an animal" (Boyce et al. 2002; Lele et al. 2013).

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Introduction

Territoriality and territory turnover

The general currency of evolution is the animal's fitness, *i.e.* the ability one individual has to produce viable offspring and contribute to future generations (Mackenzie et al. 2001). One way for animals to increase fitness is to be territorial, *i.e.* to obtain exclusive occupancy by excluding potential competitor from the area containing resources (Brown & Orians 1970). Both individuals and groups compete for exclusive occupancy of areas of space, known as territories and home ranges (Brown & Orians 1970). There are different kinds of territories. Some animals establish general purpose territories where all activities occur (*e.g.* feeding, mating, and rearing of young); many songbird species have these kinds of territories (Mackenzie et al. 2001). In contrast there are more specialized territories, such as leks. The latter are short-lived and closely aggregated territories that occurs solely for the purpose of breeding (Jiguet et al. 2000). Lekking occurs in bird, amphibians and mammals (Mackenzie et al. 2001).

Territories are established and sometimes defended. Commonly individuals or mating pairs defend a territory (Mackenzie et al. 2001), but for social animals *e.g.* gray wolves (*Canis lupus*) can defend a common territory (Cordoni & Palagi 2008; Mech 1999). Territories are not held by the same individual(s) indefinitely, territory or spatial turnover takes place when new individuals take over territories that have previously been held by another individual (Arcese 1989). Turnover happens either when a territory owner dies due to natural or human causes and leave their home range empty, or when territory owners are unable to defend their territories and are either driven out or killed by a challenger/competitor (Arcese 1987; Arcese 1989). The latter is often called territory takeover.

Wolverine spatial ecology and conservation

The wolverine (*Gulo gulo*) is a rare and elusive animal with solitary and territorial behaviour. Wolverine in Scandinavia show intrasexual territoriality, male home ranges are usually totally exclusive and female home range are either exclusive or with little overlap (Persson et al. 2010). Wolverines occur at low densities due to large home ranges size ($100 - 2000 km^2$) and territorial behaviour (Aulagnier et al. 2009). Previous studies from south-central Norway found that male home ranges (663 ± 194 km^2 (Landa et al. 1998); mean 669 km^2 (Persson et al. 2010)) were significantly larger then female home ranges (274 ± 122 km^2 (Landa et al. 1998); mean 170 km^2 (Persson et al. 2010)), and that male home ranges encompass parts of up

to five female home ranges (Persson et al. 2010). Home ranges of male wolverines overlap with the home ranges of a few females, but there is no overlap between individuals of the same sex (Hedmark et al. 2007). This suggests that home range overlap for wolverine is most likely explained by intra-sexual tolerance and kinship (Persson et al. 2010).

Wolverines are sensitive to human disturbance, selecting den-sites and home ranges in areas without human disturbance and infrastructure (May et al. 2006). Wolverines are believed to be particularly selective when it comes to choosing reproductive den-sites. Magoun and Copeland (1998) found that with few exceptions wolverine dens have been located in alpine, subalpine, taiga or tundra habitats. One of the most important requirement for den-site selection seems to be a deep snow bank that provide stable snow conditions for winter and spring (Copeland et al. 2010; Magoun & Copeland 1998; May et al. 2012).

Wolverines are opportunistic predators and facultative scavengers that often depend on scavenging (Mattisson et al. 2011; van Dijk et al. 2008). However wolverines are also polyphagous, switching between different food sources when one prey becomes scarce (Landa et al. 1997). Wolverines are known to scavenge kills of wolves (van Dijk et al. 2008) and lynx (*Lynx lynx*) (Mattisson et al. 2011) in Scandinavia. A diet shift has been observed in wolverines following the recolonizationby wolves (van Dijk et al. 2008).

Information about territory turnover in wolverine is limited. what is known comes from studies of different but related topics *e.g.* wolverine dispersal (Vangen et al. 2001). Wolverine is found to be capable of filling gaps in the current species distribution (Vangen et al. 2001). When a territory becomes vacant there will be reduced or eliminated exclusion of conspecifics, which could eventually lead to territory turnover.

The current national management goal for wolverine in Norway is set to 39 annual reproductions, *i.e.* number of females that reproduce (Stortingsmelding nr 15 (2003-2004)) this goal is not treated as an upper or lower limit but as absolute targets (Bischof et al. 2012). During the last decade, the estimated number of annual reproductions has exceeded the national goal, varying between 50-70 reproductions during 2009 – 2012 (Brøseth & Tovmo 2013) and management has been unable to reach their management goals (Bischof et al. 2012).

Monitoring

Monitoring challenges

Wolverines are challenging to monitor; they have a wide distribution range, low population density, and inhabit remote areas that are hard to access (Aulagnier et al. 2009). This makes

wolverines hard to find and observe, and studying them expensive (Magoun et al. 2011). GPS and VHF have been used for monitoring of individual wolverines in Norway (May et al. 2008; Odden et al. 2012), these methods require that the animal is captured and marked with a GPS collar or VHF implant. There are some advantages and disadvantages with monitoring wolverines with GPS and VHF. GPS collars are expensive and in some cases have a short lifespan, mostly depending on size and battery capacity (Mattisson et al. 2010). Therefore store-on board GPS collars that automatically drop-off when the battery expires have an advantage because they can be reused (Mattisson et al. 2010). VHF implants are more affordable and have a longer lifespan, but here much fieldwork is needed because for every position you need to physically go out and track the animals (Schmidt 2008).

Non-invasive genetic sampling

Non-invasive monitoring methods have become an affordable alternative to traditional methods, such as telemetry. DNA samples from wildlife can be obtained through (1) destructive sampling (the animal is killed) (2) capture and non-destructive collection of a tissue or hair sample, and (3) non-invasive sampling, which is when the DNA source is left behind by the animal (Taberlet et al. 1999). Non-invasive genetic sampling (NGS) uses noninvasively collected DNA samples from scat, hair, feathers etc. to identify the individual and sex of an animal (Taberlet et al. 1999; Waits & Paetkau 2005). NGS monitoring is being increasingly used in wildlife management in many countries around the world. NGS has many different applications *e.g.* detecting rare species (Romain-Bondi et al. 2004), estimating population size and sex ratio (Bonesi et al. 2013; Kohn et al. 1999; Taberlet et al. 1997), evaluating social structure (Garnier et al. 2001), genetic diversity and gene flow (Goossens et al. 2005), detecting hybridization (Adams et al. 2003), detecting disease (Whittier et al. 2004), detecting diet items (Taberlet & Fumagalli 1996), and predator identification of kills (Ernest et al. 2002). See Waits and Paetkau (2005) for a review.

NGS monitoring has been shown to be a suitable method for monitoring wolverines. DNA from scat (Flagstad et al. 2004; Hedmark et al. 2004) and hair (Magoun et al. 2011) has been used for both sex and individual identification of wolverines, which in turn has led to estimates of demographic parameters and relatedness (Flagstad et al. 2004; Hedmark & Ellegren 2007).

Potential of NGS to evaluate spatial patterns

The potential for NGS to evaluate spatial patterns has been mentioned by review articles on NGS (Kohn & Wayne 1997; Kohn et al. 1999). A study on Eurasian lynx in Białoweiża

Primeval Forest, Poland, compared NGS and VHF derived home ranges to evaluate the reliability of NGS for assessing spatial patterns (Davoli et al. 2012). With NGS data from hair snaring and VHF data from the same individuals, Davoli et al. (2012) found an average overlap of 86.4 % between NGS and VHF derived home ranges.

A study by Vili et al. (2013) evaluated turnover rate for the Imperial eagle (*Aquila heliaca*) in north-east Hungary. By collecting and genotyping shed feathers, this study revealed a higher turnover rate than suggested by studies using traditional methods (*i.e.* intensive field surveys) and studies on other raptor species.

Research objective and questions

The main objective of this study is to assess home ranges, territoriality and spatial turnover for the wolverine with NGS data in southern Norway. Wolverines are an important predator on domestic sheep (*Ovis aries*) in Norway (Landa et al. 1997), and has been subject to human persecution and poaching (Persson et al. 2009). It is important to study wolverines in Norway, gathering information about the wolverine territorial behaviour and determine what happens after the territory owner dies. This will provide valuable knowledge about wolverine territory dynamics and can be a stepping stone for more research on territory turnover in the future. More knowledge about territory dynamics can improve the management and conservation of wolverines, and also give managers and stakeholders (*e.g.* farmers) guidelines on how to avoid heavy predation from wolverine on domestic animals, and this can in turn alleviate human persecution and poaching of wolverine.

The main objective of my research is to assess the home ranges, territoriality and potential turnover in wolverines, by examining non-invasive monitoring data that have been collected over many years. Therefore, I ask three specific questions, shown with associated predictions:

Q1. Does NGS yield reliable information about spatial patterns?

   P1. There is a substantial overlap between wolverine home range estimates derived from NGS and GPS data.

Q2. Is there evidence of territory exclusion of conspecifics?

   P2. Scats of conspecifics found in the neighbourhood are less likely to be located within a focal individual's home ranges than predicted by chance.

   P3. Exclusion or avoidance between same sex individuals is expected to be more pronounced than between individuals of the same sex.

   P4. Evidence of territoriality will be strongest when both the focal individual and the neighbour are males.

Q3. Is there evidence of diminished or eliminated territory exclusion of conspecifics following the death of the territory owner?

    P5. Greater selection of the home range area by neighbouring individuals after the territory owner's death.

    P6. Conspecifics found in the neighbourhood are more likely to be located within a focal individual's home range after the focal individual has died.

Materials and methods

Study system

The wolverine is the largest terrestrial mustelid (Aulagnier et al. 2009), and has a circumpolar distribution, corresponding with the Boreal zone of the northern hemisphere and are rarely found below 60°N (In:Abramov et al. 2009). Wolverines are well-equipped for colder climates having thick fur with long hairs. Wolverines have big paws that assist movement in powdery snow (Aulagnier et al. 2009) and can dig tunnels in hard packed snow (Brøseth et al. 2012).

Little is known about the social structure of wolverines. They are solitary animals that keep large territories (Brøseth et al. 2012). The wolverine has a polygamous mating system and breeding pairs have overlapping territories (Hedmark et al. 2007). Hedmark et al. (2007) showed that males produced offspring with more than one female in a single year and females often reproduced with the same male in subsequent breeding years. Females sometimes change partners, as a consequence of turnover of territory-holding males in the area (Hedmark et al. 2007). Usually wolverines breed at the end of winter (Aulagnier et al. 2009) and on account of delayed embryo-development cubs are born during February – March (Brøseth et al. 2012).

The wolverine feeds on small and large prey, and wild and domesticated animals in winter time (Aulagnier et al. 2009). Landa et al. (1997) found that although small rodents constituted the main factor explaining variation in cub numbers, the main prey during the denning period was reindeer (*Rangifer tarandus*). Hares (*Lepus timidus*) accounted for a significant part of the diet during the denning period (Landa et al. 1997). In Norway wolverine is an important predator on sheep. However, Landa et al. (1997) found no evidence that sheep are an essential part of the wolverine's diet. Lambs are more vulnerable to wolverine predation then adult sheep (Landa et al. 1999).

Study area

The main study area was located in south-central Norway (62°N 10°E) (Figure 1b), mainly the counties of Oppland and Hedmark. This area makes up a substantial part of the wolverines distribution range in Southern Norway. The main study area cover approximately 41487 km^2 of land (Figure 1b), encompassing remote mountains in the west to more accessible forests in the east. This is a region with intense open-range sheep grazing in the summer (June - September; May et al. 2008). The mountain ranges mainly consists of deep valleys and tundra plateaus with peaks up to 2000 - 2286 m (May et al. 2008; May et al. 2012). Forest areas are made up of hills or low mountains and wide valleys; mixed forests of birch, spruce and pine

are scattered, intermixed with open bogs and crop lands (May et al. 2008; May et al. 2012). Snow is present in the study area from October/November until May/June depending on elevation (May et al. 2008; May et al. 2012). Infrastructure is mainly concentrated at lower elevations, with recreational cabins and private roads at higher elevations (May et al. 2012). For a detailed description of the study area see Brøseth et al. (2010); Landa et al. (1998); May et al. (2006); May et al. (2008); May et al. (2012).
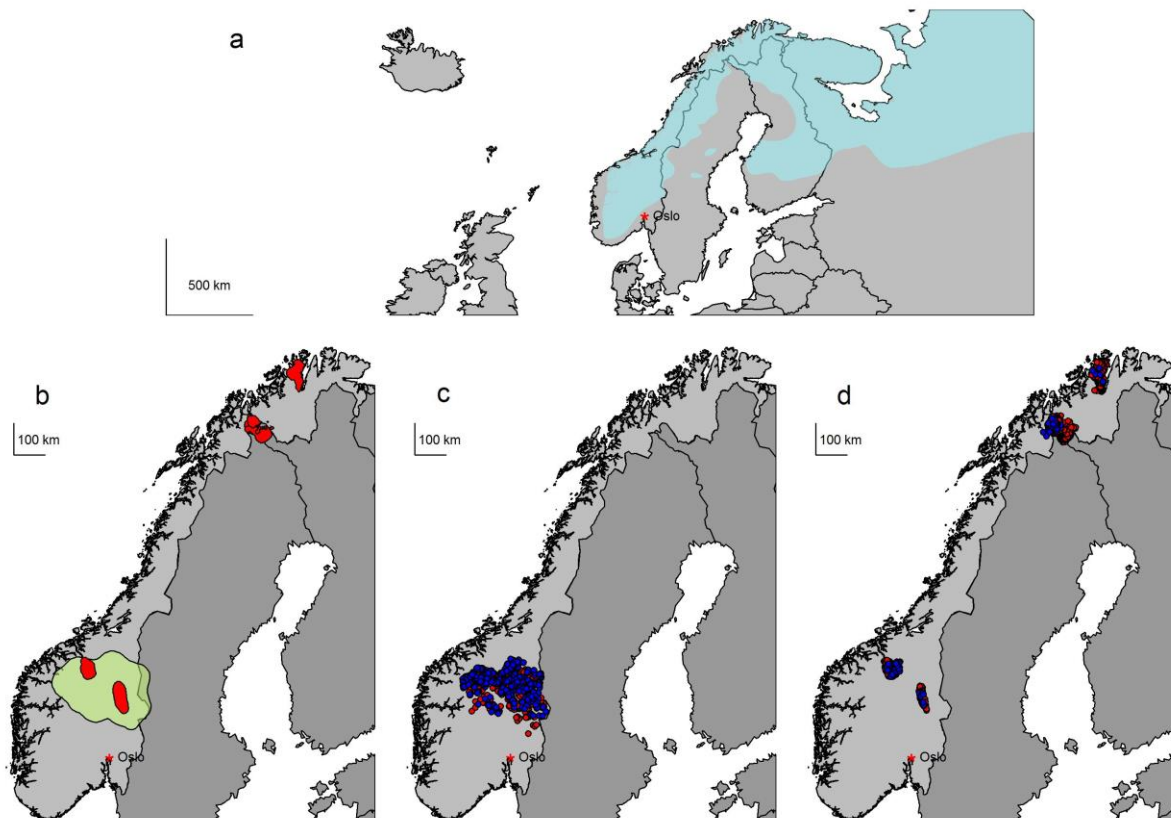
Figure 1: *(a) Map of the wolverine range in Fenoscandia (blue, IUCN). (b) Main study area (yellow) and areas with both GPS and NGS data (red). (c) Locations of male (blue) and female (red) scats with individual identification in the main study area, and (d) GPS (red) and NGS (blue) spatial points spread across Norway.*

Data collection

NGS data collection and genotyping

Altogether, 2250 faeces samples, with wolverine as the suspected host, were collected in the main study area in south-central Norway from 2000 – 2012. In total, 1422 faecal samples were successfully genotyped, representing 288 unique wolverine individuals.

Most faecal samples were collected during snow tracking between February and June. Some sampling also occurred during October to January for each season. During the first sampling year additional faecal samples were collected between July and October on bare ground (Flagstad et al. 2004). GPS position, date, and time of the sampling event were recorded for each faecal sample.

The collection of the faecal samples was performed by the Norwegian nature inspectorate (Statens Naturoppsyn SNO). The DNA analyses and the subsequent individual and sex determination were performed in the DNA laboratory at the Norwegian Institute of Nature Research (NINA). This project is part of the National monitoring program for wolverines in Norway.

GPS data collection

The GPS data used in my thesis were collected by the Scandinavian lynx project (Scandlynx, http://scandlynx.nina.no/, N=4) and The Norwegian Wolverine project (http://www.jerv.info/, N=2) (Table 1). I used GPS data from six male wolverines where I had GPS data over a period of one – three years (Table 1). Of the 6 wolverines, 1 survived to the end of the study period, 4 died and the fate of one is unknown because the GPS collars battery expired in august 2011 (Table 1).

Wolverines were immobilized by darting from helicopter and from ground with a mixture of ketamine and medetomidine (Mattisson et al. 2010; Mattisson 2013) and equipped with GPS collars. The 4 wolverines from the Scandlynx project used 20-channel store-on-board GPS collars (Televilt Prosrec C300, TVP positioning AB, Lindesberg, Sweden) which gave 7 positions per day and the GPS collars were programed to drop-off when the battery expired (Mattisson et al. 2010). The 2 wolverines from the Norwegian Wolverine project were marked with GPS radio collars (Televilt Prosrec 300; Lotek 3300SL GPS collars) which provided 7 – 15 positions per day, these collars had a lifespan of 5 months and would automatically drop off the animal (May et al. 2008).

A separate dataset of NGS spatial data was used for the NGS and GPS comparison, since there were insufficient GPS data available from the main study area at the same time period as NGS collection. Table 1 shows the NGS spatial data used in comparison of NGS and GPS home ranges. NGS data from six individuals collected between 2002 and 2013 were included in this analysis. Two of these individuals (Ind71 and Ind90) were located inside the main study area while the rest were scattered across the northern part of Norway (*i.e.* Finnmark and Troms) (Table 1).

Table 1: *Data for individuals that were used in NGS and GPS home range comparison.*

GPS-ID	DNA-ID	Sex	Status	GPS data		NGS data	
				n	Years	n	Years
S49-05 [2]	Ind90	Male	Dead	587	2005 − 2005	45	2002 − 2011
S34-03 [2]	Ind71	Male	Dead	153	2004 − 2004	10	2002 − 2008
J1006 [1]	Ind2273	Male	Dead	3870	2010 − 2012	7	2009 − 2012
J1104 [1]	Ind2331	Male	Alive	3179	2011 − 2013	20	2010 − 2013
J1105 [1]	Ind2044	Male	Unknown	1083	2011 − 2011	24	2008 − 2011
J1103 [1]	Ind2282	Male	Dead	2433	2011 − 2012	13	2011 − 2012

[1] = GPS data from the Scandinavian Wolverine project.   [2] = GPS data from the Norwegian Wolverine project.

n = number of relocations in total.

Data analysis

All statistics were performed in the statistical programming environment R 3.0.3 (R Development Core Team 2011) and functions contained in various R packages.

Q1. NGS comparison with GPS

To determine degree to which the spatial configuration of scat samples associated with an individual reflect area use, I compared NGS with GPS spatial data. For this comparison, I choose the 95 and 50 % kernel contour for all 6 individuals both visually and quantitatively. First, two multiple-year home range were estimated for all individuals, one from GPS data and one from NGS data (Table 1) using R function "kernelUD" (package "adehabitat" (Calenge 2006)). All wolverine GPS spatial points that were not inside Norway and not in areas where scat sampling had occurred was excluded from the study, to ensure that the same spatial extent of monitoring was considered for both GPS and NGS. Home range overlap was estimated using two home range contours were used; 95 and 50 % contour. To determine the similarity of the two home ranges they were compared using the R function "kerneloverlap" (package "adehabitat" (Calenge 2006)). Fieberg and Kochanny (2005) reviewed the different indices that this function uses to estimate overlap, the method "HR" is the simplest method and only considers the spatial domain of the individuals and ignores the utilization distribution (probability density). Home ranges are overlaid, and per cent overlap may be used to quantify the degree of fidelity/similarity.

Data preparation for GLMM

A list of individuals with ≥ 5 relocations and a known date of death was compiled (*i.e.* "focal individuals"). Kernel home range were calculated for all focal individuals (Figure 2b), this was estimated using the R function "kernelUD" (package "adehabitat" (Calenge 2006)). All home

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ranges were inspected and was checked for outliers and potential problem years (years where the individual was far from the 95 % kernel). If there were outlier or problem years for an individual this year was removed from the dataset. Home range size (area) was estimated for all focal individuals with the R function "kernel.area" in the statistical package "adehabitat" (Calenge 2006).

To test territory exclusion by conspecifics, I adapted approaches from resource selection functions (Boyce et al. 2002). Resource selection functions (RSF) are defined as any function that is proportional to the probability of use by an animal (Boyce et al. 2002; Lele et al. 2013). RSF are typically used for habitat selection studies (Lele et al. 2013), and have been used for wolverine studies in Norway (May et al. 2008; May et al. 2010; May et al. 2012). By establishing a baseline from randomly generated spatial points I could determine if scat locations of neighbour individuals had a higher or lower probability of being inside the focal individual's home range than predicted by chance (baseline).

A buffer-area with radius 75 km was added to all focal individual home ranges (Figure 2b) and all individuals that had spatial points located inside this buffer-area became part of the selection (i.e. "neighbours") for that specific focal individual (Figure 2c). A Minimum Convex Polygon (MCP) was calculated using all spatial points from neighbour individuals that was inside the buffer area (Figure 2c). Random spatial points was simulated for each of the neighbour individuals, this means that for every real spatial point we generate one random spatial point that is a copy of the real point expect that the coordinates was randomly selected from the MCP (Figure 2d). For every scat location of a neighbour individual, I generated one simulated location via random spatial sampling within the MCP. For each point (real and random) I determined whether it fell within or outside the focal individual's home range (95% and 50% kernel contour) (Figure 2c & 2d).
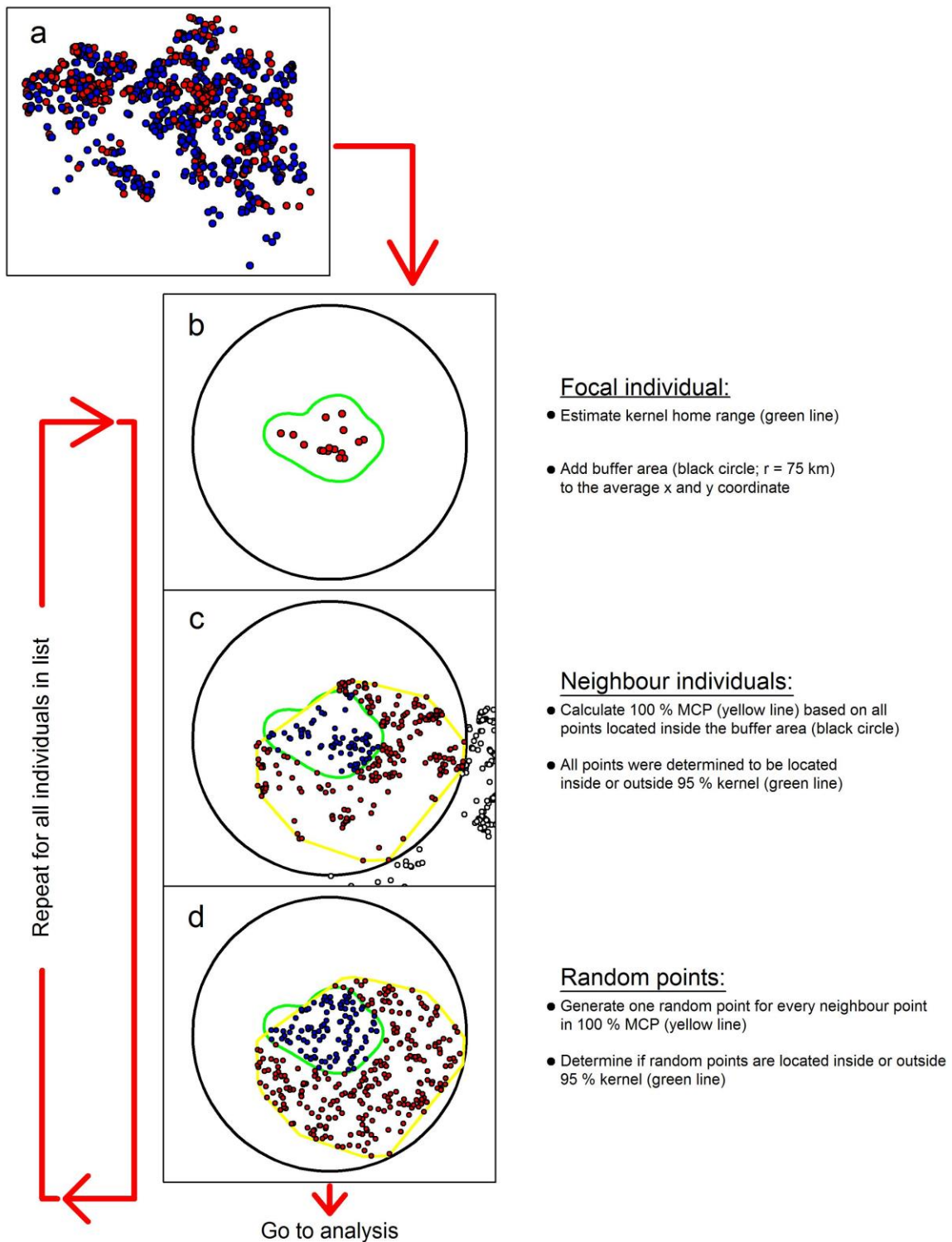
Figure 2: *Schematic illustrating the main steps involved in data preparation for GLMM. These steps were performed for all focal individuals.*

Q2. Territory exclusion of conspecifics

To test if wolverine excluded conspecifics, I used Generalized Linear Mixed Effects (GLMM) regression with a logit link (logistic regression). R function "glmer" (package "lme4" (Bates et al. 2013)) and only included spatial points from focal individual collected 1-3 years before death. I used probability of being inside 95 % kernel home range as the response, real/random points and sex (neighbour individuals) and sex (focal individuals) as the fixed effects, and individual ID for focal and neighbour individuals as the random effect. I selected the random effects structure using ANOVA (Analysis of Variance) test and I used the R function "Dredge" (package "MuMIn" (Barton 2013)) to select fixed effects. The reason "Dredge" was used for model selection was because I had no reason not to consider any particular covariate combination, and therefore I used a "brute force" approach (fitting and comparing all possible combinations of fixed effects under the most complex model considered).

Q3. Territory exclusion following the death of the territory owner

To test spatial turnover in wolverines after the territory owner died, I used an almost identical approach as for Q2, with the addition of another predictor/fixed effect *i.e.* before/after death and allowing for all possible interactions between predictors in the most complex model considered. This model was fit to a dataset including records 3 years before and after death of each focal individual.

Results

General summary

The main dataset for this thesis is the NGS scat data from Oppland and Hedmark County sampled from 2000 – 2012, after data preparation the dataset contains the GPS positions of 1389 faecal samples. Among these samples there are 282 unique individual wolverines, 146 males and 136 females. Among those 282 individuals 32 (17 males, 15 females) met the conditions to be included in the analysis as focal individuals. Note that NGS home ranges are based on multiple years of relocation data and not always the same number of years, this makes comparisons of home ranges difficult (Figure 3).

Males home ranges had a mean size 2108 ± 286 km^2 with a core area of mean size 544 ± 82 km^2, and female home ranges had a mean size 1050 ± 249 km^2 with a core area of 266 ± 64 km^2 (Figure 4). Male and female home range sizes were significantly different ($t = 2.79$, d.f $= 29.9$, $p < 0.01$). Sample size for multiple-year home ranges varied from $5 - 24$ spatial points (Figure 4), collected over a period of $1 - 7$ years (Figure 3 and 4).
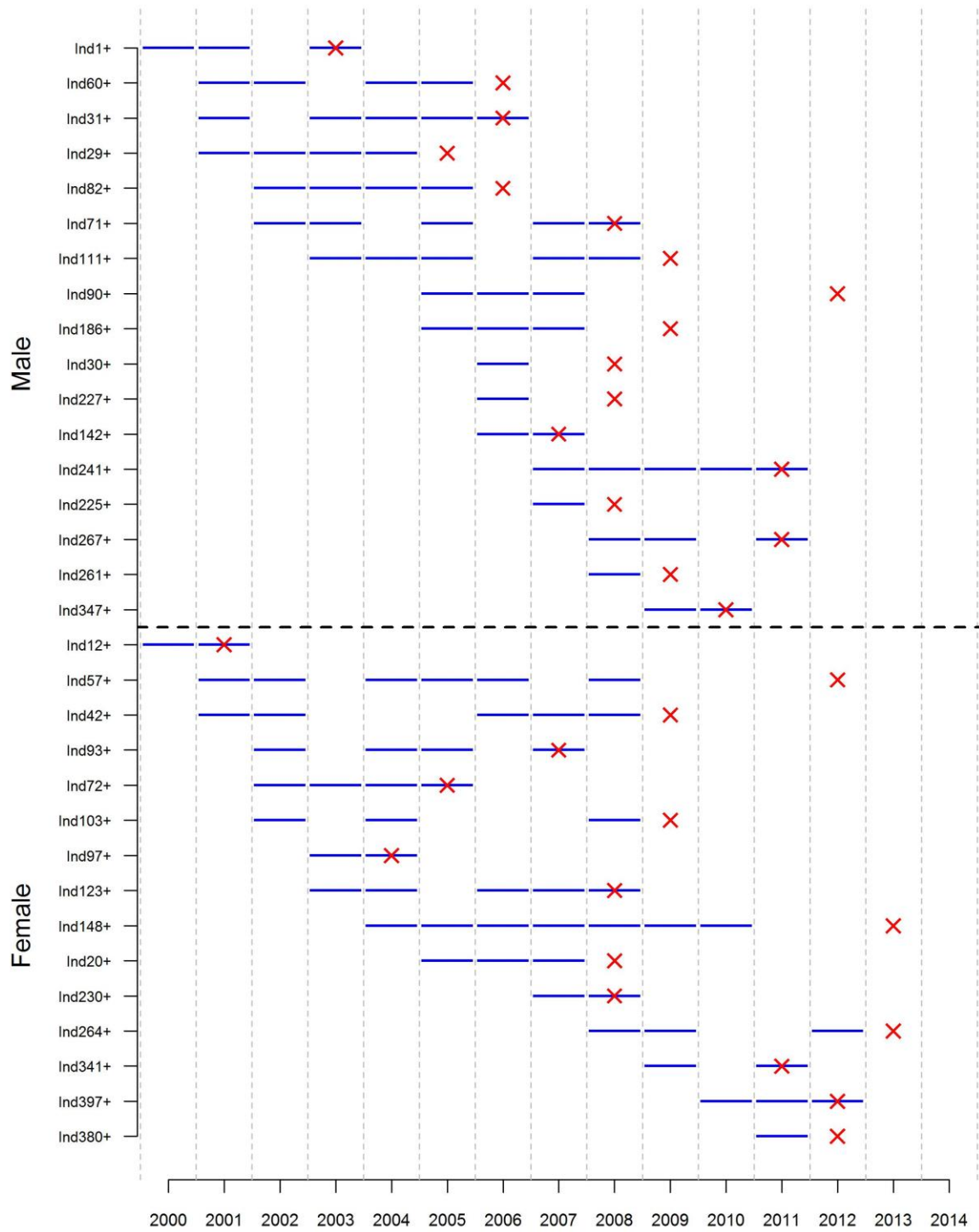
Figure 3: *Temporal scope of NGS data used to calculate home ranges for each focal individual. Each row represents the detection history of one focal individual. Years with at least one genetic detection of the focal individual are marked with blue segments and the year in which the individuals died is marked with a red "x".*
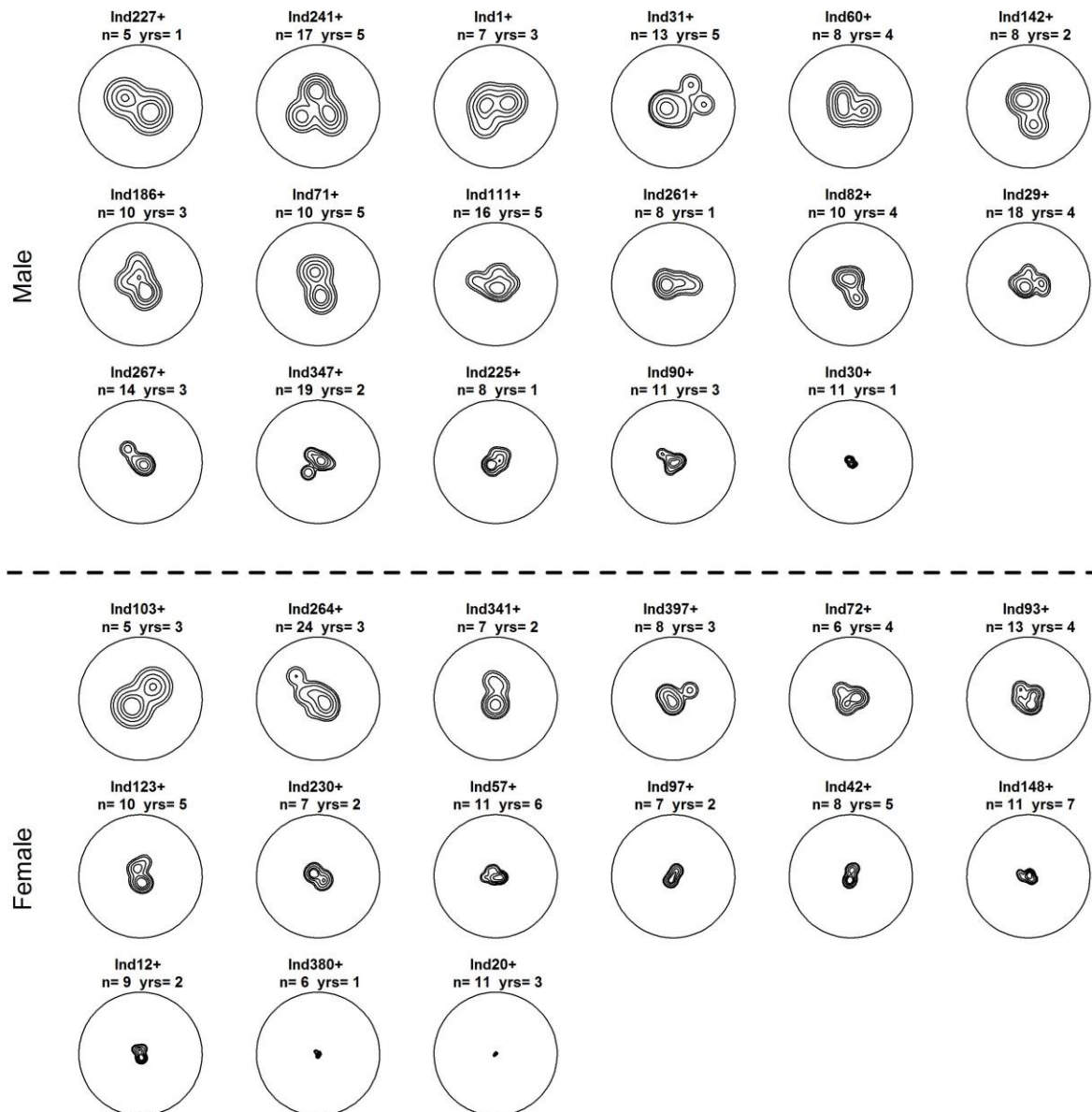
Figure 4: *Kernel home range estimates derived from scat-based non-invasive genetic sampling for all focal individuals included in the study, with buffer area (r = 75 km). 25%, 50%, 75%, 90% and 95% contour lines are included for every focal individual. Numbers of relocations (n) and numbers of years (yrs) that are used to estimate kernel home range.*

Q1. NGS comparison with GPS

Visual and quantitative comparison revealed a high overlap between NGS and GPS derived home ranges (Table 2, Fig. 5). NGS derived home ranges (95% kernel) were on average 1.5 times larger than GPS home ranges (Table 2).

Table 2: *Area estimates for non-invasive genetic sampling (NGS) and GPS kernel home ranges, and GPS-NGS overlap estimates for 95 and 50 % home range contours, in addition to mean, SEM and median for all variables.*

	NGS Area (km^2)		GPS Area (km^2)		NGS covers GPS		GPS covers NGS	
ID	95 %	50 %	95 %	50 %	95 %	50 %	95 %	50 %
Ind90	2772	733	1885	529	0.76	0.12	0.52	0.09
Ind71	2591	717	2476	663	0.82	0.64	0.78	0.59
Ind2273	3190	792	1931	271	0.83	0.84	0.50	0.29
Ind2331	593	159	1101	269	0.50	0.38	0.93	0.65
Ind2044	1686	272	1441	412	0.61	0.44	0.52	0.67
Ind2282	3157	584	666	154	1.00	0.93	0.21	0.25
Mean	2332	543	1583	383	0.75	0.56	0.58	0.42
SEM	413	108	265	77	0.07	0.12	0.10	0.10
Median	2681	651	1663	341	0.79	0.54	0.52	0.44
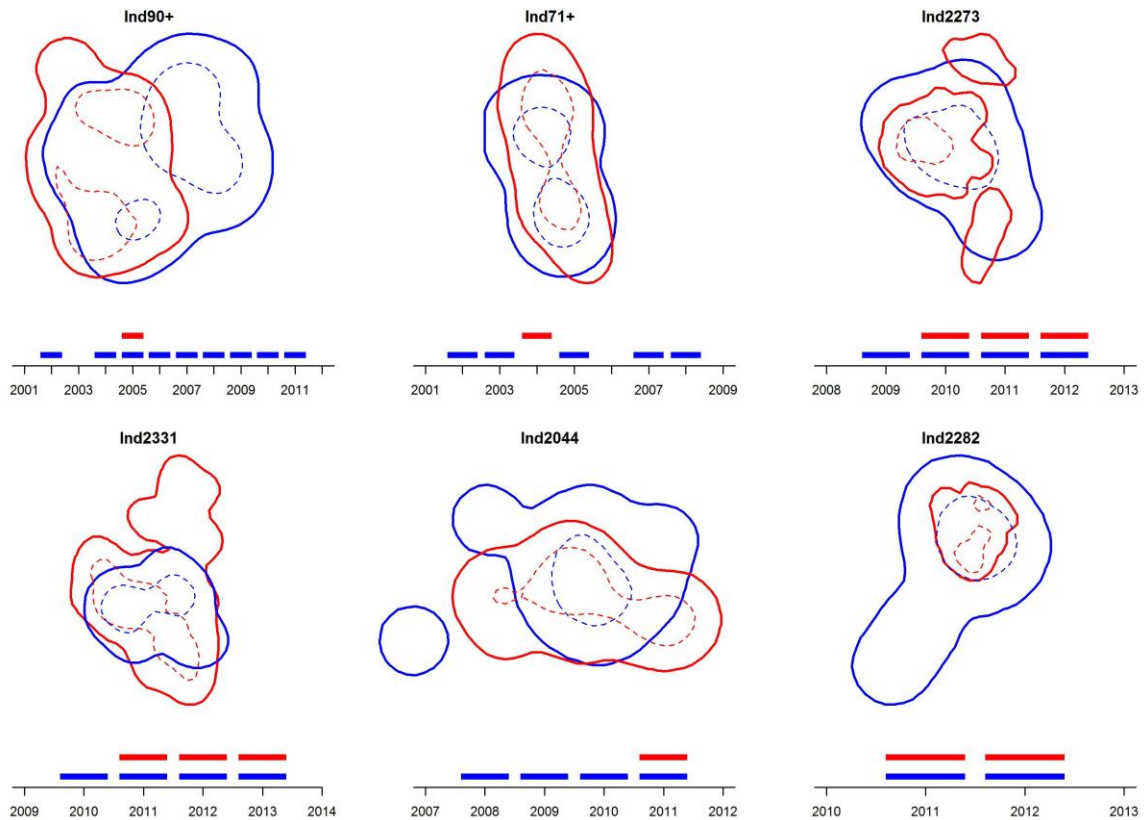
Figure 5: *Comparison of GPS (red lines) and NGS (blue lines) derived home ranges, two home range contour were compared for each individual, 95% (solid line) and 50% (dotted line). Temporal scope of spatial data for GPS (red segments) and NGS (blue segments) is displayed below each individual's home range plot.*

Q2. Territoriality

The most complex model considered had the lowest AICc, by a wide margin (ΔAICc to the next best model = 17.6, Table 3). The most complex model include all possible interactions

between the fixed effects; real or simulated points, sex (Focal individual), and sex (neighbour individual).

Table 3: *Comparison of generalized mixed effect models for assessing territoriality in wolverines. Only the intercept model (y~1) and candidate models with $\Delta AIC_c < 25$ are shown.*

#	Model[a]	d.f	LogLik	AIC_c	ΔAIC_c	w_i
1	~ real * f.sex * n.sex	12	-2953.5	5931.1	*0.00*	1
2	~ real + f.sex * n.sex	9	-2965.3	5948.7	17.57	0
3	~ f.sex * real + n.sex * f.sex	10	-2965.1	5950.3	19.20	0
4	~ n.sex * real + n.sex * f.sex	10	-2965.2	5950.4	19.26	0
5	~ n.sex * real + n.sex * f.sex + f.sex * real	11	-2965.0	5951.9	20.84	0
6	~ real + f.sex	7	-2971.0	5955.8	24.73	0
7	~ 1	5	-2982.1	5974.2	43.13	0

[a] = Fixed effects: real = real or simulated, f.sex = focal individuals sex, and n.sex = neighbour individual sex

All models was run with the same random effect structure; (1 | focal ID) + (1 | neighbour ID).

GLMM revealed that scats from both male and female wolverines were less likely to be located inside the home range of a same-sex individual (negative coefficient of selection, Table 4; Figure 6). In cases where the neighbour individual's sex was different from that of the focal individual, the selection coefficient was either not significantly different from 0 (male:female) or it was positive (female:male, Figure 6). Although female:female were slightly lower than male:male, there were detected no significant difference between the two same-sex pairings (Figure 6).

Table 4: *Parameter estimates for the top GLMM model. One level of each categorical variable serves as the contrast ($\beta = 0$) for the remaining levels for that variable (Focal sex = Female; Neighbour sex = Female; Real = FALSE).*

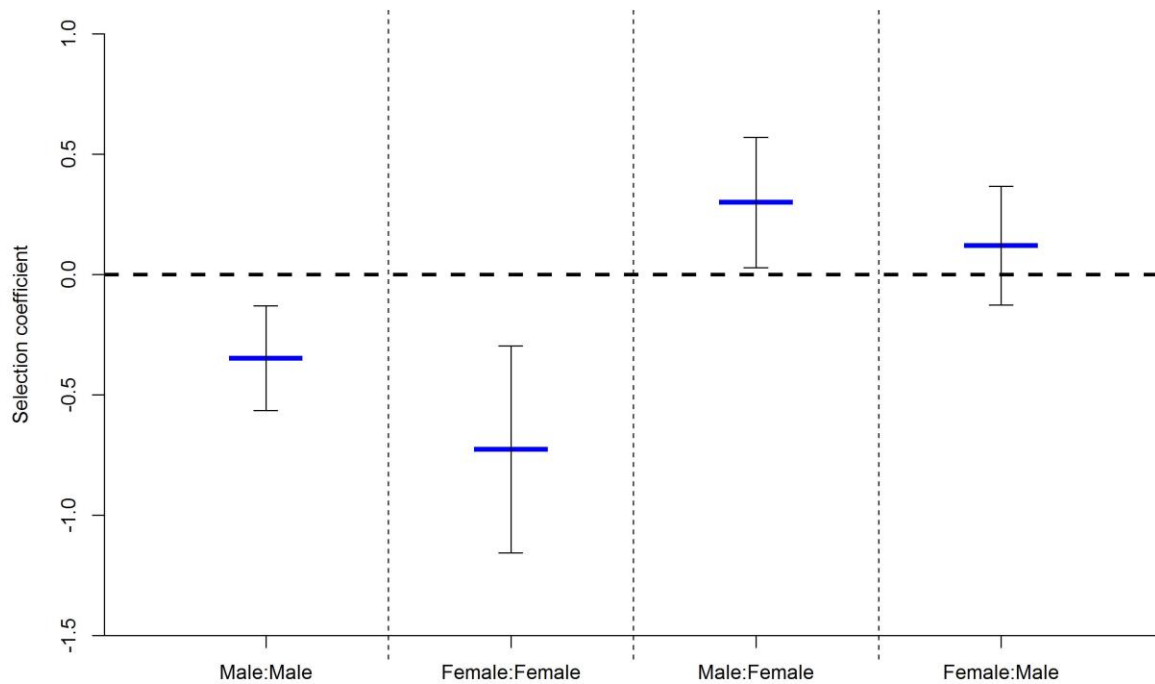| Model term	Parameter value (β)	SE	z-value	p-value
(Intercept)	-2.59	0.28	-9.39	< 0.001
Real TRUE	-0.73	0.22	-3.31	0.009
Neighbour sex Male	-0.13	0.18	-0.68	0.494
Focal sex Male	0.72	0.36	2.01	0.044
Real TRUE: Neighbour sex Male	1.03	0.26	3.96	< 0.001
Real TRUE: Focal sex Male	0.85	0.25	3.35	< 0.001
Neighbour sex Male: Focal sex Male	0.13	0.21	0.64	0.522
Real TRUE: Neighbour sex Male: Focal sex Male	-1.49	0.31	-4.84	< 0.001

Figure 6: *Log-odds of scat from neighbours to be located inside the focal individual's home range compared to chance (dotted line). Values below the dotted line indicated avoidance or exclusion and above the dotted line indicates tolerance or attraction. All pairings are arranged as focal:neighbour.*

Q3. Reduced avoidance following the death of the territory owner

The most complex model considered had the lowest AICc, by a wide margin (ΔAIC$_c$ to the next best model = 4.18, Table 5). The most complex model include all possible interactions between the fixed effects; real/ simulated points, before/after focal individuals death, sex (Focal individual), and sex (neighbour individual).

Table 5: *Comparision of generalized mixed effect models for assessing territory exclusion before and after focal individuals death. Only the intercept model (y~1) and candidate models with $\Delta AIC_c <10$ are shown.*

#	Model[a]	d.f	LogLik	AIC_c	ΔAIC_c	w_i
1	~ real*death*f.sex*n.sex	18	−5601.2	11238.5	*0.00*	0.777
2	~death*real+(death+real)*f.sex*n.sex	15	−5606.3	11242.6	4.18	0.096
3	~death*real*f.sex+(death+real)*f.sex*n.sex	16	−5606.0	11244.0	5.54	0.049
4	~death*real*n.sex+(death+real)*f.sex*n.sex	16	−5606.1	11244.3	5.81	0.042
5	~death*real*(n.sex+f.sex)+(death+real)*f.sex*n.sex	17	−5605.8	11245.7	7.22	0.021
6	~ 1	3	−5634.4	11274.8	36.37	0

[a] = Fixed effects: real = real or simulated, death = before/after focal ID death, f.sex = focal individuals sex, and n.sex = neighbour individual sex.

All models was run with the same random effect structure; (1 | focal ID) + (1 | neighbour ID).

GLMM revealed that scats from neighbour individuals were more likely to be located inside the home range of another individual of the same sex after that individual had died (Table

6; Figure 7). There was no significant effect of death when the neighbour and focal individual were of different sex.

Table 6: *Parameter estimates for the top GLMM model. One level of each categorical variable serves as the contrast ($\beta = 0$) for the remaining levels for that variable (Focal sex = Female; Neighbour sex = Female; Real = FALSE; Focal death = TRUE).*

| Model term	Parameter value (β)	SE	z-value	p-value
(Intercept)	-2.63	0.29	-9.25	< 0.001
Real TRUE	-0.73	0.22	-3.31	< 0.001
Focal death TRUE	-0.33	0.22	-1.51	0.130
Focal sex Male	0.74	0.37	1.99	0.047
Neighbour sex Male	-0.14	0.18	-0.78	0.441
Real and Focal death TRUE	0.93	0.31	2.98	0.002
Real TRUE: Focal sex Male	0.85	0.25	3.35	< 0.001
Focal death TRUE: Focal sex Male	0.18	0.25	0.70	0.485
Real TRUE: Neighbour sex Male	1.03	0.26	3.96	< 0.001
Focal death TRUE: Neighbour sex Male	0.22	0.27	0.79	0.428
Focal and Neighbour sex Male	0.13	0.21	0.63	0.527
Real and Focal death TRUE: Focal sex Male	-0.70	0.36	-1.94	0.052
Real and Focal death TRUE : Neighbour sex Male	-1.14	0.39	-2.92	0.003
Real TRUE: Focal and Neighbour sex Male	-1.49	0.31	-4.84	< 0.001
Focal death TRUE: Focal and Neigbour sex Male	0.01	0.32	0.02	0.981
Real and Focal death TRUE: Focal and Neighbour sex Male	1.39	0.45	3.07	0.002
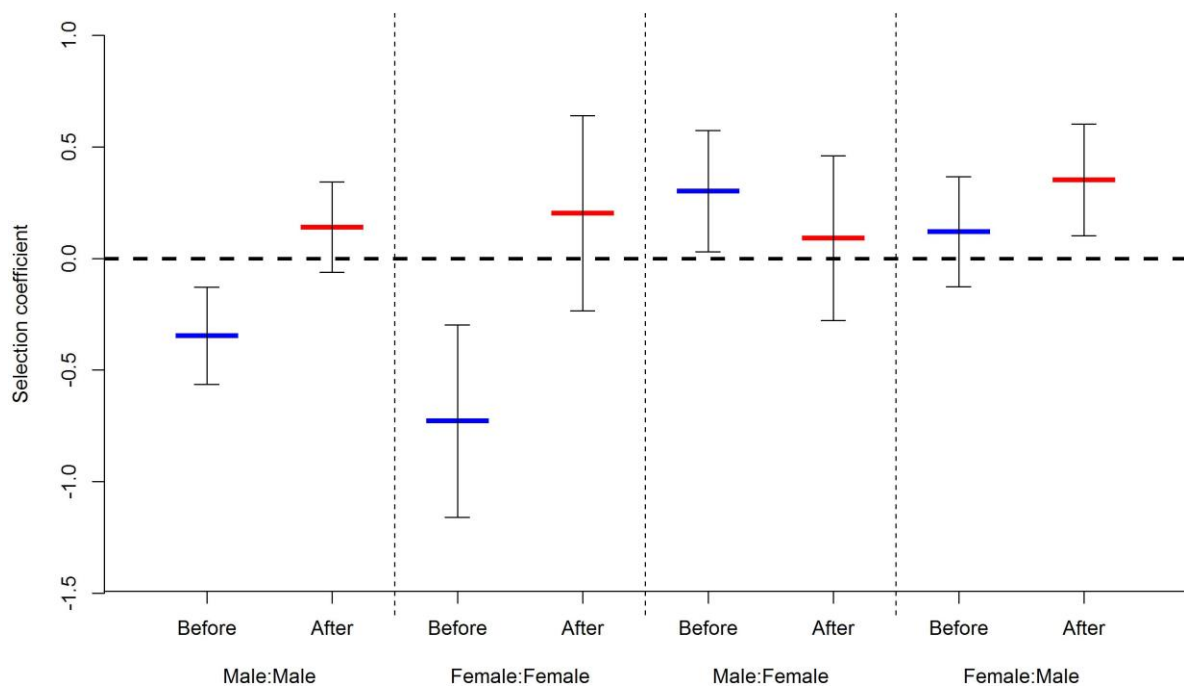
Figure 7: *Log-odds of scat from neighbours to be located inside the focal individual's home range compared to chance (dotted line), before (blue segment) and after (red segment) focal individual's death. Values below the dotted line indicated avoidance or exclusion and above the dotted line indicates tolerance or attraction. All pairings are arranged as focal:neighbour.*

Discussion

This thesis revealed patterns that suggest that conspecifics of the same sex are excluded from wolverine territories and that this effect is reduced after the territory owner dies. It is particularly noteworthy, that these patterns were pronounced enough to be detected using scat-based NGS data. Comparison of NGS and GPS derived home ranges, showed that NGS data can be used to evaluate territoriality and spatial behaviour of the wolverine.

Territoriality

The results of the analyses indicate intra-sex avoidance/exclusion and inter-sex tolerance or even affinity in area use by wolverines (P2, P3). I did not detect a significant difference between males and females in terms of avoidance/exclusion of same-sex individuals (P4). The results are consistent with what has previously been reported about wolverine territorial behaviour. Home range choice for solitary carnivores is determined by different resources for each sex; females are expected to select home ranges depending on food resources availability and males are expected to select home ranges depending on the number and distribution of females (Persson et al. 2010). Male home ranges overlap with one or more female home ranges (Persson et al. 2010). This thesis did not find evidence of exclusion between the sexes. This would be an interesting study for the future, looking at and assessing interactions between male and female wolverines using NGS scat data. The data set used in this thesis has the potential to addressing such interactions.

What happens after focal individual dies? (Turnover or gap-filling)

I identified patterns that neighbouring individuals are more likely to enter/use another territory following its owner's death (P5). This pattern was only detected for conspecifics of the same sex (P6). I did not find a significant difference for different-sex individuals in terms of avoidance/exclusion before and after a territory owner's death. The data set used to fit the model only included 3 years before and after the territory owner died, which indicates that neighbouring individuals enter/use another territory $1 - 3$ years after a territory owner dies.

After a territory owner's death, a new individual can partly or fully take over the owner's territory (*i.e.* territory turnover). The territory could be taken over by a young, non-territorial individual that is establishing a territory for the first time, or already territorial individuals could expand or shift their territory. Previous studies have found that wolverines have the capacity to fill gaps (*i.e.* vacant territories) in the current species distribution (Vangen et al. 2001). The removal/death of adult females from established home ranges has been found

to have an effect on dispersal patterns of young females (Vangen et al. 2001). However, territories can stay vacant or as a gap in the distribution for several years after the owner dies (Vangen et al. 2001).

My results do not show explicitly that territory turnover (*i.e.* a vacant territory is partly or fully taken over by another individual) between conspecifics occurs. However, a diminished exclusion of conspecifics after territory owner dies, would be the mechanism that eventually leads to territory turnover. Although the approach used herein was unable to show that territory turnover takes place, the data set used have the potential to address this question.

The wolverine's ability to fill gaps left by a removed territory owner have important relevance to wolverine management, especially population control. Removing a dominant territory owner that keep other, less dominant individuals out, can cause more animals to invade the territory and lead to more predation on domestic sheep and reindeer. In other animal populations, selective removal can be more effective and long lasting than random removal, *e.g.* coyotes (Conner et al. 2008). A better understanding of territory dynamics can aid wolverine conservation and management, and may reduce the predation caused by wolverine on domestic animals. Information about territory turnover is important for managers when dealing with conservation and population control. What happens after a territory owner is removed? Will younger individuals take over? Would it be a better management solution to remove individuals without a defined home range?

Using NGS to study spatial ecology

Although based on a relatively small sample size (N=6), the results from the comparison of NGS and GPS multiple-year home ranges in this thesis shows strong consistency. There was substantial overlap between NGS and GPS derived home ranges (P1). It is important to clarify that these estimates are based on multiple years of both NGS and GPS data and not always the same years. Despite the difference in how the data were collected, the resulting home range estimates are surprisingly similar. Interpretation beyond a general similarity should proceed cautiously, due to differences in years surveyed and possibly sample size, although kernel utilization distribution estimates should be less sensitive to this. A similar study on lynx also showed consistency between home ranges derived from NGS and VHF, with an average overlap of 86.4 % (Davoli et al. 2012). This study used NGS data from hair snaring compared with VHF data, and the home ranges were estimated by using MCP (Davoli et al. 2012).

This thesis found that male home ranges were significantly larger than female home ranges. This difference have been observed by previous studies on wolverine in Scandinavia

(Landa et al. 1998; Persson et al. 2010). The mean home range size reported by this thesis is 2 − 3 times higher than that previous studies. This is likely a consequence of constructing home ranges from NGS data collected over multiple years. Home ranges sizes that have been reported from Scandinavia before are 663 ± 194 km^2 for male and 274 ± 122 km^2 for female in south-central Norway (Landa et al. 1998), and a mean size of 669 km^2 for males and 170 km^2 for females in northern Sweden (Persson et al. 2010).

Combining NGS with other monitoring methods

NGS monitoring has great potential as a flexible method for long-term monitoring of cryptic and elusive species. NGS data can provide insight into demographic, population genetic and genomic, and spatial patterns. For long-term monitoring NGS pays off, at least if the problems with imperfect detection is accounted for analytically and a sampling protocol is followed. Compared to NGS, GPS is able to show animal movement in greater detail (higher resolution) for individual animals.

NGS can be combined with other non-invasive and invasive monitoring methods (Bischof & Swenson 2012). A pilot study successfully integrated and tested motion-detection cameras and hair snags for the wolverine (Magoun et al. 2011). This method captures both hair for microsatellite DNA genotyping, and takes a picture of the wolverine's ventral pattern at the same moment, providing two ways to identify individuals. Combined methods may complement each other and can be used for validation.

Limitations and considerations

There are various challenges associated with NGS, in part depending on the quality of the sampling schemes and DNA identification protocols that are used. These include imperfect detection (Waits & Paetkau 2005), sub-optimal quality of the genetic materials used, and genotyping errors (Hedmark et al. 2004). Problems regarding quality of DNA samples and genotyping errors are still being addressed and standardized protocols has been developed to minimize these challenges (Hedmark et al. 2004; Waits & Paetkau 2005).

One of the biggest challenges with NGS and most wildlife monitoring methods today is handling imperfect detection, *i.e.* cannot be sure that all animals are detected. There is one way to register a detection; the organism is there and is detected, but two different ways to get a non-detection; (1) the organism is not present and therefore it is not detected, or (2) the organism is present and is not detected (MacKenzie et al. 2009). The fact that we did not detect an animal does not mean that it does not occupy the area. Capture-recapture analysis can account for imperfect detection. In the case of NGS capture-recapture models including an

explicit spatial component can be a good approach, such as spatially explicit capture-recapture (SECR) methods which includes the spatial information inference (Borchers 2012).

During NGS monitoring there is no observation or interaction with the wolverine. Therefore it is difficult to know when or if a wolverine dies. However, when an animal stops being detected there are three options; (1) the animal is dead, (2) the animal moved out of the study area, or (3) the animal is still there but no scats were retrieved. Estimating turnover and mortality rates with NGS data are therefore possible. NGS data has been used to estimate turnover rates in imperial eagles, and can be used to estimate mortality rates (Vili et al. 2013). Estimates of adult survival based on NGS data have already been obtained for the wolverine in Scandinavia (Brøseth et al. 2010). One interesting approach could be to use mortality estimation from open population CMR models and additional information on potential mortality from change in spatial patterns of neighbouring individuals to estimate mortality rates. This could be a topic for future study.

Management implications

Contemporary Norwegian wolverine management has been unable to reach management targets; culling/hunting does not seem to be sufficient for wolverine population control. Wolverine population size and reproduction dropped in 2013 (Brøseth & Tovmo 2013). This drop in population size and reproductions can be attributed to bad snow conditions and a low number of breeding females that year, as well as hunting. In the 2012/13 hunting season 157 wolverines were shot or died of other causes, this is an increase of 45 from the season before and the highest wolverine mortality since the 1870's (Statistics Norway (SSB) 2013). Therefore there would be expected lower than usual predation on sheep and reindeer in 2013 since there is both less reproductions and lower population size. However, there was a slight increase in sheep predation from 2012 to 2013 (*Rovebase 3.0* 2014). This indicates that newly vacant territories could be taken over rather quickly after the owner's death. In Norway the hunting season for wolverine is between September – February (Bischof et al. 2012) and the grazing season is mostly constrained to the summer/fall months. This gives neighbouring wolverines 4 – 9 months to recolonize the vacant territory of a removed wolverine. This should be explored by future studies, one question can be how much time proceeds before a vacant territory is recolonized by a neighbouring individual?

In Norway population control of the wolverine is implemented through recreational hunting and culling. In some cases, reproducing females and/or cubs are removed (Stortingsmelding nr 15 (2003-2004)). Using hunters to reduce wildlife population is the most

cost-effective method available (Conover 2001). Hunting is usually non-selective or random, *i.e.* both territorial and non-territorial individuals are removed. The issue of removal of territorial carnivore individuals for damage control/prevention can have the opposite effect by allowing more, less dominant individuals to move in and cause even more damage, *i.e.* more predation on sheep and reindeer. In North America, selective removal of individual coyotes (*i.e.* problem individuals) has been shown to reduce predation on livestock more than non-selective removal (Conner et al. 1998). The timing of removal seems to also be important when reducing predation on livestock by coyotes (Conner et al. 2008). Timing wolverine removal with the summer grazing season could alleviate predation on domestic animals if new individuals do not have time to occupy the area before the grazing season ends.

Poaching is a significant part of the wolverine population dynamics in Norway, especially during the snow season (Persson et al. 2009). Wolverine conservation in Scandinavia is challenging because wolverine (and other large carnivores) live in conflict with sheep and reindeer husbandry practices. The animal husbandry practices are in turn in conflict with the dominating society, which is in favour of conservation and objects to killing of wolverine as a proactive depredation control strategy (Persson et al. 2009).

An interesting research question is; can selective removal of non-territorial wolverine individuals reduce predation on domestic animals? One approach to this would be to try different management strategies in different areas, one control area with the same strategies as now, one area with only removal of young and non-territorial wolverine, and one area with removal of older and territorial wolverines.

Future study

A natural next step after this thesis will be to study if and how territory turnover proceed in the wolverine. How much time passes after the territory owner dies until the territory is taken over? Is there a period if instability/uncertainty, or does the new territory become established quickly? Does one neighbour take over the entire home range, or is the home range divided between multiple neighbours? And does the shape of the territory change with change in ownership? One interesting approach could be to combine NGS with GPS monitoring, using GPS monitoring on a few individuals both for control and detailed movement patterns.

Conclusions

NGS can be useful for evaluating spatial patterns in wolverine and other carnivores. Spatio-temporal patterns in scat locations suggest intrasexual territoriality, the effect of which was reduced once the territory owner died. The results indicate that the wolverine are capable of filling/using vacant territories in the species distribution. Diminished or eliminated exclusion would be a mechanism that eventually leads to territory turnover. Future studies on home range and territory dynamics in wolverine is needed to assess territory turnover, i.e. the replacement of the former territory owner by a new owner that continues to exclude same-sex conspecifics from the same or a similar area in space. I conclude that NGS is a reliable monitoring method that is sensitive enough to detect patterns of territoriality in wolverines.

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