OF TURKU

INSIGHTS FROM UNSEEN INDIVIDUALS – USING NON-INVASIVE APPROACHES TO STUDY POPULATION BIOLOGY OF WHITE-TAILED DEER IN FINLAND

Jenni Poutanen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 367 | BIOLOGICA – GEOGRAPHICA – GEOLOGICA | TURKU 2020

UNIVERSITY OF TURKU

INSIGHTS FROM UNSEEN INDIVIDUALS – USING NON-INVASIVE APPROACHES TO STUDY POPULATION BIOLOGY OF WHITE-TAILED DEER IN FINLAND

Jenni Poutanen

TURUN YLIOPISTON JULKAISUJA – ANNALES UNIVERSITATIS TURKUENSIS
SARJA – SER. AII OSA – TOM. 367 | BIOLOGICA – GEOGRAPHICA - GEOLOGICA | TURKU 2020

University of Turku

Faculty of Science and Engineering
Department of Biology
Section of Ecology
Doctoral programme in Biology, Geography and Geology (BGG)

Supervised by

Professor, Jon E. Brommer
Department of Biology
University of Turku
Finland

Reviewed by

Assistant professor Rahel Sollman,
Department of Fish, Wildlife and Conservation Biology
University of California, Davis
U.S.A.

Professor Göran Ericsson
Department of Wildlife, Fish and Environmental Studies
Swedish Agricultural University, Umeå
Sweden

Opponent

Senior Scientist Mervi Kunnasranta
Natural Resources Institute Finland
(Luke) Joensuu
Finland

The originality of this publication has been checked in accordance with the University of Turku quality assurance system using the Turnitin OriginalityCheck service.

Cover picture: wildlife camera picture of white-tailed deer taken during this thesis research

ISBN 978-951-29-8043-7 (PRINT)
ISBN 978-951-29-8044-4 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)
Painosalama Oy, Turku, Finland 2020

UNIVERSITY OF TURKU
Faculty of Science and Engineering
Department of Biology
Section of Ecology
JENNI POUTANEN: Insights from Unseen Individuals – Using Non-invasive Approaches to Study Population Biology of White-tailed Deer in Finland
Doctoral Dissertation, 150 pp.
Doctoral programme in Biology, Geography and Geology (BGG)
April 2020

ABSTRACT

Density, adult sex ratio and fecundity are biologically important population parameters, whose estimation is also essential for wildlife management and conservation. These parameters describe population viability and predict its future composition. Density of animals is dependent on the surrounding habitat structure as animals rarely use all the available habitat types equally. Thus, understanding habitat preferences is also a significant challenge when estimating population parameters, such as density. Animal populations have been traditionally surveyed. for instance, by physically capturing and marking individuals. Non-invasive methods, such as DNA sampling or wildlife camera trapping, provide alternative to obtain information from populations without disturbing the animals. These methods are also cost-effective and provide population-wide inferences.

In this thesis, I use non-invasive fecal DNA sampling and wildlife cameras to estimate populations of white-tailed deer (*Odocoileus virginianus*) in Finland. I analyze the data collected with these approaches by using Spatial Capture Recapture (SCR) and Spatial Capture (SC) methods to examine white-tailed deer density, fecundity, adult sex ratio and habitat preferences. White-tailed deer is an important game species, whose population size has grown rapidly after introduction in Finland from North America in 1930s. I start this thesis by reviewing current scientific literature about this species to examine what is known about the biology of white-tailed deer in its distribution range within Europe. In this first chapter, the focus is on Finnish population as introductions to other European countries has not been as successful.

The results of this thesis show that using non-invasive DNA collection with SCR analysis provides reasonable estimates on white-tailed deer pre-harvest densities. Although, the approach has its challenges mainly related to low quality of non-invasive DNA. Estimating white-tailed deer populations by fecal DNA-based SCR provided generally higher density estimates than wildlife camera data analyzed by SC. SC requires auxiliary information on space use. For this, three different approaches were used and their results provided plausible information on white-tailed deer density, sex ratio and fecundity. The three approaches to obtain space use information for SC were based on 1) literature values, 2) simultaneous fecal DNA sampling analyzed by SCR, and 3) movement of adult males identified from camera pictures and that data analyzed by SCR, when female and fawn estimates were from DNA-based SCR. The models, where adult male and adult female space use was

allowed to differ from each other (2, 3), estimated population to have a female-biased sex ratio.

Wildlife cameras and DNA were found to estimate sex and age classes of white-tailed deer differently. The inability of DNA to distinguish age groups caused challenges for estimating space use of population because DNA-based SCR could not detect differences in movement between sexes. For instance, fawns are large part of the DNA data and they have home ranges with more comparable size to their mothers, and this hampers estimating adult male movement because large fraction of males in DNA data are actually fawns instead of being adult males. However, when estimating by camera-based SC, male movement was found to be three times larger than of females. Related to this issue, DNA also seems to capture shorter movement of white-tailed deer and was not able to capture larger movements of adult males, even though the sampling scheme was similar to wildlife camera trapping. This might lead to the higher density estimates of DNA-based SCR compared to estimates from camera-based SC.

By modelling white-tailed deer habitat preferences using DNA-based SCR, I found that in late summer white-tailed deer prefer having their home ranges on agricultural fields and mixed forests, probably because they provide easily accessible food. Inside their home ranges, they select to be close to fields but also near transitional woodlands. If white-tailed deer density was modelled without considering the landscape heterogeneity in the study area but assuming homogeneous landscape, SCR would have underestimated density. This highlights the importance of taking habitat preferences and landscape structure into account when estimating animal densities.

In conclusion, estimating populations by non-invasive DNA-sampling and SCR provides reasonable density estimates of white-tailed deer population. However, it is a laborious method, which would not necessarily be an applicable option in a larger-scale sampling that would be relevant to management of white-tailed deer. However, this approach could be used to provide a baseline reference when developing survey schemes based on other approaches, such as wildlife camera trapping. Indeed, camera-based SC provided reasonable estimates on density, adult sex ratio and fecundity of white-tailed deer. This would be an approach to be considered also in a larger-scale sampling scheme. Moreover, as SC-based camera trapping scheme would require auxiliary information on space use of animals, DNA-based SCR sampling conducted occasionally in some areas might be an applicable alternative.

TURUN YLIOPISTO
Luonnontieteiden ja tekniikan tiedekunta
Biologian laitos
Ekologia
JENNI POUTANEN: Havaintoja DNA:n ja riistakameroiden kautta – ei-invasiivisten menetelmien käyttö valkohäntäpeuran populaatiobiologisessa tutkimuksessa
Väitöskirja, 150 s.
Biologian, maantieteen ja geologian tohtoriohjelma
Huhtikuu 2020

TIIVISTELMÄ

Eläinten tiheyden, aikuisten sukupuolten lukumääräsuhteen ja populaation tuottavuuden arviointi ovat tärkeitä populaatioista arvioitavia tekijöitä, jotka on erityisen tärkeää huomioida eläinten kannanhoidossa ja suojelussa. Nämä tekijät kuvaavat populaation hyvinvointia ja niiden avulla voidaan ennustaa sen rakennetta tulevaisuudessa. Eläinten tiheys riippuu niiden elinympäristön rakenteesta, sillä eläimet käyttävät vain harvoin kaikkia elinympäristöjä samanlaisesti. Siksi populaation rakennetta ja tiheyttä arvioitaessa on tärkeää tietää minkälaista elinympäristöä eläimet suosivat. Perinteisesti eläinpopulaatioita on tutkittu esimerkiksi fyysisesti pyydystämällä ja merkitsemällä yksilöitä esimerkiksi korvamerkein tai radiopannoin. Non-invasiiviset menetelmät, kuten DNA-näytteiden keräys ja riistakameroiden käyttö, ovat sen sijaan vaihtoehtoja, jotka eivät häiritse eläimiä. Nämä menetelmät ovat lisäksi kustannustehokkaita ja tuottavat tietoa yksilötason sijaan koko populaation laajuisesti.

Tässä väitöskirjassa käytän non-invasiivista DNA-keräystä ja riistakameroita arvioidessani valkohäntäpeurapopulaatioiden (*Odocoileus virginianus*) rakennetta Suomessa. Analysoin näillä menetelmillä kerätyn aineiston Spatial Capture Recapture (SCR) ja Spatial Capture (SC) analyysimenetelmiä käyttäen arvioidakseni valkohäntäpeurojen tiheyttä, tuottavuutta, aikuisten sukupuolten lukumääräsuhdetta ja elinympäristön valintaa. Valkohäntäpeura on tärkeä riistaeläin, jonka kannan koko on kasvanut nopeasti sen jälkeen, kun se siirtoistutettiin Suomeen Pohjois-Amerikasta 1930-luvulla. Väitöskirjani alussa vedän yhteen tämän hetkisen tieteellisen kirjallisuuden lajin biologiasta selvittääkseni, mitä valkohäntäpeurasta tiedetään sen Euroopan sisäisellä levinneisyysalueella. Tässä ensimmäisessä osatyössä keskityn Suomen valkohäntäpeurapopulaatioon, koska siirtoistutukset muualle Eurooppaan eivät ole olleet yhtä onnistuneita.

Tämän väitöskirjan tutkimukset osoittavat, että non-invasiivinen DNA-keräys yhdessä SCR-analyysimenetelmien kanssa tuottaa vertailukelpoisen arvion valkohäntäpeurakannan tiheydestä ennen metsästyskauden alkua. Siitä huolimatta, menetelmässä on haasteensa liittyen erityisesti non-invasiivisissa näytteissä olevaan heikkolaatuiseen DNA:han. Ulostenäytteiden DNA:han ja SCR-menetelmiin pohjautuva valkohäntäpeuran tiheysarvio oli suurempi kuin riistakamera-aineistoon ja SC-menetelmiin perustuva arvio. SC-analyysi tarvitsee toimiakseen lisätietoa eläinten liikkuma-alueen laajuudesta. Tässä väitöskirjassa käytettiin kolmea eri vaihtoehtoa saada tämä tieto liikkuma-alueen koosta lisättyä analyyseihin, jotta

saatiin arvioitua valkohäntäpeuran tiheys, sukupuolten lukumääräsuhde ja tuottavuus. Yksilöiden liikkuma-alueen kokoa arvioitiin 1) tieteellisestä kirjallisuudesta saataviin arvoihin perustuen, 2) riistakameroiden kanssa yhtäaikaisesti kerättyjen ulostenäytteiden DNA:sta SCR-menetelmin saatujen arvojen perusteella, ja 3) tunnistamalla aikuiset urokset riistakamerakuvista ja arvioimalla niiden liikkuma-alueen koko SCR-menetelmin, jolloin naaraiden ja vasojen liikkuma-alueet perustuivat DNA:han ja SCR-menetelmiin.

Riistakameroihin ja DNA:han perustuvat menetelmät arvioivat valkohäntäpeuran eri sukupuoli- ja ikäryhmiä hieman eri tavalla. DNA:n avulla ei voida tunnistaa eri ikäryhmiä toisistaan, mikä aiheuttaa haasteita arvioitaessa yksilöiden liikkuma-alueiden kokoa, koska DNA:han perustuvan SCR-menetelmän avulla ei voida tunnistaa eroja urosten ja naaraiden liikkumisessa. Vasat ovat suuri osa DNA-aineistoa ja niiden liikkuma-alueet ovat kooltaan lähempänä niiden emien kuin urosten liikkuma-alueiden kokoja. Tämä vaikeuttaa esimerkiksi aikuisten urosten liikkumisen tutkimista DNA:n perusteella, koska suurin osa DNA aineiston uroksista on itseasiassa vasoja eikä aikuisia uroksia. Sen sijaan riistakamera-aineistoon perustuvan SC-menetelmän avulla huomattiin, että aikuiset urokset liikkuvat kolme kertaa laajemmilla alueilla kuin aikuiset naaraat. Tähän ongelmaan liittyen, DNA:n avulla pystyttiin tunnistamaan ainoastaan pienellä alueella tapahtuvat liikkumiset ja tätä edellämainittua riistakameroiden avulla havaittavaa urosten laajaa liikkumista ei havaittu DNA-aineistossa ollenkaan, vaikka DNA-keräysalueiden ja riistakameroiden väliset etäisyydet ja asettelu maastoon olivat samanlaiset. Todennäköisesti tästä johtuen DNA:han ja SCR-menetelmään perustuvat tiheysarviot olivat suuremmat verrattuna riistakameroihin ja SC-menetelmään perustuviin arvioihin.

Kun mallinsin valkohäntäpeuran elinympäristön valintaa DNA:n ja SCR-menetelmien avulla, löysin, että myöhään kesällä valkohäntäpeurat valitsevat liikkuma-alueensa viljelypelloille tai sekametsiin. Näitä elinympäristöjä suosittiin todennäköisesti niiden tarjoaman helposti saatavan ravinnon vuoksi. Näiden liikkuma-alueidensa sisällä valkohäntäpeuroja havaittiin todennäköisemmin lähellä peltoja, mutta lisäksi lähellä harvapuustoista metsämaata (esimerkiksi entiset hakkuualueet). Sen sijaan valkohäntäpeura ei suosi esimerkiksi havumetsää. Jos valkohäntäpeurojen tiheyttä olisi mallinnettu ilman, että oltaisiin otettu elinympäristön rakenteen vaihtelevuus huomioon, valkohäntäpeurojen tiheys olisi aliarvioitu. Tämä osoittaa, että eläinten elinympäristön valinta on tärkeä ottaa huomioon niiden tiheyksiä arvioitaessa.

Yhteenvetona, non-invasiivinen DNA-keräys yhdessä SCR-menetelmän kanssa tuottaa vertailukelpoisen arvion valkohäntäpeurojen tiheydestä. Se on kuitenkin työläs menetelmä, joka ei välttämättä ole järkevä vaihtoehto lajin laajempaan valtakunnalliseen kannanarviointiin sovellettaessa. Siitä huolimatta, tällä menetelmällä saataisiin luotettava vertailukohta esimerkiksi kehitettäessä kannanarviointia muihin menetelmiin, kuten esimerkiksi riistakameroihin, perustuen. Tässä väitöskirjassa riistakameroihin ja SC-analyyseihin perustuva menetelmä tuotti vertailukelpoiset arviot valkohäntäpeurojen tiheydestä, aikuisten sukupuolten lukumääräsuhteesta ja kannan tuottavuudesta. Riistakameramenetelmä voisikin olla hyvä vaihtoehto laajempaan valkohäntäpeuran kannanseurantaan huomioiden kuitenkin tarpeen esimerkiksi koko ajan kehittyvälle automaattiselle kuvantunnistukselle. Koska SC-analyyseihin pohjautuva kameramenetelmä kuitenkin vaatisi lisätietoa yksilöiden liikkuma-alueiden koosta, yksi sovellettava vaihtoehto voisi olla toteuttaa joillakin alueilla satunnaisesti DNA:han ja SCR-menetelmiin perustuva arviointi valkohäntäpeurojen liikkumislaajuudesta.

Contents

List of Original Publications (I–IV)

This thesis is based on the following publications and manuscripts, which are referred to by their Roman numerals in the text:

I **Poutanen J**, Wikström M & Brommer JE (in press) White-tailed deer (chapter in "Handbook of the mammals of Europe", edited by Klaus Hackländer and Frank E. Zachos, Springer)

II **Poutanen J**, Pusenius J, Wikström M & Brommer JE (2019). Estimating population density of the white-tailed deer in Finland using non-invasive genetic sampling and spatial capture–recapture. In Annales Zoologici Fennici (Vol. 56, No. 1–6, pp. 1–16).

III **Poutanen J,** Fuller AK, Pusenius J, Royle JA, Wikström M, Brommer JE (submitted) Density-habitat relationships of white-tailed deer (Odocoileus virginianus) in Finland

IV Brommer JE, **Poutanen J**, Pusenius J, Wikström M (submitted) Estimating pre-harvest density, adult sex ratio and fecundity of white-tailed deer using wildlife cameras

Author contributions to the original publications:

	I	II	III	IV
Original idea	JEB	JEB, **JPo**, MW, JPu	**JPo**, JEB, MW, JPu	JEB, **JPo**, MW, JPu
Data collection	**JPo**, JEB, MW	**JPo**, JEB	**JPo**	**JPo**
Data analyses (DNA and/or picture)	-	**JPo**	**JPo**	**JPo**
Statistical analyses	-	**JPo**, JEB	**JPo**, AKF, JAR	JEB
Writing	**JPo**, JEB	**JPo**, JEB, MW, JPu	**JPo**, JEB, MW, JPu, AKF, JAR	JEB, **JPo**, MW, JPu

JPo= Jenni Poutanen, JEB= Jon E. Brommer, MW= Mikael Wikström, JPu= Jyrki Pusenius, AKF= Angela K. Fuller, JAR= J. Andrew Royle

1 Introduction

1.1 Population biology

Estimating population parameters such as density, sex ratio and fecundity is one of the core aspects in population biology as well as part of sustainable wildlife management (Andrewartha & Birch 1954, Caughley & Sinclair 1994). This demographic information is crucial for effective long-term population management plans and also for conservation actions. Population size is the number of individuals in a population and it can be viewed to describe population viability (Reed et al. 2003). Furthermore, especially for wildlife management, it is important to know population density i.e. the number of individuals per unit area (e.g. individuals/km^2). With that information, it is possible to determine necessary management actions by defining target-densities for managed population. Additionally, sex ratio, fecundity and age structure are important demographic parameters, which can predict future composition and sustainability of the population. Estimating these requires information on sex- and age-specific densities. Sex ratio and fecundity are often impacted when harvesting animals and the effect of harvesting on those parameters should be thoroughly investigated. For instance, in the Nordic countries harvested ungulate populations tend to have more females than males, which may cause several reproductive issues (Langvatn & Loison 1999, Sæther et al. 2004). These issues may result from changes in the mating behavior that again alters the sex and age structure of the population (Sæther et al. 2004). When ungulate population sex ratio is female-biased and age composition of males is more towards young males, it may cause e.g. decreased pregnancy rates and delayed reproduction resulting in juveniles with smaller body size and poorer survival (Holand et al. 2006, Milner et al. 2007, Noyes et al. 1996, Solberg et al. 2002). Furthermore, when mostly young males reproduce, it may further bias offspring sex ratio towards more females than males (Sæther et al. 2004). In Finland, there are some indications that white-tailed deer population may lack old males (Kekkonen et al. 2016).

Another important aspect of wildlife management is to understand the spatial distribution of animals. Animals rarely use all the available habitats equally and their densities are often dependent on the landscape structure (Allen & Singh 2016, Bjørneraas et al. 2012, Fretwell 1969, Maier et al. 2005). Hence, understanding

habitat selection of animals is important when extrapolating density estimates of animal populations over different landscapes.

1.2 Population estimation methods

The first step for managing wildlife population is to assess its population structure. Traditionally, abundance have been estimated using count-based surveys, which does not require individual identification of animals (Sutherland 2006). In ungulates surveys have been done, for example, by counting animals in the fields by road-based or aerial surveys (Beaver et al. 2014, Drake et al. 2005, Millette et al. 2011). However, this has been shown to often produce biased estimates (Collier et al. 2013, McCorquodale 2001, Pollock & Kendall 1987). Other traditional methods for estimating animal abundances are track or dung counts (Mooty et al. 1984). For ungulates, tracking is especially difficult as they usually walk the same paths making it impossible to count individual numbers. Even though, dung counts have been shown to provide estimates comparable to other approaches (Bailey & Putman 1981, Batcheler 1975, Neff 1968, Pfeffer et al. 2018) it can be error-prone especially because dungs of different sympatric species may be difficult to distinguish. Moreover, sexes cannot be distinguished by track or dung counting.

One challenge in count-based surveys is that the number of individuals, which were not detected, remains unknown. This can be overcome by using capture-recapture methods (Otis et al. 1978), which require identification of individuals. Capture-recapture provides estimates of total abundance based on the probability of capturing individuals. Numbers of uncaptured individuals are estimated by using the capture probability counted by marking and recapturing part of the population. Traditionally, this has been done by live-capturing animals and physically marking them using e.g. collars or ear tags (Jung et al. 2019, Oyster et al. 2018, Smith, J. B. et al. 2016). Apart from being harmful for the animal itself, capturing and marking animals may also bias the survey. Handling often changes the behavior of animal causing, for example, so-called trap-shyness. This leads to avoidance of traps by animals after being caught, and decreases the probability of further recapturing the individual (Jolley et al. 2012). Moreover, live-capturing sufficient number of individuals, in order to get a representative sample of the study population, is laborious and resource consuming. Handling of animals requires highly trained personnel and in case of large animals, such as ungulates or large predators, live-capturing requires anesthesia and veterinary care. Still, the operation can be potentially life-threatening to animals. To overcome these issues, non-invasive methods have become more common in population estimation (Smith & Wang 2014, Waits & Paetkau 2005). These approaches do not require physical capturing or even

direct observation of the animal itself. They can be used independently for surveying populations or they can complement traditional methods (Liberg et al. 2012).

Two common non-invasive approaches for assessing animal populations are non-invasive DNA sampling and wildlife camera trapping, which are also methods used in this thesis. Non-invasive DNA is usually extracted from feces (Biffi & Williams 2017, Brazeal et al. 2017, Fuller et al. 2016), urine (Hausknecht et al. 2007, Rehnus & Bollmann 2016) or hair (Mullins et al. 2010) that individuals have left to their environment. DNA allows identification and sexing of individuals. With proper sampling design, non-invasive DNA provides information on individual encounter history indicating which individual has moved on which sampling location and when. In cases where species identification morphologically from feces is difficult, DNA can be used to distinguishing the species and exclude non-target species from the analysis. Furthermore, non-invasive genetics enables assessing, for instance, genetic structure, diversity and pedigree of individuals (Granroth-Wilding et al. 2017, Honnen et al. 2015).

Wildlife cameras have become more common and their numbers have been rapidly growing (Burton et al. 2015). Potential of wildlife cameras for population estimation is immense. Species identification is relatively easy from camera pictures. Moreover, if animals have visible individually unique characteristics, such as in the case of bobcats (*Lynx rufus*) (Young et al. 2019), also different individuals can be distinguished. Many species also have sex-specific characteristics, such as antlers of ungulates, allowing estimation of sex-specific estimates. Unlike from DNA, aging between juveniles and adults is also often possible from camera pictures. In addition to surveying one species, also simultaneous assessment of multiple species by camera trapping is possible. Wildlife cameras also provide possibilities for larger citizen science projects (Sun et al. 2019).

Traditional capture-recapture analysis provides population size estimates but the area in which individuals live remains unknown. Thus, it is difficult to estimate the density. There are some approaches attempting to estimate the area used by animals of the study population *post-hoc* but the precise definition of the effective sampling area is impossible and there remains difficulty to decide which buffer area and resulting density estimates are the most appropriate (Royle et al. 2018, Sutherland et al. 2016a). Recently, capture-recapture has been extended to include the spatial encounter information on individuals. These Spatial Capture-Recapture (SCR) methods (Efford 2004, Efford & Fewster 2013, Royle et al. 2014) are based on the assumption that probability to capture an individual is related to the distance between the home range center and the location where the individual was detected. With that information, it is possible to infer where home range centers are located and how large they are. Consequently, the size of an effective sampling area i.e. where the study population actually lives, can be estimated. Hence, the population density is

the number of home range centers found inside the effective sampling area divided by the size of the sampling area. SCR can also incorporate spatial covariates such as information about landscape structure into the models. This allows inferring, for instance, habitat selection (Royle et al. 2013b) or landscape connectivity (Fuller et al. 2016, Royle et al. 2013a, Sutherland et al. 2015). SCR has been used together with non-invasive sampling for assessing populations of e.g. large predators (Roffler et al. 2016, Young et al. 2019), ungulates (Brazeal et al. 2017) and small mammals (Romairone et al. 2018).

SCR requires individual identification. When individuals cannot be identified, for example, from wildlife camera pictures when animals do not have unique visible characteristics, Spatial Capture (SC) is one possible alternative (Chandler & Royle 2013) for analyzing method. It is essentially an SCR approach with same assumption of parameters but it requires information on only total counts of animals instead of counts of identified individuals. SC infers density based on spatial correlation between counts made at locations that are close enough to each other so that same individuals could potentially move between them. SC approach requires prior or auxiliary information on the space use of the focal species.

2 Aims of This Thesis

Overarching aim of this thesis is to examine the use of non-invasive methods to study population biology of white-tailed deer (*Odocoileus virginianus*) in Finland. White-tailed deer is an introduced species in Finland and the abundance of the species has grown rapidly after the introduction in 1930s. It has established its status as common and important game species. The National Strategy on Invasive Alien Species by Finnish Ministry of Agriculture and Forestry (2012) states that white-tailed deer is potentially or locally harmful and in need of monitoring, and that the spreading of the species from Finland to other countries must be prevented. One of the biggest damages that white-tailed deer causes in Finland are deer-vehicle collisions. In addition, in the densest population areas, white-tailed deer cause also damages to agriculture, forestry and gardens. In order to minimize these damages the population size is regulated by intensive hunting and the management of the species is regulated by Finnish hunting legistlation. The greatest challenge for white-tailed deer management is to further develop methods to control population growth. Given this challenge, research into improved methods to estimate population size and structure of white-tailed deer is be important.

In this thesis, I first provided an overview of white-tailed deer biology and investigated what is known about the ecology of this species in Europe (**I**). Then, I applied non-invasive fecal DNA sampling and wildlife camera trapping with Spatial Capture Recapture and Spatial Capture approaches for estimating biologically relevant population parameters of white-tailed deer such as density, sex ratio, fecundity and habitat use (**II-IV**), which are also essential for management of the species.

This thesis consists of four chapters (**I–IV**), whose objectives are:

I: To provide an overview of white-tailed deer biology and describe what is currently known about this introduced North-American species in Europe (Finland).

II: First, to develop a protocol for fecal DNA-based individual identification of white-tailed deer in Finland. Second, to evaluate the applicability of Spatial Capture Recapture with fecal DNA sampling for inferring pre-hunt density of white-tailed deer in Finland.

III: First, to understand how white-tailed deer use available habitat types in late summer prior to its hunting season in Finland. Second, to evaluate the importance of including habitat covariates for density estimation by comparing the standard Spatial Capture Recapture model assuming homogeneous distribution over space to inhomogeneous models considering a heterogeneous landscape.

IV: To evaluate the applicability of Spatial Capture on wildlife camera data for inferring pre-hunt population density, adult sex ratio and fecundity of white-tailed deer in Finland.

3 Materials and Methods

3.1 White-tailed deer as a study species

White-tailed deer is a North-American ungulate, which was introduced in Finland in 1934. It has been introduced also to a few other European countries (Czech Republic, Romania and Serbia), but most introductions failed (Halls 1984). In the Czech Republic, a small population of about 1000 individuals still exists. In Finland, the first introduction consisted of only four individuals, one male and three females, which survived and reproduced. There was a second introduction in 1940s, but the survival of these individuals remains unknown. Thus, it is possible that only four individuals founded the current white-tailed deer population in Finland. Despite the small founder population, white-tailed deer in Finland is genetically diverse. This results from a quick increase in population size after the introduction (Kekkonen et al. 2012). Nowadays, white-tailed deer is an abundant and important game species in Finland whose population size is estimated to be 112 000 individuals in winter 2018–2019 with 7% increase from the previous year. Mean density was 0.5 individuals per km^2, but on species' core areas post-harvest densities of roughly 5 – 10 individuals per km^2 occurred (Kukko & Pusenius 2019). About half of the population is harvested annually. Population estimation methods of the species in Finland can be improved and developed further. White-tailed deer population size has been estimated by integrating e.g. hunting statistics, hunters' estimates on the population size in their hunting areas after the hunting season, deer-vehicle collision statistics and estimates on productivity in a population dynamical model. Still, there is a need for methods to complement the current, only recently applied approaches. For example, hunters have gathered white-tailed deer observations during the moose hunt, which has been shown to bias the white-tailed deer estimates when compared to observations done during white-tailed deer hunt. Therefore, collecting observations primarily targeting on white-tailed deer e.g. by direct sightings by human or by wildlife cameras could be a potential improvement. Moreover, basic ecological aspects such as white-tailed deer adult sex ratio, habitat preferences and, for instance, possible competition with other most common sympatric ungulates, particularly roe deer (*Capreolus capreolus*) and moose (*Alces alces*), or the effect of predation by main predators lynx (*Lynx lynx*) and wolves (*Canis lupus*), remain obscure.

3.2 Data collection

3.2.1 Literature review (I)

Chapter **I** of this thesis describes the current knowledge on the biology of the white-tailed deer in Finland. In this chapter, scientific literature from the white-tailed deer in Finland but also literature from the original distribution range of this North American species was reviewed.

3.2.2 Non-invasive fecal DNA (II, III, IV)

White-tailed deer fecal samples were collected for the chapters **II**, **III** and **IV**. Samples were collected non-invasively in the field by four to five persons each year. From the samples, DNA was extracted in the laboratory to obtain individual identities. Sampling was conducted in a clustered design where feces were collected from sampling plots of 20 m x 20 m in size. Each cluster included four plots, which were 100 m (**II**) or 60 m (**III, IV**) apart from each other. Distance between the center coordinates of the clusters was 500 m (**II**) or 300 m (**III, IV**). Encounter histories of individuals were obtained by collecting feces from the same plots with one-week (**II**, and first sampling for **III** and **IV**) or four-day (second sampling for **III** and **IV**) interval. Plots were initially cleaned from the feces one week or four days, respectively, before the first sampling visit as well as after each visit. This ensured that the feces accumulated only during the preceding time interval. Plots were visited two (first sampling of **III** and **IV**), three (**II**) or five times (second sampling of **III** and **IV**) (Table 1). Sampling was done each year just prior to the white-tailed deer hunting season. The timing ensures the assumption of closed population without emigration, immigration, births or harvest-based deaths.

Table 1. Overview of the sampling of white-tailed deer non-invasive fecal DNA for Chapters **II, III** and **IV** with study area and sampling year, distances between centrals of sampling clusters and between the four plots of each cluster, sampling interval and number of sampling visits to each plot.

Study area	Year	Chapter	Cluster spacing	Samping interval	No of visits
Tammisaari	2015	II	clusters 500 m, plots 100 m	7 days	3
Loimaa	2016	III, IV	clusters 300 m, plots 60 m	7 days	2
Loimaa	2017	III, IV	clusters 300 m, plots 60 m	4 days	5

Sampling was first designed for Chapter **II**, which was conducted in Tammisaari, Uusimaa region, in southern Finland in September 2015. There, 45 sampling clusters (180 plots) were surveyed. Based on results of this study, the design was modified and applied for data collection for Chapters **III** and **IV**. For these two studies, samples were collected simultaneously in a same sampling grid with wildlife camera trapping (for Chapter **IV**), in Loimaa, southwestern Finland during two consecutive years in September 2016 and August 2017. There, 23 clusters (92 plots) were surveyed. Based on the results on white-tailed deer movement scale in Chapter **II**, the distance between the sampling clusters was decreased from 500 m to 300 m and between the plots from 100 m to 60 m. Aim of this was to allow more spatial recaptures of individuals. Sampling in Loimaa in 2016 was still conducted with one-week interval and two sampling occasions. When final DNA and Spatial Capture Recapture (SCR) analysis of Chapter **II** were finished, the results suggested decreasing sampling interval for four days and increasing the number of visits to five for the 2017 sampling in Loimaa. Aim of more frequent sampling was potentially to allow more temporal recaptures of individuals and simultaneously increase genotyping success by reducing the time fecal samples were laying on the field and exposed to weather, which further increases DNA degradation (Brinkman et al. 2010). Both Tammisaari (2015) and Loimaa (2016 and 2017) samples were collected in resealable plastic bags and stored in -20°C until laboratory analyses.

3.2.3 Wildlife camera pictures (IV)

Wildlife camera trapping for Chapter **IV** was conducted simultaneously and integrated in the same sampling grid with DNA sampling in Loimaa in September 2016 and August 2017. 36 (35 in second year) wildlife cameras (Uovision UV595) were placed approximately in the middle of distinct DNA sampling clusters and had about 300 m between the adjacent cameras. They took pictures whenever animal movement was detected in front of them. The manufacturer's estimate for the detection distance is up to 15 meters. Picture were taken with bursts of three pictures with 5 s delay between each burst if there were subsequent movement of animals. In 2016, cameras were operational during 16 days and in 2017 22 days. From each picture, the species, number of adult white-tailed deer females, adult males and fawns were counted (Figure 1). Obtained data was further analyzed with Spatial Capture (SC) approaches. Further, adult males were individually identified from pictures whose quality allowed identification based on antler characteristics. Identification was based on e.g. antler size, shape and number of points in antlers. This allowed further SCR analysis of the male encounters. For SC analysis, consecutive pictures that were taken within 1 hour were considered non-independent,

intending that there could potentially be same individuals in these pictures. Therefore, pictures with less than 1-hour time interval between them were grouped as belonging to one encounter event. The number of females, males and fawns per encounter event was inferred to be the maximum number of white-tailed deer individuals in these groups that could be counted in one picture of that event. Each 24-hour period was considered as one sampling occasion.

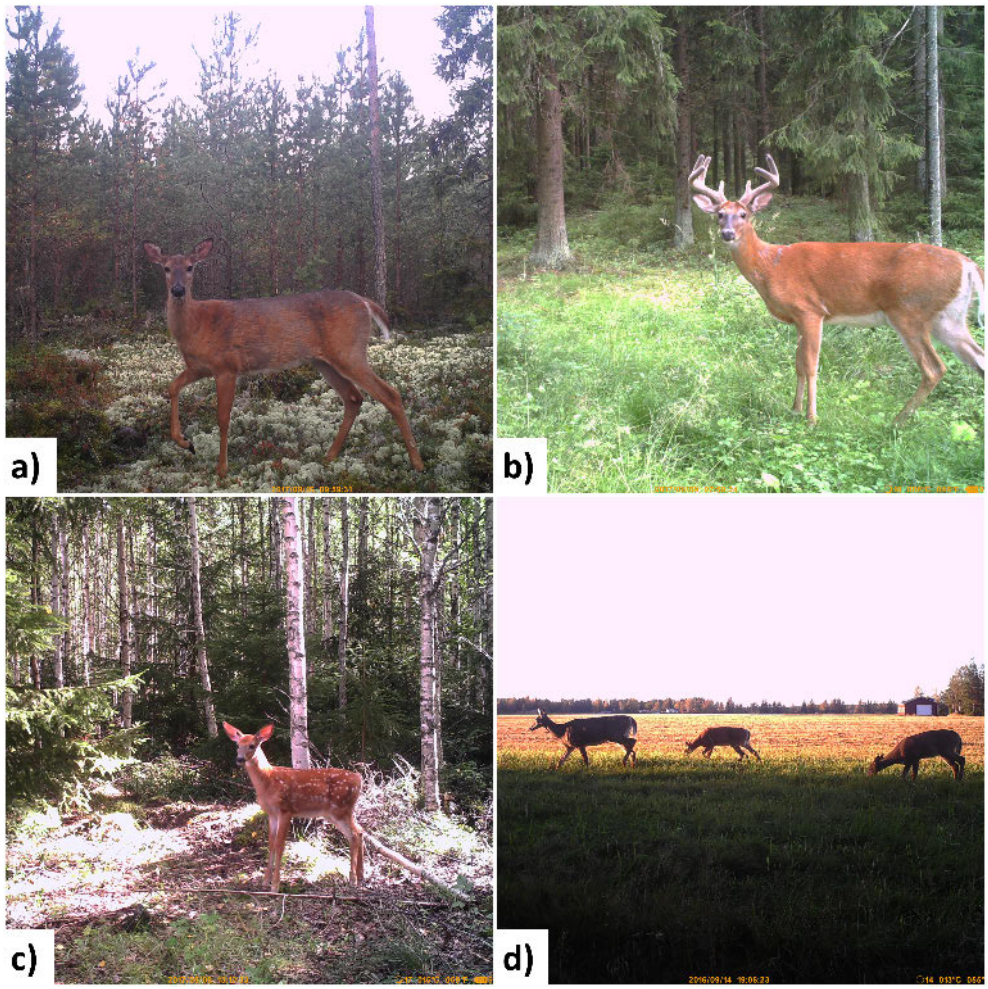

Figure 1. Examples of white-tailed deer wildlife camera pictures in Loimaa study area in 2017. **a)** female, **b)** male, **c)** fawn and **d)** white-tailed deer female with two fawns.

3.3 Laboratory analyses for DNA extraction and individual identification

DNA was extracted from non-invasively collected fecal samples using a commercially available DNA extraction kit (QIAamp DNA Stool Mini Kit, Qiagen, Valencia, California, USA). Provided ready-made extraction protocol was modified so that elution volume was decreased from 200 µl to 100 µl and incubation time was increased from 1 min to 5 min. One extraction was done for each sample.

Laboratory protocol for DNA-based individual identification was developed in Chapter **II** and applied further for Chapters **III** and **IV**, with only minor modifications on primer and BSA concentration. In summary, the identification was based on 14 microsatellite markers and sex identification on a X- and Y-chromosome-specific primer pair. Multitube approach with three PCR replicates for each marker was used in order to minimize genotyping errors typical to fragmented non-invasive DNA (Taberlet et al. 1996). Heterozygote loci were accepted to final genotype if alleles were amplified at least two times and homozygote loci if amplified three times. Based on estimated probability of identify (PI) values, genotypes with successful amplification on at least 11 (**III, IV**) or 12 (**II**) microsatellites were used in subsequent identification analysis. Genotypes were matched to the same individual so that maximum of two mismatches between alleles were allowed in two distinct loci. In Chapter **II**, also the protocol for distinguishing white-tailed deer DNA from roe deer DNA was developed. Species identification was based on amplifying one white-tailed deer DNA-specific primer pair and one roe deer-DNA-specific primer pair, which were targeted for mitochondrial 12S rRNA gene.

3.4 Statistical analyses

3.4.1 Spatial Capture Recapture (II, III, IV)

Spatial Capture Recapture (SCR) was applied in this thesis on Chapters **II**, **III** and **IV** to estimate white-tailed deer density, space use and density-habitat relationships (**III**) based on individual encounter histories obtained from genotypes from non-invasive fecal DNA. Further, in Chapter **IV**, SCR was also used to estimate density of adult white-tailed deer males from their encounter histories from wildlife camera pictures, where individual identification was based on antler characteristics.

SCR requires spatial encounter history data which has a record of when (sampling occasion) and where (trap location) individuals are captured. Animals are assumed to have a specific home range center whose location can be denoted by the vector **s**. According to the half-normal function, the probability to detect individual

at a specific trap with location **x** whose Euclidian distance |**x** – **s**| from the home range center is defined (Royle et al. 2014) as,

$$p(x, s) = p_0 \exp\left(-\frac{|\mathbf{x} - \mathbf{s}|^2}{2\sigma^2}\right)$$

where p_0 is the baseline probability to detect the animal, and σ is a parameter scaling the rate at which detection probability declines with distance from the home range center. Therefore, this formulation accounts for heterogeneity in capture probabilities meaning that, for example, an individual captured in the peripheral location on its home range has smaller probability of being captured than another individual captured at the core area of its home range, where the capture probability is at its highest. Parameters that can be estimated by SCR modelling are p_0, σ, N (number of individuals) and D (density). Density of individuals can be derived from the number of individuals (i.e. home range centers) per certain area, which is usually referred to as the state-space. The state-space consists of the sampling area and a certain buffer around it resulting in an area that could potentially cover home range centers of all individuals in the study population.

Furthermore, in Chapter **II**, white-tailed deer density inferred by SCR was also compared with estimates from dung count method (Koda et al. 2011, Pfeffer et al. 2018). The fecal accumulation rate method was used, where density is,

$$D = \frac{n}{a \times t \times d}$$

where n is the number of fecal pellet groups counted, a is the sampling area (km^2), t is the accumulation time of pellets (days) and d is the defecation rate, which is number of pellet groups produced per day based on literature values.

In Chapter **III,** SCR was used to infer density-habitat relationship of white-tailed deer. SCR incorporates spatially explicit information on locations of both traps and individual encounters. Using explicit spatial locations allows estimating dependency of encounter probabilities and densities on surrounding habitat type by including landscape covariate in the models. Landcover types were included as covariates to estimate habitat preferences on two different levels. Firstly, to infer 2nd order habitat selection, i.e. how habitat preferences affect the selection of home range area locations of individuals (Johnson 1980), landcover type was added as a covariate on state space for modelling density. Secondly, habitat was included as trap-level covariate to model capture probability (p_0) in order to infer 3rd order habitat selection, i.e. individual habitat preferences inside their home ranges (Johnson 1980). For density modelling, three different landscape covariates were used. First, a categorical habitat class variable with four levels: agricultural areas (fields), coniferous forests, mixed forests and transitional woodland/shrub (mainly clear cuts in the study area).

Second, distance to anthropogenic habitats (e.g. buildings, roads and other artificially surfaced areas) and third, the nearest distance to water bodies. For modelling capture probability, four different covariates were used. First was a categorical habitat class variable with three levels: coniferous forest, mixed forests and transitional woodland/shrub (hereafter: transitional woodland). Other three covariates were distance to agricultural areas, distance to anthropogenic habitats, and distance to water.

Habitat covariates were chosen so that they would be ecologically relevant for white-tailed deer. White-tailed deer uses variety of different habitats including, for example, agricultural fields, various forest types, grasslands and swamps, including both open and closed vegetation types (Beier & McCullough 1990, Brinkmann et al. 2005, Halls 1984). Here, field and main forest types of the area (coniferous, mixed and transitional woodland) were expected to provide food, and forests also cover, for white-tailed deer. By using different forest types instead of merging those to one habitat class would potentially show if different forest types have different effect on white-tailed deer density or detection probability. The effect of anthropogenic habitats was investigated to determine whether white-tailed deer would avoid or prefer this type of human activity in the rural areas on the scale of this study.

In Chapters **II** and **IV**, bias and precision of SCR-derived parameters were evaluated by *a posteriori* simulation given the spatial layout of the sampling. In Chapter **II**, different scenarios were simulated, where sampling occasions varied between four and six visits, and the distance between the sampling plots was scaled by 0.5, 1.5 or 2.0. In simulations for Chapter **IV**, the effect of increasing the number of sampling occasions was estimated.

All SCR-models were implemented using the R package oSCR (Sutherland et al. 2016b) in RStudio (RStudio Team 2018) and secr (Efford 2018) in R (R Core Team 2018). Simulations were implemented using secrdesign package (Efford 2019) in R.

3.4.2 Spatial Capture (IV)

In Chapter **IV**, data based on wildlife camera pictures of white-tailed deer were analyzed using Spatial Capture (SC) in order to infer density, sex ratio and fecundity. SC approaches are fundamentally the same as SCR without the requirement of individual identification. Instead of the individual encounter histories, the SC data consists of counts of animals in traps during capture occasions. Still, there underlies same assumption as in SCR about declining capture probability between individual's home range center and distance to the trap. Thus, SC approaches were applicable in encounter history data set of counts of adult males, adult females and fawns in camera pictures. For estimating densities, SC requires additional information on the scale of space use of animals. This was included in the models by three different

approaches: 1) Estimating space use by fecal DNA-based SCR and assuming it to be equal for all age and sex classes. 2) Using literature estimates on space use, where adult males have larger home ranges than adult females and fawns, whose space usage was assumed to be identical. 3) including information on space use from SCR of individually identified adult males on wildlife camera pictures and using female and fawn space usage (assumed identical) estimated from fecal DNA-based SCR. SC models were implemented with Bayesian MCMC model in JAGS (Plummer 2003).

4 Results and Discussion

4.1 White-tailed deer in Europe (I)

Chapter **I** provides an overview of the scientific knowledge on biology of white-tailed deer in Finland. White-tailed deer is an introduced species whose population likely originates from only four individuals, one male and three females, introduced in 1934 from North America. Despite the fact that white-tailed deer is currently an abundant species and important game animal in Finland, the literature review revealed that white-tailed deer population biology is not well-studied in Finland. In species' original distribution range, its ecology is thoroughly researched. However, what is found in North American populations does not necessarily apply to white-tailed deer in Finland, because population biology of species depend partly on abiotic and biotic factors of the environment where the species lives. Abiotic factors affecting population parameters are, for instance, climate and weather conditions. Biotic factors are, for instance, quality and availability of food, shelter and other resources. Furthermore, predators, diseases and sympatric species competing on same resources have effect on e.g. population density, fecundity and movement. Hence, when discussing about populations living in completely different continents, even though being populations of same species, findings of studies on white-tailed deer in North America cannot be straightly inferred being comparable to the population in Finland.

We found that there is a lack of knowledge even on basic population parameters of the white-tailed deer in Finland such as precise adult sex ratio and fecundity. Furthermore, there is a need for proper complementary methods to estimate these parameters and also to complement current density estimates. Previous studies show that Finnish white-tailed deer populations may lack older males possibly due to Nordic hunting regulations, which does not allow culling of female with fawns (Kekkonen et al. 2016). Possibly, trophy hunting may also cause higher hunting pressure on older males compared to old females. Sex ratio is an important factor determining population viability. Female-biased sex ratio may cause several reproductive issues in ungulate populations. This phenomenon is well-studied on, for instance, moose (Sæther et al. 2004) and red deer (*Cervus elaphus*) (Langvatn &

Loison 1999) in Nordic countries, but there is a lack of studies on smaller ungulates such as white-tailed deer and roe deer.

Furthermore, competition between white-tailed deer and roe deer has not been generally considered to have substantial impact on the populations of these species in Finland. However, there is no scientific literature on competition between white-tailed deer and sympatric ungulates in Finland. Measured by abundance, in addition to roe deer other potential competing ungulate for white-tailed deer is moose. White-tailed deer is an adaptive species and can live in various different environments. In its original distribution range, species exist, for example, in forests, savannas, deserts and coastal marine environments (Halls 1984).

In Finland, there are currently no published studies on white-tailed deer habitat preferences before Chapter **III** of this thesis. Moreover, research on movement and home range sizes of Finnish white-tailed deer are basically restricted to one thesis on 32 GPS-collared individuals (11 males, 21 females) which were followed on four different regions (Honzová 2013). More studies with higher sample size is needed to gather more extensive information on white-tailed deer space use in Finland.

We found that one explanation for the success of white-tailed deer introduction and further rapidly expanded population size is that no diseases that would significantly hinder population growth exist. Especially fortunate is that the nematode, meningeal worm (or brainworm, *Parelaphostrongylus tenuis*), which is a common parasite of white-tailed deer in North America, did not become established in Finland during the introduction (Anderson 1964). Despite the small founder population, white-tailed deer in Finland still has unexpectedly high genetic diversity. Although, the bottleneck reduced allelic richness. High genetic diversity might be a consequence of rapid growth in population size after the introduction (Kekkonen et al. 2012).

4.2 Non-invasive fecal DNA-based identification of white-tailed deer with Spatial Capture Recapture to infer population density (II)

In Chapter **II**, we developed a protocol for sampling non-invasive fecal DNA to identify white-tailed deer individuals for Spatial Capture Recapture (SCR) analysis. Moreover, protocol for distinguishing white-tailed deer DNA from roe deer DNA was developed. With three weekly sampling visits, 245 fecal samples were collected. Only 15% of the samples were successfully genotyped and used in identification analysis. Genotyping success was lower than previously found in studies using non-invasive feces of ungulates (Brinkman et al. 2010, Goode et al. 2014, Harris et al. 2010). There are three possible explanations for low genotyping

success. First, in this study 12 microsatellites of 14 were needed to amplify in order to reliably identify white-tailed deer individuals. In the study by Goode et al. (2014) only 6 microsatellite markers were used. When white-tailed deer was introduced in Finland allelic richness reduced due to bottleneck effect (Kekkonen et al. 2012). Lower allelic richness leads to the need for using more microsatellite markers, which lowers the genotyping success when analyzing fragmented DNA. Secondly, non-invasive samples are exposed to environment, which risks DNA preservation. During this study, the weather was rainy and this together with long sampling interval of one week may have led to rapid DNA degradation. Brinkman et al. (2010) and Goode et al. (2014) found also decrease in genotyping success when ungulate fecal samples were exposed to rain. Finally, diet may affect functioning of PCR as some plant material includes secondary components that act as PCR-inhibitors (Kohn & Wayne 1997, Monteiro et al. 1997). There might be some differences in inhibitors between plant species consumed by white-tailed deer in Finland and in North America.

Even though the genotyping success was low and we were able to identify only 27 white-tailed deer of which seven were recaptured, this data set allowed SCR analysis. SCR produced density estimate of 3.5 (95% CI = 2.0–6.4) individuals per km^2, which was comparable to larger-scale national estimates of the area, and also comparable to results provided by dung count method. From seven recaptured individuals, only two were males. Thus, due to the restricted data set we did not provide sex-specific estimates on density or space use.

Although, non-invasive fecal DNA sampling with SCR provided reasonable pre-hunt estimates of the white-tailed deer, the approach has its challenges. Based on simulations conducted in this study, we suggested sampling with shorter time intervals and placing DNA sampling plots and clusters closer to each other. This would potentially lead to higher genotyping success due to shorter time that samples are exposed to weather in the field. Also, more temporal recaptures of individuals would be obtained. Furthermore, decreasing the distance between sampling plots and clusters, may allow more spatial recaptures. During this study, the SCR-based movement scale (σ) of white-tailed deer was about 190 m. Sun et al. (2014) suggested that distance between the centers of sampling clusters should be minimum twice the movement scale. Thus, the distance between the clusters in this study was possibly too large (500 m) to obtain more encounters. These above-mentioned changes in sampling design would allow collection of more data and result in more recaptures of individuals. This would further lead to more precise estimates of SCR-based density and σ. These changes were implemented in Chapters **III** and **IV**.

4.3 Density-habitat relationships of white-tailed deer (III)

In Chapter **III**, we investigated the relationship between habitat and density of white-tailed deer using SCR. White-tailed deer preferred agricultural fields and mixed forests, as population densities were highest in these landcover types. In opposite, densities were smallest in coniferous forests and transitional woodlands. This preference describes second-order habitat selection so where animals select their home ranges to be. Moreover, third-order habitat selection revealed that inside their home ranges, white-tailed deer prefer being close to agricultural fields and transitional woodlands. Preferred habitat types are selected likely because they provide easily accessible food. Fields in the study area are mainly grain fields that especially prior to harvest in late summer, when the sampling was done, provide large amount of food for white-tailed deer. Transitional woodlands in the area are mainly clear-cuts with, for example, plenty of seedlings, shrubs and grass. Furthermore, undergrowth in mixed forest may provide more food for white-tailed deer than coniferous forests. Notable is that this study describes white-tailed deer habitat selection at that particular time of the year when sampling was done. For instance, snow cover and temperature during winter affects food availability (Andersson & Koivisto 1980).

Including habitat covariates into SCR models was important when estimating white-tailed deer density. When expecting landscape to be homogeneous, the density estimates were drastically lower. Increase in density when including landscape heterogeneity to models was probably due to the largest fraction of the study area consisting of fields, which was among the most preferred landcover types. Moreover, the sampling did not took place on fields but instead in lower density habitats. Thus, under the homogeneous SCR model there were no information to be provided to the model that would allow it to estimate higher densities in the surrounding of the traps. Supposedly, if the landscape had consisted mostly on, for example, coniferous forest, which was least preferred habitat, the density estimate of homogeneous models would have been lower than of heterogeneous models. This underlines the importance of accounting for habitat preferences when estimating animal densities.

4.4 Wildlife cameras and Spatial Capture for inferring density, sex ratio and fecundity of white-tailed deer (IV)

In Chapter **IV**, the use of wildlife cameras and Spatial Capture (SC) in estimating white-tailed deer population density, sex ratio and fecundity was evaluated. Estimates from three different approaches to incorporate space use to SC models provided plausible estimates of these population parameters. The auxiliary

movement information that is needed to implement SC approach was based on 1) literature values, 2) simultaneous fecal DNA sampling and analysis on SCR, and 3) adult male movement estimated from individually identified males from camera pictures and analyzing data by SCR, and in this case female and fawn space usage (assumed identical) estimates were based on fecal DNA-based SCR. SC-based density estimates were lower than estimated based on SCR on fecal DNA, especially on the second study year (2017), but the estimates were still reasonable. Thus, SC on wildlife camera data achieved to provide conservative density estimates of white-tailed deer. *A posteriori* simulations of fecal DNA-SCR showed that five sampling occasions, as in 2017, was sufficient to provide unbiased estimates of density and increasing number of occasions from that does not further affect bias. Two sampling occasions in 2016 resulted in overestimation of density by 9 %, which would have decreased to 0 % with five occasions. Estimates of movement parameter σ was unbiased in both years.

Interestingly, wildlife camera-based approaches inferred population space use differently than DNA-based SCR. First, fecal DNA-SCR did not find any difference in space use between different sexes of white-tailed deer. Nevertheless, SCR on adult males from camera pictures found male space use being three-times larger than of females, which is expected, regarding ungulate population biology and previous studies on white-tailed deer (Honzová 2013). DNA infers space use differently probably because genotype data consists of both juveniles and adults, and DNA cannot distinguish different age classes. At the time of the sampling, fawn movement is still restricted to movement of their mothers. DNA does not capture heterogeneity in movement between adult males and adult females, because substantial part of the population actually consists of juveniles, which cannot be distinguished from DNA data. Secondly, DNA seem to capture shorter movement of white-tailed deer individuals than wildlife cameras do, which may also explain why DNA-based density is higher. Wildlife cameras were placed at same distances from each other as were also adjacent DNA clusters. Regarding movement scale of white-tailed deer estimated by fecal DNA-SCR in this study, these distances are optimal to what is suggested for a SCR sampling design (Sun et al. 2014). Still, cameras detect large movement of adult males while DNA sampling fails to detect it. This might be related to different nature of sampling between these two approaches. Here, DNA captures individuals based on feces left on the ground, while wildlife cameras take pictures when they detect moving animals in front of them. These different capture methods may actually record different movement behaviors of individuals. That is, cameras somehow capture adult males when they are moving over larger distances and DNA captures shorter movement of females and fawns but probably also adult males when they are moving shorter distances. Females and fawns, especially at this time of the year, may spend more time roaming around in same small area leaving

feces there. Whereas, adult males may move longer distances at a time. DNA may capture adult males only when they are moving around more restrictedly in more constricted area.

Wildlife camera-based SC approaches, where adult female and male space use was allowed to differ from each other (literature-based values or adult male movement estimated from camera-based SCR), found female-biased sex ratio in adult white-tailed deer in the study area. This area may be attractive to females with fawns, for example, because of some particular resource it provides at this time of the year. Nevertheless, Nordic hunting regulations put more pressure on shooting males than females, because females with calves cannot be harvested. Lack of older male compared to old females have been found in Finnish white-tailed deer (Kekkonen et al. 2016). However, due to restricted size of the study area and relatively small number of individuals in the study, any conclusions around this issue cannot be made here. Fecundity estimates produced by SC were plausible, although on the second study year slightly higher than usually estimated on white-tailed deer. Nevertheless, probably large part of population consist of young females and thus the population may have high reproductive potential (cf Kekkonen et al. 2016).

5 Conclusions, Future Recommendations and Applications to Wildlife Management

In this thesis, I evaluated the use of non-invasive DNA and wildlife camera trapping in estimating white-tailed deer populations in Finland. First, in Chapter **I**, I provided an overview of the white-tailed deer as an introduced species in Finland. In Chapters **II**–**IV**, I used Spatial Capture Recapture (SCR) and Spatial Capture (SC) methods with fecal DNA sampling and wildlife camera trapping (**IV**) to provide estimates of density, space use, sex ratio and fecundity, as well as estimated density-habitat relationships of white-tailed deer (**III**). For these chapters, I applied the sampling and laboratory protocol developed in Chapter **II**.

In Chapter **II**, we found that using the sampling and laboratory protocols developed during this research, non-invasive fecal sampling together with SCR provided reasonable inferences on white-tailed deer pre-hunt densities during a short three-week sampling period just before hunting season. However, this approach has its challenges, in particularly regarding sampling low quality and quantity DNA such as in non-invasive feces. Indeed, in Chapter **II** genotyping success was very low (15%), which we hypothesized being partly result of rainy weather during the sampling. Genotyping success of the following two years of sampling in another study area (**III**, **IV**) was 32%. Regardless the shortened sampling interval (four days instead of seven days) on the second year, the genotyping success did not increase further. Increase in genotyping success from Chapter **I**, may be a result of weather being more favorable during sampling. Still, 32 % success rate is low compared to what has been found in ungulate studies (Brinkman et al. 2011, Goode et al. 2014, Harris et al. 2010). One possible explanation is that in this thesis 11 (**III**, **IV**) to 12 (**II**) microsatellite markers were needed to amplify in order to reliably determine individual identities. The require for more microsatellites than used for example in North America (Goode et al. 2014) might be a consequence of reduced allelic richness in Finnish white-tailed deer (Kekkonen et al. 2016). This issue may be solved in the future studies by designing even shorter microsatellite markers. Here, we used markers which resulted in amplicons of about 190 bp in average size (range 97 bp – 242 bp) in final genotypes, while marker size closer to 100 bp might be more

favorable because shorter fragments amplify better in non-invasive DNA (Broquet et al. 2007). One potential alternative in population monitoring by non-invasive genetics is to use Single Nucleotide Polymorphism (SNP) markers (Carroll et al. 2018, Morin et al. 2004). SNPs generally provide shorter amplicons than microsatellites, which potentially results in higher amplification rate, yet also lower rates than with microsatellites have been found (Fitak et al. 2015, Goossens et al. 2016, von Thaden et al. 2017). However, microsatellites typically have higher allelic diversity than bi-allelic SNPs and are therefore more informative for examining genetic variation and genetic structure of populations, especially when populations are closely related. To achieve the same information as with microsatellites, larger number of SNPs are needed. The issues with genotyping errors related to low quality and quantity DNA of non-invasive samples are similar to both SNPs and microsatellites. Further, one possibility is to use a combination of both SNPs and microsatellites (Czarnomska et al. 2008, Fabbri et al. 2012, Goossens et al. 2016, Narum et al. 2008)

An interesting challenge often encountered during this thesis work was that DNA and wildlife cameras provide, to some extent, inferences of different parts of the population. One strength of using DNA is that sexes of identified individuals can be distinguished. However, the inability of DNA to distinguish age groups caused challenges for estimating space use of population because DNA-based SCR could not detect differences in movement between sexes (**IV**). Nevertheless, simultaneous wildlife camera trapping showed larger space use of adult males compared to females and fawns, based on SCR on individually identified males by their antler characteristics. DNA might tend to capture shorter movement of white-tailed deer than wildlife cameras do regardless of similar sampling design. This phenomenon of capturing heterogeneity in movement between age and sex classes by different trapping methods is an interesting issue which should be taken into account in future studies.

Even though wildlife cameras provide the advantage of distinguishing white-tailed deer adults and juveniles from pictures, the disadvantage of camera trapping is that individuals without unique visible characteristics cannot be identified. This applies to white-tailed deer females and fawns. Moreover, sexes of fawns cannot be distinguished from pictures. The timing of sampling for this thesis allowed estimating densities of different age groups as fawns still move with their mothers. Thus, population fecundity can be estimated. Moreover, males have their antlers making it possible to distinguish them from females based on camera pictures, and thus to estimate adult sex ratio. Furthermore, antler characteristics enable individual identification of males. If sampling had been done after the hunting season, which ends in Finland in February, males would have already started to shed their antlers.

Some studies have integrated count and SCR data to same hybrid models. For example, Furnas et al. (2018) combined DNA-based SCR with N-binomial mixture modeling of camera data for ungulate density estimation. Already mentioned challenge with combining two types of data collected in Chapter **IV** is that the methods identify sex and age classes differently. In future research, one potential approach would be recently developed spatial partial identity models (SPIM) (Augustine et al. 2018). SPIM would also allow using partial identities from incomplete genotypes. Furthermore, at the time of the sampling, most fawns still have spotted, apparently individually unique, pattern on their fur before it starts fading. When categorizing pictures for this thesis, I also examined the possibility of individually identifying fawns based on their spots. However, our camera design has only one camera per trap, which leads to one-sided pictures of animals. This decreases the amount of data available for identification by restricting the pictures to either left- or right-sided images, which would be necessary in order to avoid duplicate captures of same animal. However, SPIM modelling would also allow using this type of incomplete data sets.

Estimating habitat preferences using DNA and SCR is quite novel method. Chapter **III** highlighted the importance of accounting for landscape heterogeneity and habitat preferences when estimating animal densities. This is especially considerable in wildlife management or conservation when extrapolating densities over the landscapes. Thus, for the management of white-tailed deer, it would be important not only to estimate densities, but also to understand how different habitat types affect species densities. Traditionally, habitat selection has been studied by using telemetry. However, telemetry usually provides information on only a few individuals while non-invasive DNA with SCR provide population-wide inferences. Integrating this data by hybrid modelling with e.g. camera trapping data would potentially provide information on age-specific habitat preferences (Furnas et al. 2018). Moreover, combining telemetry-based inferences on space use together with non-invasive sampling may improve precision of estimates (Linden et al. 2018, Royle et al. 2013b, Sollmann et al. 2016).

Collecting population-level information based on non-invasive methods can potentially be of lower cost and causes less risk to animals than research with traditional invasive methods requiring physical captures of animals such as in the case of telemetry. Even laborious non-invasive DNA sampling has been shown to be, under certain conditions, a cost-effective method for producing reliable density estimates as compared with traditional methods (Goode et al. 2014, Roffler et al. 2016, Solberg, K. H. et al. 2006). In addition, genotype data provides information for also studying, for instance, genetic diversity and structure of populations (Granroth-Wilding et al. 2017, Hagemann et al. 2018, Sun et al. 2017). In Chapter **IV**, we found that wildlife camera-based sampling scheme together with SC

approaches could provide reasonable method for larger, potentially nation-wide, population estimation of white-tailed deer. Wildlife cameras would provide sufficient amount of information for estimating density, sex ratio and fecundity, which is information of relevance to wildlife biology. This information can be extracted from pictures by SC methods. The amount of wildlife cameras that people own is rapidly growing (Burton et al. 2015). In Finland, according to a survey made by Finnish Wildlife Agency (unpublished, 2018) the amount of wildlife cameras that Finnish hunters own and the willingness of the hunters to voluntarily participate in white-tailed deer population estimation using their own cameras, suggest that there is potential for wildlife manager and researcher-organized wildlife camera sampling in a larger scale. Furthermore, many hunters already use their wildlife cameras for surveying game animals moving in their hunting area. As there are already multiple cameras in the field constantly recording valuable information of wildlife, one potential alternative for population estimation is to use this already existing wildlife camera data. This independently gathered picture data could also be used as a complementing approach for designed SC-based sampling. Although, the usefulness of this type of disorganized random sampling scheme would need further investigation.

Implementing nationwide population estimation of white-tailed deer, or any other abundant game species, with wildlife cameras results in vast amounts of pictures. In order to provide biologically relevant information, pictures would need to be effectively analyzed and further interpreted. In practice, extracting information from larger amount of pictures would require automatic identification. Currently, there are projects worldwide focusing on developing automatic identification of pictures and new technologies and software emerge (Norouzzadeh et al. 2018). Regarding white-tailed deer population estimation with SC, there are different categories of information that automatic identification would need to be able to record. First, wildlife cameras sometimes take empty pictures, which would need to be automatically filtered. Second, software would need to distinguish white-tailed deer on species-level from other sympatric non-target species, e.g. roe deer. Third, for estimating sex ratio and fecundity, different age and sex classes would need to be distinguished.

Using fecal DNA sampling for estimating densities of abundant species such as white-tailed deer in Finland may not be realistic in larger nationwide management. Sampling in the field and subsequent DNA analysis in the laboratory can be laborious. Nevertheless, when developing evaluating other methods such as wildlife camera-based estimation, the use of DNA together with SCR can provide baseline reference estimates of density. Such baseline information is needed also when comparing estimates from other non-invasive approaches such as wildlife camera trapping (Furnas et al. 2018, Gopalaswamy et al. 2012). For instance, applying

wildlife cameras with SC for estimating white-tailed deer populations for wildlife management purposes would still require auxiliary information on space use of the animals. For this, local smaller-scale DNA sampling with SCR would be reasonable option for providing that information. Home range sizes of animals are dependent on e.g. population densities and surrounding habitat. Thus, density estimates cannot be extrapolated between areas with very different white-tailed deer densities or different landscapes. Accordingly, auxiliary space use information for SC-based wildlife camera sampling would need to be collected from populations under different circumstances. The DNA-based SCR sampling could possibly be conducted only occasionally, as Chandler & Clark (2014) showed that collecting SC data in some years combined with SCR data in other years cost-effectively improved temporal monitoring.

One important advantage of using wildlife cameras in larger-scale population estimation is that it would potentially allow simultaneous survey of populations of other sympatric species as well (Figure 2). However, the sampling design would need to be careful planned in relation to animal movement, so that it allows recapturing of individuals of multiple species, at least in case of analyzing data with SC or SCR approaches. Resulting wildlife pictures are also attractive for public and may attract people to volunteer in picture-based citizen science projects. There are examples of successful web-based projects where people can identify animals from wildlife camera pictures and the categorized pictures are subsequently analyzed by researchers to provide inferences of animal populations (Hsing et al. 2018, Swanson et al. 2015). Moreover, pictures provide interesting insights into wildlife and can be used for drawing attention when for example popularizing science and communicating about the research to broader public. Therefore, wildlife pictures may potentially even increase general interest for example in wildlife conservation.

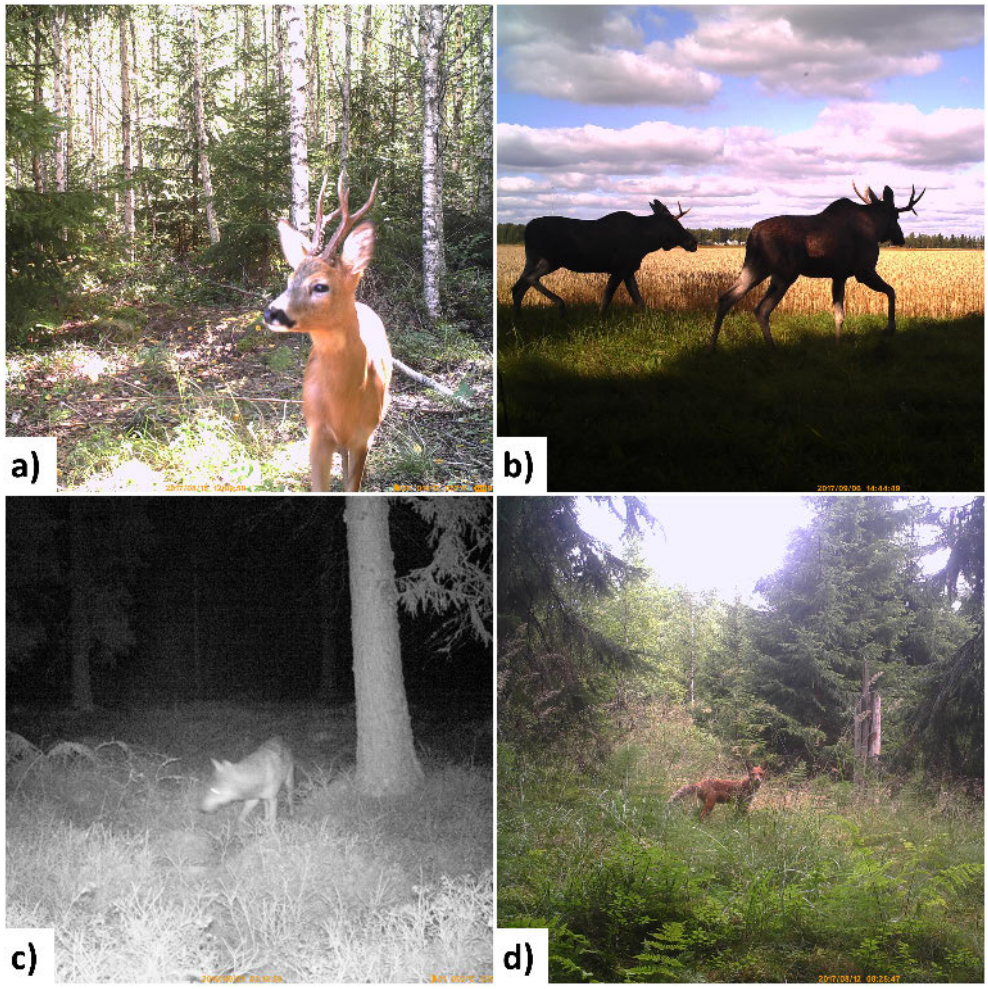

Figure 2. Examples of wildlife camera pictures of non-target species recorded during white-tailed deer camera trapping in Loimaa study area in 2016 and 2017. **a)** roe deer male (*Capreolus capreolus*), **b)** two male moose (*Alces alces*), **c)** wolf (*Canis lupus*) and **d)** red fox (*Vulpes vulpes*).

Acknowledgements

First of all, I would like to thank my supervisor Jon Brommer. You have supported me with every aspects related to this thesis. Without your guidance, this thesis would not have been possible to do. I am also very happy that I have had the possibility to work in collaboration with Suomen Riistakeskus and Luonnonvarakeskus. I want to thank especially Micke and Jyrki for close collaboration. I would also like to thank the landowners in Tammisaari and Loimaa, and two hunting clubs of Loimaa and Pöytyä for their valuable help with the fieldwork. I also wish to thank Angela and Andy. It was a pleasure to visit you in Cornell University in Ithaca, USA. Your guidance, and of course your research on SCR, have guided me during SCR analyses.

I am very grateful that after initially working with multiple smaller grants, I received a funded doctoral candidate position for three years from Doctoral Programme in Biology, Geology and Geography (BGG) Graduate School. Of course, I would like to acknowledge the smaller grants I was lucky to get, and which helped me to start this work: Societas Pro Fauna et Flora Fennica, Suomen Riistanhoito-säätiö, Jenny and Antti Wihuri Foundation, and funding by the joint research between Luonnonvarakeskus and University of Turku. I would also like to thank Suomen Metsästäjäliitto for a collaboration with funding for wildlife cameras.

I want to thank my hard-working field assistants. Without you, I would not have gathered hundreds of samples of study material, at least not so efficiently. Two Novia students helped me and Jon in Tammisaari. Maiju, Jorma and Roosa were collecting the samples with me in Loimaa. We got a chance to enjoy the beautiful sunny weather (contrarily to weather in Tammisaari) and to collect enormous amounts of mushrooms during the long field days. Roosa worked also with DNA samples in the laboratory and categorized thousands of wildlife camera pictures. It was nice to notice that we are not only great friends, but it was also fun to work together during those six months.

In addition to happy and easy workdays, there have been times when I have also been struggling with balancing with PhD work and life. I am always thankful especially for Pauliina, Laura, Roosa and Jouni who have helped me with maintaining my sanity and being able to also enjoy life and forget worries at those times. I am also happy to have a group of beautiful ladies around me who are my

closest friends outside the university: Anna, Ilona, Mari, Niina, Noora, Petra and Saara. I am thankful to have you and your sense of humor in my life. Finally, I want to thank my family, but especially my husband who has always been there for me. Kalle, kiitos kun olet ollut siinä ja tukenut kaikessa. Oli myös hauska tehdä kenttätöitä yhdessä ja kiitos kun kannoit välillä mun puolesta painavaa rinkkaa täynnä riistakameroita pitkin Loimaan metsiä.

April 2020
Jenni Poutanen

References

Allen AM & Singh NJ (2016) Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution* 3.

Anderson RC (1964) Neurologie disease in moose infected experimentally with pneumostrongylus tenuis from white-tailed deer. *Pathologia Veterinaria* 1:289–322.

Andersson E & Koivisto I (1980) Valkohäntäpeuran talviravinto ja vuorokausrytmi (white-tailed deer's winter food and diurnal rhythm). *Suomen Riista* 27:84–92.

Andrewartha HG & Birch LC (1954) *The distribution and abundance of animals* University of Chicago Press.

Augustine BC, Royle JA, Kelly MJ, Satter CB, Alonso RS, Boydston EE & Crooks KR (2018) Spatial capture–recapture with partial identity: An application to camera traps. *The Annals of Applied Statistics* 12:67–95.

Bailey RE & Putman RJ (1981) Estimation of fallow deer (dama dama) populations from faecal accumulation. *Journal of Applied Ecology* 18:697–702.

Batcheler CL (1975) Development of a distance method for deer census from pellet groups. *The Journal of Wildlife Management* 39:641–652.

Beaver JT, Harper CA, Kissell RE, Muller LI, Basinger PS, Goode MJ, Van Manen FT, Winton W & Kennedy ML (2014) Aerial vertical-looking infrared imagery to evaluate bias of distance sampling techniques for white-tailed deer. *Wildlife Society Bulletin* 38:419–427.

Beier P & McCullough DR (1990) Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:3–51.

Biffi D & Williams DA (2017) Use of non-invasive techniques to determine population size of the marine otter in two regions of Peru. *Mammalian Biology - Zeitschrift Für Säugetierkunde* 84:12–19.

Bjørneraas K, Herfindal I, Solberg EJ, Sæther B, van Moorter B & Rolandsen CM (2012) Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia* 168:231–243.

Brazeal JL, Weist T & Sacks BN (2017) Noninvasive genetic spatial capture-recapture for estimating deer population abundance. *The Journal of Wildlife Management* 81:629–640.

Brinkman TJ, Deperno CS, Jenks JA, Haroldson BS & Osborn RG (2005) Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture, *The Journal of Wildlife Management* 69:1099–1111.

Brinkman TJ, Schwartz MK, Person DK, Pilgrim KL & Hundertmark KJ (2010) Effects of time and rainfall on PCR success using DNA extracted from deer fecal pellets. *Conservation Genetics* 11:1547–1552.

Broquet T, Ménard N & Petit E (2007) Noninvasive population genetics: A review of sample source, diet, fragment length and microsatellite motif effects on amplification success and genotyping error rates. *Conservation Genetics* 8:249–260.

Burton AC, Neilson E, Moreira D, Ladle A, Steenweg R, Fisher JT, Bayne E & Boutin S (2015) REVIEW: Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52:675–685.

Carroll EL, Bruford MW, DeWoody JA, Leroy G, Strand A, Waits L & Wang J (2018) Genetic and genomic monitoring with minimally invasive sampling methods. *Evolutionary Applications* 11:1094–1119.

Caughley G & Sinclair ARE (1994) *Wildlife ecology and management* Blackwell Science.

Chandler RB & Clark JD (2014) Spatially explicit integrated population models. *Methods in Ecology and Evolution* 5:1351–1360.

Chandler RB & Royle JA (2013) Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics* 7: 936–954.

Collier BA, Ditchkoff SS, Ruth CR & Raglin JB (2013) Spotlight surveys for white-tailed deer: Monitoring panacea or exercise in futility? *The Journal of Wildlife Management* 77:165–171.

Czarnomska SD, Jędrzejewska B, Borowik T, Niedziałkowska M, Stronen AV, Nowak S, Mysłajek RW, Okarma H, Konopiński M, Pilot M, Śmietana W, Caniglia R, Fabbri E, Randi E, Pertoldi C & Jędrzejewski W (2013) Concordant mitochondrial and microsatellite DNA structuring between Polish lowland and Carpathian Mountain wolves. *Conservation Genetics* 14: 573–588.

Drake D, Aquila C & Huntington G (2005) Counting a suburban deer population using forward-looking infrared radar and road counts. *Wildlife Society Bulletin* 33:656–661.

Efford M (2004) Density estimation in live-trapping studies. *Oikos* 106:598–610.

Efford MG & Fewster RM (2013) Estimating population size by spatially explicit capture–recapture. *Oikos* 122:918–928.

Efford MG (2018) secr: Spatially explicit capture-recapture models. R package version 3.1.6. https://CRAN.R-project.org/package=secr

Efford MG (2019) secrdesign: Sampling Design for Spatially Explicit Capture-Recapture. R package version 2.5.7. https://CRAN.R-project.org/package=secrdesign

Fabbri E, Caniglia R, Mucci N, Thomsen HP, Krag K, Pertoldi C, Loeschcke V & Randi E (2012) Comparison of single nucleotide polymorphisms and microsatellites in non-invasive genetic monitoring of a wolf population. *Archives of Biological Sciences* 64:321–335.

Finnish Ministry of Agriculture and Forestry (2012) Finland´s National Strategy on Invasive Alien Species. https://mmm.fi/documents/1410837/1894125/Finlands_national_strategy_on_invasive_alien_species.pdf/61137cdf-92ad-4ac8-8b6d-0feaeaedfe74

Fitak RR, Naidu A, Thompson RW & Culver M (2015) A new panel of SNP markers for the individual identification of north american pumas. *Journal of Fish and Wildlife Management* 7:13–27.

Fretwell SD (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:45–52.

Fuller A, Sutherland CS, Royle AJ & Hare MP (2016) Estimating population density and connectivity of american mink using spatial capture—recapture. *Ecological Applications* 26:1125–1135.

Furnas BJ, Landers RH, Hill S, Itoga SS & Sacks BN (2018) Integrated modeling to estimate population size and composition of mule deer. *The Journal of Wildlife Management* 82:1429–1441.

Goode MJ, Beaver JT, Muller LI, Clark JD, Manen FTv, Harper CA & Basinger PS (2014) Capture—recapture of white-tailed deer using DNA from fecal pellet groups. *Wildlife Biology* 20:270–278.

Goossens B, Sharma R, Othman N, Kun-Rodrigues C, Sakong R, Ancrenaz M, Ambu LN, Jue NK, O'Neill RJ, Bruford MW & Chikhi L (2016) Habitat fragmentation and genetic diversity in natural populations of the bornean elephant: Implications for conservation. *Biological Conservation* 196:80–92.

Gopalaswamy AM, Royle JA, Delampady M, Nichols JD, Karanth KU & Macdonald DW (2012) Density estimation in tiger populations: Combining information for strong inference. *Ecology* 93:1741–1751.

Granroth-Wilding H, Primmer C, Lindqvist M, Poutanen J, Thalmann O, Aspi J, Harmoinen J, Kojola I & Laaksonen T (2017) Non-invasive genetic monitoring involving citizen science enables reconstruction of current pack dynamics in a re-establishing wolf population. *BMC Ecology* 17:44.

Hagemann L, Boesch C, Robbins MM, Arandjelovic M, Deschner T, Lewis M, Froese G & Vigilant L (2018) Long-term group membership and dynamics in a wild western lowland gorilla population (gorilla gorilla gorilla) inferred using non-invasive genetics. *American Journal of Primatology* 80:e22898.

Halls LK (1984) *White-tailed deer: Ecology and management.* Stackpole Books.

Harris RB, Winnie J, Amish SJ, Beja-Pereira A, Godinho R, Costa V & Luikart G (2010) Argali abundance in the afghan pamir using Capture–Recapture modeling from fecal DNA. *Journal of Wildlife Management* 74:668–677.

Hausknecht R, Gula R, Pirga B & Kuehn R (2007) Urine — a source for noninvasive genetic monitoring in wildlife. *Molecular Ecology Notes* 7:208–212.

Holand Ø, Mysterud A, Røed KH, Coulson T, Gjøstein H, Weladji RB & Nieminen M (2006) Adaptive adjustment of offspring sex ratio and maternal reproductive effort in an iteroparous mammal. *Proceedings of the Royal Society B: Biological Sciences* 273:293–299.

Honnen A, Roos A, Stjernberg T & Zachos FE (2015) Genetic analysis of eurasian otters (lutra lutra) reveals high admixture in finland and pronounced differentiation in sweden. *Mammalian Biology* 80:47–53.

Honzová M (2013) *Analysis of habitat size and migration of roe and white-tailed deer in finnish lake district, finland.* Retrieved from http://is.mendelu.cz/zp/index.pl?podrobnosti=50543

Hsing P, Bradley S, Kent VT, Hill RA, Smith GC, Whittingham MJ, Cokill J, Crawley D & Stephens PA (2018) Economical crowdsourcing for camera trap image classification. *Remote Sensing in Ecology and Conservation* 4:361–374.

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

Jolley WJ, Campbell KJ, Holmes ND, Garcelon DK, Hanson CC, Will D, Keitt BS, Smith G & Little AE (2012) Reducing the impacts of leg hold trapping on critically endangered foxes by modified traps and conditioned trap aversion on san nicolas island, california, USA. *Conservation Evidence* 9:43–49.

Jung TS, Boonstra R & Krebs CJ (2019) Mark my words: Experts' choice of marking methods used in capture-mark-recapture studies of small mammals. *Journal of Mammalogy*

Kekkonen J, Wikström M, Ala-Ajos I, Lappalainen V & Brommer JE (2016) Growth and age structure in an introduced and hunted cervid population: White-tailed deer in finland. *Annales Zoologici Fennici* 53:69–80.

Kekkonen J, Wikström M & Brommer JE (2012) Heterozygosity in an isolated population of a large mammal founded by four individuals is predicted by an individual-based genetic model. *Plos One* 7:e43482.

Koda R, Agetsuma N, Agetsuma-Yanagihara Y, Tsujino R & Fujita N (2011) A proposal of the method of deer density estimate without fecal decomposition rate: A case study of fecal accumulation rate technique in japan. *Ecological Research* 26:227–231.

Kohn MH & Wayne RK (1997) Facts from feces revisited. *Trends in Ecology & Evolution* 12:223–227.

Kukko T & Pusenius J (2019) *Valkohäntäpeurakanta talvella 2018 – 2019.* Natural Resources Institute Finland.

Langvatn R & Loison A (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer cervus elaphus in central norway. *Wildlife Biology* 5:213–223.

Liberg O, Aronson Å, Sand H, Wabakken P, Maartmann E, Svensson L & Åkesson M (2012) Monitoring of wolves in scandinavia. *Hystrix, the Italian Journal of Mammalogy* 23:29–34.

Linden DW, Sirén APK & Pekins PJ (2018) Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. *Ecosphere* 9:e02203.

Maier JAK, Ver Hoef J,M., McGuire AD, Bowyer RT, Saperstein L & Maier HA (2005) Distribution and density of moose in relation to landscape characteristics: Effects of scale. *Canadian Journal of Forest Research* 35:2233–2243.

McCorquodale S (2001) Sex-specific bias in helicopter surveys of elk: Sightability and dispersion effects. *The Journal of Wildlife Management* 65:216.

Millette TL, Slaymaker D, Marcano E, Alexander C & Richardson L (2011) AIMS-thermal—a thermal and high resolution color camera system integrated with GIS for aerial moose and deer census in northeastern vermont. *Alces* 47:27–37. Retrieved from https://alcesjournal.org/index.php/alces/article/view/52

Milner JM, Nilsen EB & Andreassen HP (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology* 21:36–47.

Monteiro L, Bonnemaison D, Vekris A, Petry KG, Bonnet J, Vidal R, Cabrita J & Mégraud F (1997) Complex polysaccharides as PCR inhibitors in feces: Helicobacter pylori model. *Journal of Clinical Microbiology* 35:995–998. Retrieved from http://jcm.asm.org/content/35/4/ 995.abstract

Mooty JJ, Karns PD & Heisey DM (1984) The relationship between white-tailed deer track counts and pellet-group surveys. *The Journal of Wildlife Management* 48:275–279.

Morin PA, Luikart G & Wayne RK (2004) SNPs in ecology, evolution and conservation. *Trends in Ecology & Evolution* 19:208–216.

Mullins J, Statham MJ, Roche T, Turner PD & O'Reilly C (2010) Remotely plucked hair genotyping: A reliable and non-invasive method for censusing pine marten (martes martes, L. 1758) populations. *European Journal of Wildlife Research* 56:443–453.

Neff DJ (1968) The pellet-group count technique for big game trend, census, and distribution: A review. *The Journal of Wildlife Management* 32:597–614.

Narum SR, Banks M, Beacham TD, Bellinger MR, Campbell MR, Dekoning J, Elz A, Gurthiere III CM, Kozfkay C, Miller KM, Moran P, Phillips R, Seeb LW, Smith CT, Warheit K, Young SF, Garza JC (2008) Differentiating salmon populations at broad and fine geographical scales with microsatellites and single nucleotide polymorphisms. *Molecular Ecology* 17: 3464–3477.

Norouzzadeh MS, Nguyen A, Kosmala M, Swanson A, Palmer MS, Packer C & Clune J (2018) Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. *Proceedings of the National Academy of Sciences* 115:E5716–E5725.

Noyes JH, Johnson BK, Bryant LD, Findholt SL & Thomas JW (1996) Effects of bull age on conception dates and pregnancy rates of cow elk. *The Journal of Wildlife Management* 60:508–517.

Otis DL, Burnham KP, White GC & Anderson DR (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 3–135. Retrieved from http://www.jstor.org/stable/3830650

Oyster JH, Keren IN, Hansen SJK & Harris RB (2018) Hierarchical mark-recapture distance sampling to estimate moose abundance. *The Journal of Wildlife Management* 82:1668–1679.

Pfeffer SE, Spitzer R, Allen AM, Hofmeester TR, Ericsson G, Widemo F, Singh NJ & Cromsigt, Joris P. G. M. (2018) Pictures or pellets? comparing camera trapping and dung counts as methods for estimating population densities of ungulates. *Remote Sensing in Ecology and Conservation* 4:173–183.

Pollock KH & Kendall WL (1987) Visibility bias in aerial surveys: A review of estimation procedures. *The Journal of Wildlife Management* 51:502–510.

Reed DH, O'Grady JJ, Brook BW, Ballou JD & Frankham R (2003) Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113:23–34.

Rehnus M & Bollmann K (2016) Non-invasive genetic population density estimation of mountain hares (lepus timidus) in the alps: Systematic or opportunistic sampling? *European Journal of Wildlife Research* 62:737–747.

Roffler GH, Waite JN, Flynn RW & Larson KR (2016) Estimation of wolf population density using spatial capture-recapture: Refining methods for monitoring cryptic species. *PeerJ Preprints* 4: e1946v1. doi.org/10.7287/peerj.preprints.1946v1

Romairone J, Jiménez J, Luque-Larena JJ & Mougeot F (2018) Spatial capture-recapture design and modelling for the study of small mammals. *Plos One* 13:e0198766.

Royle JA, Chandler RB, Gazenski KD & Graves TA (2013a) Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology* 94:287–294.

Royle JA, Chandler RB, Sun CC & Fuller AK (2013b) Integrating resource selection information with spatial capture–recapture. *Methods in Ecology and Evolution* 4:520–530.

Royle JA, Chandler RB, Sollmann R & Gardner B (2014) *Spatial capture-recapture*. Oxford, UK: Elsevier.

Royle JA, Fuller AK & Sutherland C (2018) Unifying population and landscape ecology with spatial capture–recapture. *Ecography* 41:444–456.

RStudio Team (2018) RStudio: Integrated development for R. RStudio, inc., Boston, MA. URL http://www.rstudio.com/

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sæther B-E, Solberg EJ, Heim M, Stacy JE, Kjetill SJ & Olstad R (2004) Offspring sex ratio in moose alces alces in relation to paternal age: An experiment. *Wildlife Biology* 10:51–57.

Smith JB, Windels SK, Wolf T, Klaver RW & Belant JL (2016) Do transmitters affect survival and body condition of american beavers castor canadensis? *Wildlife Biology* 22:117–123.

Smith O & Wang J (2014) When can noninvasive samples provide sufficient information in conservation genetics studies? *Molecular Ecology Resources* 14:1011–1023.

Solberg EJ, Loison A, Ringsby TH, Sæther B & Heim M (2002) Biased adult sex ratio can affect fecundity in primiparous moose alces alces. *Wildlife Biology* 8:117–128.

Solberg KH, Bellemain E, Drageset O, Taberlet P & Swenson JE (2006) An evaluation of field and non-invasive genetic methods to estimate brown bear (ursus arctos) population size. *Biological Conservation* 128:158–168.

Sollmann R, Gardner B, Belant JL, Wilton CM & Beringer J (2016) Habitat associations in a recolonizing, low-density black bear population. *Ecosphere* 7:e01406.

Sun CC, Royle JA & Fuller AK (2019) Incorporating citizen science data in spatially explicit integrated population models. *Ecology* 100:e02777.

Sun CC, Fuller AK, Hare MP & Hurst JE (2017) Evaluating population expansion of black bears using spatial capture-recapture. *The Journal of Wildlife Management* 81:814–823.

Sun CC, Fuller AK & Royle JA (2014) Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. *Plos One* 9:e88025.

Sutherland C, Fuller AK, Royle JA & Gimenez O (2015) Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks. *Methods in Ecology and Evolution* 6:169–177.

Sutherland C, Muñoz DJ, Miller DA & Grant EHC (2016a) Spatial capture–recapture: a promising method for analyzing data collected using artificial cover objects. *Herpetologica* 72:6–12.

Sutherland C, Royle JA & Linden DW (2016b) oSCR: Multi-session sex-structured spatial capture-recapture models. R package version 0.30.0. URL https://Github.com/jaroyle/oSCR

Sutherland WJ (2006) *Ecological census techniques: A handbook, 2nd ed.* Cambridge: Cambridge University Press.

Swanson A, Kosmala M, Lintott C, Simpson R, Smith A & Packer C (2015) Snapshot serengeti, high-frequency annotated camera trap images of 40 mammalian species in an african savanna. *Scientific Data* 2:1–14.

Taberlet P, Griffin S, Goossens B, Questiau S, Manceau V, Escaravage N, Waits LP & Bouvet J (1996) Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research* 24:3189–3194.

von Thaden A, Cocchiararo B, Jarausch A, Jüngling H, Karamanlidis AA, Tiesmeyer A, Nowak C & Muñoz-Fuentes V (2017) Assessing SNP genotyping of noninvasively collected wildlife samples using microfluidic arrays. *Scientific Reports* 7:1–13.

Waits LP & Paetkau D (2005) Noninvasive genetic sampling tools for wildlife biologists: A review of applications and recommendations for accurate data collection. *The Journal of Wildlife Management* 69:1419–1433.

Young JK, Golla JM, Broman D, Blankenship T & Heilbrun R (2019) Estimating density of an elusive carnivore in urban areas: Use of spatially explicit capture-recapture models for city-dwelling bobcats. *Urban Ecosystems* 22:507–512.

UNIVERSITY OF TURKU

Painosalama Oy, Turku, Finland 2020

ISBN 978-951-29-8043-7 (PRINT)
ISBN 978-951-29-8044-4 (PDF)
ISSN 0082-6979 (Print)
ISSN 2343-3183 (Online)