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Johanna Suutarinen

ECOLOGY OF LAWBREAKING

EFFECTS OF POACHING ON LEGALLY HARVESTED WOLF POPULATIONS IN HUMAN-DOMINATED LANDSCAPES

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU, FACULTY OF SCIENCE;
NATURAL RESOURCES INSTITUTE FINLAND (LUKE);
SCANDINAVIAN WOLF RESEARCH PROJECT SKANDULV

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Effects of poaching on legally harvested wolf populations in human-dominated landscapes

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Abstract

Illegal killing of wolves (hereinafter 'wolf poaching') in human-inhabited areas, where wolves are also legally harvested is a special case of wildlife crime. This doctoral thesis examines wolf poaching in Finland and Sweden from the ecological perspective. In the first paper, we examined the causes of mortality among collared Finnish wolves and the role of estimated poaching rates on population changes. The second paper related the likelihood of being poached to covariates expressing different dimensions of the wolf conflict at two spatial scales (territory and country level) in Finland. Third paper turns the focus to Sweden, where we examined the disappearances of adult wolves in relation to population size, legal harvest and inbreeding. The first two studies were done in collaboration with the Natural Resources Institute Finland (Luke) and the third with the Scandinavian Wolf Research Project SKANDULV. Poaching outnumbered other causes of death. Most poaching cases were unverified. Other causes of death were legal harvest, traffic and natural mortalities. Both populations had a relatively high number of wolves with unknown fates. Inbreeding was not related to the disappearances of adult wolves in Sweden. Remoteness to human inhabitation and the detectability of the wolves from the forest roads (road crossings by wolves) increased the likelihood of poaching in Finland. Adult wolves suffered high risk of poaching in both populations. Risk was highest in early spring in Finland. Larger population size increased and the number of legally harvested wolves decreased poaching in both countries. Poaching seemed to limit the study populations despite the management efforts that used legal hunting as a tool to increase tolerance towards wolves.

Keywords: Canis lupus, carnivore conflict, game management, population ecology, wildlife crime

Suutarinen, Johanna, Laittomuuksien ekologia. Salametsästyksen vaikutukset luvallisesti metsästettäviin susipopulaatioihin ihmisen hallitsemassa elinympäristössä
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Tiivistelmä

Suden ja ihmisen rinnakkainelo johtaa konflikteihin, joiden lievittämiseksi susikantoja rajoitetaan usein luvallisella metsästyksellä. Suteen kohdistuu lisäksi laitonta tappamista eli salametsästystä. Tämä väitöstutkimus selvittää salametsästyksen ekologisia vaikutuksia Suomen ja Ruotsin susipopulaatioihin. Ensimmäisessä osatyössä selvitimme suomalaisten pantasusien kuolinsyitä, arvioimme salametsästyksen voimakkuutta ja sen vaikutuksia populaatiotasolla. Toisessa osatyössä tarkastelimme susikonfliktiin liittyvien ennustetekijöiden vaikutusta laittomasti tapetuksi tulemisen riskiin reviiritasolla ja koko Suomen mittakaavassa. Kaksi ensimmäistä osatyötä tehtiin Luonnonvarakeskuksen (Luke) suurpetotutkimuksessa. Kolmas osatyö tehtiin osana skandinaavista susitutkimushanketta (SKANDULV). Siinä selvitimme populaatiokoon, luvallisen pyynnin ja sukusiittoisuuden vaikutuksia aikuisten susien katoamiseen Ruotsissa. Salametsästys oli susien yleisin kuolinsyy, mutta suurin osa tapauksista jää toteen näyttämättä. Muita kuolinsyitä olivat luvallinen metsästys, liikenne ja luonnolliset kuolinsyyt. Aineistoissa oli runsaasti kohtaloltaan tuntemattomaksi jääneitä yksilöitä. Yksilöiden sukusiittoisuusaste ei ollut yhteydessä susien katoamisiin Ruotsissa. Syrjäinen sijainti ja susien havaittavuus metsätiestöltä lisäsivät laittoman tapon todennäköisyyttä Suomessa. Salametsästysriski oli korkein kevättalvella. Aikuisilla susilla oli huomattavan korkea riski tulla laittomasti tapetuksi. Tutkimuksen perusteella salametsästyksen määrää selittävät erityisesti susipopulaation kulloinenkin koko ja luvalliset pyyntimäärät. Suurempi susikanta lisäsi salametsästystä ja metsästyslupien määrä vähensi sen riskiä. Salametsästys vaikuttaa säädelleen susikantoja siitä huolimatta, että susikonfliktia on pyritty lieventämään luvallisella metsästyksellä.

Asiasanat: Canis lupus, luonnonvararikokset, populaatioekologia, riistakannat, suurpedot

"In any extensive area of suitable wolf country there will be many packs of wolves making up the population. Just as individual wolves and packs have characteristics, so do populations, and a knowledge of these is of great importance in understanding the life of the wolf."

L.David Mech, 1970, The wolf

Acknowledgements

He was a proper wolf. Men came with snowmobiles and put a collar on him on the 6th of March 2004. He was in good body condition, with 36 kilograms of strength and function; his teeth were perfect except for a piece of right lower canine tooth that had broken off at some point – maybe while catching a moose with the stamina of a young hunter. It was his first winter. He had been born in the last spring to a pack of collared wolf pair that had their territory in the forested area of eastern Finland, not far from the Russian border. The following year he met a female on some of his alone wanders. Then snow covered the ground, and he was confronted by humans again.

I was a proper biology student in my first field work season in the summer 2006. It was the 14th of June. We were driving back to the field station with our foreman. His phone rang. A fisherman had noticed a dead canid beneath a bridge. We made a U-turn. It took us an hour to reach the destination. There was a small bridge on a gravel road not far from a national park. We parked the car a few meters before the bridge. A greyish, swollen carcass of a canid lay in the water with the rounded side of the body visible and close to the surface. The carcass was heavily swollen, and the fur was already coming off the skin. The animal seemed to have something attached to its neck that kept it anchored.

We called the police. The carcass was lifted from the water. It was a wolf with a collar. It was the young male collared in the previous winter. He had been shot. The collar had been attached with a rope and a sinker, a heavy component of a car to keep the carcass under the water. I saw a poached wolf before seeing a living one in the wild.

Years (and some living wolves) later, I started this doctoral thesis on wolf poaching as suggested by my supervisor. The topic probably fitted me better than any easier path I might or should have taken, and the one I took would have been ten times the terror without the several organizations and people I wish to thank.

The Natural Resources Institute Finland (Luke) offered me the data and working facilities. The University of Oulu and the Thule Institute funded my doctoral studies with the Aurora DP. The Finnish Foundation for Nature Conservation funded the first six months and thus made it possible to start this project. The Scandinavian Wolf Research Project SKANDULV and the Grimsö Wildlife Research Station (Swedish University of Agricultural Sciences) upgraded my thesis with collaboration and hosting my research visit. In particular, I am grateful to my employer for the favor of granting me a leave of absence for the time of the doctoral studies.

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1st January 2019 Johanna Suutarinen

List of original articles

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I Suutarinen, J., & Kojola, I. (2017). Poaching regulates the legally hunted wolf population in Finland. *Biological Conservation, 215*, 11-18. doi:10.1016/j.biocon.2017.08.031

II Suutarinen, J., & Kojola, I. (2018). One way or another: predictors of wolf poaching in a legally harvested wolf population. *Animal Conservation, 21*(5), 414-422. doi:10.1111/acv.12409

III Liberg, O., Suutarinen, J., Andrén, H., Åkesson, M., Wikenros, C., Wabakken, P., & Sand, H. Blood may not cause more blood: Population size but not harvest increased wolf poaching. *Manuscript*.

The authors' contributions to the publications:

Paper	I	II	III
Original idea	IK, JS	JS, IK	OL, JS, HS
Data collection	Luke	Luke	Skandulv
Data preparation	JS	JS	JS, OL, PW, CW, MÅ, HS
Data analysis	JS	JS	JS, OL, HA
Manuscript draft	JS	JS	OL, JS
Final manuscript	JS, IK	JS, IK	OL, JS, HA, HS, CW, MÅ, PW

IK Ilpo Kojola; JS Johanna Suutarinen; OL Olof Liberg; PW Petter Wabakken; CW Camilla Wikenros; MÅ Mikael Åkesson; HS Håkan Sand; HA Henrik Andrén; Luke Natural Resources Institute Finland; SKANDULV Scandinavian Wolf Research Project

Contents

1 Introduction

1.1 Background

In most parts of the world, animals live under human dominance in human-altered landscapes (Ceballos & Ehrlich, 2002; Dirzo et al. 2014; Ripple et al. 2014). We humans control wildlife species both in number and in distribution as well as rank them according to our subjective preferences. Some species are seen beneficial and worth protecting while others are considered harmful or threatening to our ways of life (Treves & Bruskotter, 2014). Throughout the human-wildlife history, the solution to such unpleasant coexistence has been extermination (Woodroffe, 2000).

Harvesting is lethal control of wild animals; they are hunted for the goods they offer, such as meat, pelts or trophies, or just culled to get rid of them, and also to earn pride from hunting down the unwelcome beasts. Sustainable harvesting and conservation of species, even if they are not beneficial to humans, is often the goal in contemporary wildlife management (Chapron et al. 2014; Darimont, Fox, Bryan, and Reimchen, 2015). Yet, old habits and attitudes die hard especially among people who live close to large carnivores (Treves & Bruskotter, 2014).

Carnivore populations are often managed to keep them low in numbers, whereas the goal for game populations that are considered beneficial is maximized gain (Darimont et al. 2015; Williams, Nichols, & Conroy, 2002; Woodroffe, 2000). The definition of a population can vary whether we consider a genetic population, a metapopulation or a population as a management unit, which is often based on biologically artificial national borders such as the Finnish grey wolf (*Canis lupus* Linnaeus) population.

Populations are rarely closed systems. Gains and losses within the population define its dynamics (Eberhardt, 1985; Williams et al. 2002). Recruitment brings new individuals to the population through birth and immigration, and losses happen because of emigration and death. In addition to intraspecific factors, such as source-sink dynamics of the connected populations or competition for space, food and mates, populations are affected by interspecific factors, such as predation and human impact, not to forget abiotic environmental conditions (Fiesta-Bianchet & Apollonio, 2003).

From the perspective of lifetime fitness, the one thing you need to do before you die is to reproduce. Every individual will eventually die. The time you have until death is survival, and time can only go forward. For every time step, there is a certain risk of dying (Cox, 1972; Therneau & Grambsch, 2000). As you only die once, you can only die because of one cause of mortality. Therefore, the causes of death are competing risks (Andersen & Gill, 1982; Lunn & McNeil, 1995). The cause-specific mortality risk defines the probability of dying during a specified time because of a certain cause (Heisey & Patterson, 2006).

Intrinsic and extrinsic factors can increase or decrease the cause-specific mortality risk. Mortality risk can differ among social status or age groups, which can influence, for example, the length of pair bonds of monogamous species (Milleret et al. 2016), reproduction success, offspring survival (Borg, Brainerd, Meier, and Prugh, 2015; Brainerd et al. 2006) and stability of the population (Creel & Rotella, 2010). Risk varies both in time and space (Rauset et al. 2016; Sharma, Wright, Joseph, and Desai, 2014); for instance, snow cover can make catching prey easier (DelGiudice, Riggs, Joly, and Pan, 2002; Sand, Eklund, Zimmermann, Wikenros, and Wabakken, 2016), but, on the other hand, makes the tracks of the predator visible to the unfriendly human eye.

The cause-specific mortality rates in wolf populations are mostly related to the extent to which the wolf population coexists with humans (Fuller, Mech, and Cochrane, 2003; Liberg et al. 2012; Person & Russell, 2008; Treves, Artelle, Darimont, and Parsons, 2017; Treves, Langenberg, López-Bao, and Rabenhorst, 2017; Webb, Allen, and Merrill, 2011). Human-caused mortalities are often overrepresented in wolf populations that live in human-dominated landscapes. In contrast, populations in more remote areas with a low level of human contact have higher rates of natural causes of death.

Knowledge on the key factors behind the vital rates and population dynamics is essential for successful conservation efforts and sustainable harvesting, i.e., by harvesting moderately enough to avoid unwanted population decrease and loss of genetic diversity and, eventually, to avoid the risk of extinction (Darimont et al. 2015; Williams et al. 2002). Without sufficient background information, conservation and management actions are based on a trial and error approach and stochasticity often has a leading role. Although measurements on wild populations always contain some error, the patterns of life and death must be known. Wildlife population sizes can be counted in accurate numbers only in rare occasions, but most often they are rough estimates with some uncertainty about the true figures.

Rates and causes of mortality are often difficult to estimate for wildlife populations. Detectability of a mortality event may be related to the cause of death, which complicates the assessment of mortality rate and understanding the significance of different causes of mortality for the population (Liberg et al. 2012; Stenglein et al. 2015; Treves et al. 2017a). Some causes of death, such as traffic kills, are easier to discover and count, but some, such as lethal diseases and illegal kills, may, to a large extent, remain hidden. For example, a legally shot large carnivore is routinely reported to the authorities, but poaching is usually conducted in silence. We might know that the animal survived to a certain date, but then suddenly vanished, without leaving behind any tracks to the mortal incident.

1.2 Position and objectives of the study

This doctoral thesis on the magnitude and effects of poaching on wolf populations in Finland and Sweden comprises three separate studies. In the first article, we examined the causes of mortality among collared Finnish wolves and estimated the poaching rate as well as its possible role to the observed changes in population size. The second article linked the likelihood of being poached to covariates expressing different dimensions of the wolf conflict at two spatial scales. The third paper turns the focus to Sweden, where we examined the disappearance rate and risk of adult wolves in relation to population size, legal harvest and inbreeding. The first two papers were done in collaboration with the large carnivore research of the Natural Resources Institute Finland (Luke) and the third with the Scandinavian Wolf Research Project SKANDULV using data on Swedish wolves.

The wolf is one of the most studied wildlife species (Mech & Boitani, 2003). Research on wolf ecology often requires taking account of human dimensions (Chapron & Treves, 2016; Graham, Beckerman, and Thirgood, 2005; Gude et al. 2011; Moss, Allredge, and Pauli, 2016). In the areas where wolves and humans coexist, conflict is to be expected (Dickman, 2010; Dressel, Sandström, and Ericsson, 2015; Linnell et al. 2002; Skogen, Krange, and Figari, 2017; Treves, Naughton-Treves, and Shelley, 2013). The study populations of this thesis, the wolf populations in Finland and Sweden, represent populations that live in human-inhabited landscapes and are legally harvested because of the ongoing carnivore conflict (Bisi, Liukkonen, Mykrä, Pohja-Mykrä, and Kurki, 2010; Epstein, 2017; Ministry of Agriculture and Forestry, 2015).

Poaching touches the boundaries of several fields of science and practice (Challender & MacMillan, 2014; Europol, 2013; Gavin et al. 2010; Liberg et al. 2012; Peterson, von Essen, Hansen, and Peterson, 2018; Pohja-Mykrä, 2016; Treves et al. 2017c; Trouwborst, 2015). This thesis is a biological study, and, therefore, I do not consider illegality from the juridical viewpoint, i.e., whether or not the conditions of a criminal offence were fulfilled or which stage of the criminal procedure was reached, if any. I refer to poaching as the intentional killing of wolves without legitimacy in contrast to the other human-caused mortalities, such as legal harvesting, i.e., hunting, or accidental traffic kills.

The hidden nature of poaching (Liberg et al. 2012; Wellsmith, 2011) set a challenge for the methodology and interpretation of the results, but it was also the main motivation for this thesis: science is an ideal stage for questions that are difficult from the perspective of both society and investigation. The objectives of this thesis were:

1. To examine the magnitude of wolf poaching as mortality factor in the study populations.
2. To examine the predictors of wolf poaching related to human-wolf conflict.
3. To examine the importance and mechanisms of poaching for wolf population dynamics.

In Chapter 1, I will first give an overview of poaching as an example of the many-sided wildlife crime, then walk through the human-dominated landscape where legal hunting and poaching occurs, to finally review the ecological characteristics of the wolf that make it an interesting model species for a poaching study. In Chapter 2, I will approach the deadly topic from the concepts of survival and mortality, introduce the methodological solutions and describe the wolf data and the methods used in this thesis. In Chapter 3, I will report the main results of each article and discuss them in relation to the study objectives listed above. Lastly, I will discuss the main topics in Chapter 4 and the possible implications and needs for further research in Chapter 5.

1.3 Dark figure of wildlife crime

The illegal killing of wild animals is a globally significant form of wildlife crime, involving ecological, economic and social aspects (Challender & MacMillan, 2014; Elianson, 2004; Europol, 2013; Gavin et al. 2010; Hilton-Taylor, 2000). From the ecological perspective, poaching is a considerable threat to many wildlife populations (Challender & MacMillan, 2014; Leader-Williams, Albon, and Berry, 1990; Liberg et al. 2012; Maisels et al. 2013; Sharma et al. 2014). Wildlife crime occurs at several scales, from large-scale illicit trade to sporadic hunting offenses (Challender & MacMillan, 2014; Chapron & Treves, 2016; Dickman, 2010; Pohja-Mykrä, 2016).

Large carnivores are often seen in a negative light at the local level, although their conservation is valued nationally and globally (Bisi et al. 2010; Boitani et al. 2015; Dickman, 2010; Graham et al. 2005; Pohja-Mykrä & Kurki, 2014; Treves & Bruskotter, 2014; Trouwborst, 2015). In developed countries, poaching is mostly driven by social intolerance, in comparison to the well-acknowledged monetary profit and organized crime related to illicit wildlife trade from the developing countries (Gangaas, Kaltenborn, and Andreassen, 2013; Gavin et al. 2010; Treves & Bruskotter, 2014).

Poaching is mostly unreported and difficult to verify, and it has, therefore, been termed 'cryptic poaching' (Liberg et al. 2012) because of the unknown dimension and frequency of this type of crime (Biderman & Reiss, 1967; Wellsmith, 2011). Acts are kept silent to avoid consequences of the lawbreaking, and poachers often enjoy wide, at least passive, support among the local residents (Peterson et al. 2018; Pohja-Mykrä & Kurki, 2014). Hunting offenses do not directly violate human rights nor have high economic impact and, therefore, are seen as less severe illegal acts in the society. Consequently, these crimes are not among the priorities of law enforcement (Wellsmith, 2011).

Reported poaching cases are only the tip of the iceberg. Achievements in wildlife crime prevention by the authorities are usually not measurable because of the unrecorded crime described above, i.e., the dark figure of wildlife crime. There is also relatively little biological research on poaching mainly because of the difficulties in obtaining data and the methodological challenges, although several poaching studies have emerged during the recent years (Chapron & Treves, 2016; Heurich et al. 2018; Liberg et al. 2012; Person & Russell, 2008; Rauset et al., 2016; Stenglein et al. 2015; Treves et al. 2017a, 2017b).

1.4 It's a human's world

The global distribution and population sizes of large carnivores have substantially decreased relative to their historic levels because of habitat loss and human intolerance (Breitenmoser, 1998; Linnell et al. 2002; Ripple et al. 2014; Treves & Bruskotter, 2014; Woodroffe, 2000). In recent years, however, large carnivores have been expanding in many regions in North America and Europe (Chapron et al. 2014; Moss et al. 2016), although their return is a conflictual process with serious local frustration and displeasure (Dickman, 2010; Graham et al. 2005; Treves & Bruskotter, 2014).

Finland and Sweden are situated in the mid-boreal coniferous forest zone. The landscape characteristics in the rural areas are mostly built on commercial forestry and secondarily on agriculture, resulting in an extensive forest road network, which makes forested areas easily accessible for humans throughout the year. Permanent snow cover appears in mid-November and melts in early May, although this varies both annually and along latitude and altitude.

Wolves cause livestock damage (Kaartinen, Luoto, and Kojola, 2009) and attacks and killing of hunting dogs (Kojola & Kuittinen, 2002; Kojola, Ronkainen, Hakala, Heikkinen, and Kokko, 2004). Wolves also prey on large ungulates such as the moose (*Alces alces* Linnaeus), which is considered to be both the primary prey for wolves (Gade-Jørgensen & Stagegaard, 2000; Kojola et al. 2009; Sand et al. 2016) and the most valuable game species in boreal regions (Timmermann & Rodgers, 2005). Consequently, a large portion of the motivation for wolf poaching arises from the loss of domestic animals to wolves and the unwillingness to share the big game with them (Andrén et al. 2006; Graham et al. 2005; Persson, Ericsson, and Segerström, 2009; Treves & Bruskotter, 2014). In addition to personal fear, human-human conflicts between the different interest groups over the wolf issues may further strengthen the conflict between humans and wolves (Dickman, 2010; Pohja-Mykrä, 2016; Skogen et al. 2017).

Hunting has strong communal value in the rural areas of Northern Europe where human densities are low and urbanization is common (Gangaas et al. 2013; Pellikka, Lindén, Rita, and Svensberg, 2007; Skogen et al. 2017). There are approximately 300 000 hunters per country in both Finland and Sweden (human population sizes approx. 5 and 10 million people, respectively), and majority of hunters live in the countryside. Hunting is usually an important part of the lifestyle of rural people, including game husbandry, hunting dog activities and social events. Furthermore, local hunters have a major role in delivering observational abundance data on game animals in Finland, which are used, for instance, to calculate the official estimates of the wolf population size (Kojola, 2005; Kojola et al. 2014; Kojola, Heikkinen, and Holmala, 2018; Pellikka et al. 2007).

Hunting is regulated by national laws and international conventions, such as the Bern Convention on the Conservation of European Wildlife and Natural Habitats and by the European Union's Habitats Directive (Council Directive 92/43/EEC). Detailed national regulations are given, in particular, in the Hunting Act and Hunting Ordinance in Finland (615/1993 and 666/1993, respectively) and in Sweden (SFS 1987:259 and SFS 1987/905, respectively). Hunting is administered by the Ministry of Agriculture and Forestry in Finland. Swedish Environmental Protection Agency (Naturvårdsverket) was the responsible authority on wolf management in Sweden during 2009–2013, when the license hunting was launched, but partly delegated the responsibility to the County Administrative Boards for 2014–2017.

In addition to sport hunting, hunting is often used in wolf management to build public support for carnivore conservation, striving mainly to maintain populations at stable levels and reduce conflicts over property such as dogs, livestock and game animals (Treves, 2009; Olson et al. 2015). Hunting, although limited, has also been the administrative solution to ease the discomfort caused by wolves both in Sweden and Finland (Epstein, 2017; Ministry of Agriculture and Forestry, 2015; Peterson et al. 2018). Epstein (2017) describes such 'tolerance hunting' as hunting premised on the hypothesis that the negative attitudes towards wolves that lead to illegal killing will be ameliorated to the point of tolerating a greater wolf presence if people are allowed to legally hunt them.

In Finland, wolf hunting is allowed by the so-called exceptional permits. Licenses with targets are issued for removing individual wolves causing damage to, e.g., livestock (Finn. 'vahinkoperusteinen poikkeuslupa'). A second type of permit can be issued for management purposes, based on socio-political issues (Finn. 'kannanhoidollinen poikkeuslupa'). Additionally, the local police can permit a wolf hunt with an individual target in the case of danger or damage, and an act of emergency is also legitimate. In Sweden, in addition to the act of emergency, wolf hunting includes hunting to remove specific individuals prone to cause damage on domestic animals (Swe. 'skyddsjakt') and some hunting to limit population growth (Swe. 'licensjakt').

Although lethal control has been motivated by reducing poaching and increasing tolerance, wolf hunting has also been opposed by some groups in the societies. Contradictory arguments state that there is no scientific support for the tolerance-hypothesis (Epstein, 2017), that the lethal control does not inevitably increase the feeling of stewardship or tolerance over large carnivores (Browne-Nuñez, Treves, MacFarland, Voyles, and Turng, 2015; Treves, 2009), and that it may even cement a negative message about the value of wolves (Chapron & Treves, 2016; but see also Pepin, Kay, and Davis, 2017 and correspondence therein). The negative attitudes and fear of wolves (Dressel et al. 2015; Linnell et al. 2002; Treves, Naughton-Treves, and Shelley, 2013) have been also claimed to be due to hyperawareness of the risks caused by these animals (Dickman, 2010).

1.5 Study species

The wolf populations in Finland and Scandinavia are closely related (Åkesson et al. 2016; Jansson, Ruokonen, Kojola, and Aspi, 2012; Liberg et al. 2005). In Finland, wolves were extirpated in the late 19th century but recolonized the country in the 1990s (Ermala, 2003; Kojola et al. 2014; Mykrä & Pohja-Mykrä, 2015). Since the beginning of the telemetry-assisted wolf monitoring in 1998, the estimates of the population numbers have fluctuated between approximately 100 and 300 wolves (Jansson et al. 2012; Kojola et al. 2014; Figure 2 in Paper I).

The wolf population in Sweden increased from few individuals up to approximately 400 wolves since its re-establishment in the 1980s but, according to the latest estimates, has been reduced to approximately 300 wolves (Liberg et al. 2018; Figure 1 in Paper III). The Scandinavian wolf population is inbred and relatively isolated (Åkesson et al. 2016; Jansson et al. 2012; Liberg et al. 2005). Inbreeding depression can lower survival in early stages of life and decrease litter sizes (Liberg et al. 2005). Inbreeding may also be the cause of the relatively high frequency of congenital anomalies in wolf populations (Räikkönen, Bignert, Mortensen, and Curtis, 2006; Räikkönen, Vucetich, Peterson, & Nelson, 2009; Räikkönen, Vucetich, Vucetich, Peterson, and Nelson, 2013). It is noteworthy that genetic rescues of the Scandinavian wolf population in 1991 and especially in 2007 resulted in higher litter sizes and pairing success leading to increased population growth rate (Åkesson et al. 2016; Vilà, Sundqvist, Flagstad, Seddon, & Björnerfeldt, 2003) and decreased inbreeding (Åkesson & Svensson, 2018).

A family group or pack is the ecological unit of the wolf, and the territorial behavior may be considered a long-term strategy for resources and reproduction. The wolf pack usually consists of the monogamous breeding pair and their offspring. First-time breeding usually occurs at the age of two or later (Fuller et al.

2003). Females come into oestrus in January–February, and, on average, 4–6 pups are born in the late spring (Fuller et al. 2003; Kojola et al. unpublished data; Liberg et al. 2005).

Territory is defended from individual trespassers and neighboring packs. Size of the territory is approximately 1000 km^2 in Finland and Sweden with high variation, but the borders of the territory usually remain approximately the same for years (Kaartinen, Antikainen, and Kojola, 2015; Mattisson et al. 2013). During the summer, when pups are neonatal, movement patterns of the pack are concentrated in the den and rendezvous sites (Gurarie, Suutarinen, Kojola, and Ovaskainen, 2011). Towards the autumn, the movement of the pack within the territory is more flexible, as pups can join the adults. Young wolves usually leave the natal territory during their second year, to find a mate and to establish a territory of their own (Kojola et al. 2006).

Breeding adult survival is the key parameter for the recruitment rate in a wolf population (Borg et al. 2015; Fuller et al. 2003). Annual survival rates of yearling and adult wolves in study areas where humans have not purposefully tried to eliminate a high proportion of wolves vary approximately from 0.55 to 0.85 (Fuller et al. 2003). Breeder loss can have detrimental effects on the survival of the offspring and cause pack dissolution (Brainerd et al. 2008, Borg et al. 2015), alter prey selection and hunting success (Sand et al. 2006) and induce instability in population dynamics (Brainerd et al. 2008). In-time replacement of the lost breeder(s) can buffer the effects of adult mortality (Brainerd et al. 2008; Milleret et al. 2016), but high turnover rate may have genetic consequences both at the local level and to connectivity of populations (Rick, Moen, Erb, and Strasburg, 2017).

Wolves are characterized by various mechanisms that could contribute to intrinsic population regulation: territoriality, intraspecific competition, high dispersal rates and reproductive inhibition among subordinate pack members and lone wolves (Fuller et al. 2003). Prey availability, i.e., food resources for wolves, is determined by prey density and vulnerability (Fuller et al. 2003; Sand et al. 2016). Therefore, habitat quantity and quality, weather conditions and competing predators can all affect wolf numbers (Fuller et al. 2003). Density dependence has been observed in wolf populations without human impact, such as the Yellowstone and the Isle Royal wolf populations (Cubaynes et al. 2014; Fuller et al. 2003; Peterson & Page, 1988, Peterson, Thomas, Thurber, Vucetich, and Waite, 1998; Vucetich & Peterson, 2004).

Human-caused mortality is often overrepresented in areas where humans and wolves coexist (Fuller et al. 2003; Liberg et al. 2012; Person & Russell, 2008; Treves et al. 2017a, 2017b; Webb et al. 2011). The estimates of sustainable harvest rates for wolves vary from less than 30% (Adams, Stephenson, Dale, Ahgook, and Demma, 2008; Creel & Rotella, 2010) up to approximately 70% (Fuller et al. 2003; Gude et al. 2011), depending on the productivity of the wolf population and the status of the animals killed (Adams et al. 2008; Gude et al. 2011; Webb et al. 2011).

2 Material and methods

2.1 Survival analysis

Survival and mortality at different life stages are the vital rates to study in order to understand population dynamics and especially to predict future changes (Eberhardt, 1985; Williams et al. 2002). Survival and mortality can be expressed in several ways, but they are always related to time. Death is an evident consequence of life. It follows that survival and mortality are mathematically equivalent expressions in that specification of one function is sufficient to determine the form of the other (Williams et al. 2002).

Survival rate is measured as the proportion of individuals in the population that survive from one point in time to the next. It is visualized as a survivorship curve, representing temporal patterns of mortality over time. A survivorship curve is straight when mortality is roughly constant over the ages or for continuous time steps. The length of the interval gives the time to the next death in the population, and the depth of the step expresses the change in survival, i.e., mortality rate, from one time interval to the next. Individuals are excluded from the mathematical population at risk at the time of death or censoring.

Mortality and survival may also be expressed as probabilities. Probabilities are associated with random variables. For mortality and survival probabilities, the random variable is survival time (T). The mortality probability at time t, $M(t)$, is the probability that the survival at time T will be less than some specified time t. Death is an exclusive event. Therefore, the forces of mortality are competing risks. The cause-specific mortality risk defines the probability of dying during a specified time because of a certain cause (see Heisey & Patterson, 2006). It introduces a second random variable, K, which is the cause of death. Cause-specific mortality is the joint probability that death occurs before t, $T<t$, and that its cause is of type k ($K=k$). It follows that the cause-specific mortality probabilities sum to the total mortality probability. The cause-specific risk can be also expressed as a cumulative incidence that gives the overall risk for an individual to die during the study period because of a certain cause of death.

Survival analysis examines the time to an event (death) and the effect of covariates on that time. Cox proportional hazards regression (hereinafter Cox PH) is a common tool in survival analysis (Cox, 1972; Heisey & Patterson, 2006; Therneau & Grambsch, 2000). We examined the risk (Paper I) and related risk factors (Paper III) with the Andersen-Gill extension of the Cox PH in a competing risks framework (Andersen & Gill, 1982; Heisey & Patterson, 2006; Lunn & McNeil, 1995).

Data for a competing risk model is structured so that each row in the dataset is multiplied, i.e., stratified, by the number of the possible events (causes of death). A stratified analysis partitions the effects of the covariates into separate cause-specific components and estimates them separately allowing cause-specific base hazards. An event variable is coded as “1” for event and “0” for surviving the interval without event. Survived intervals with zero events are not considered as incomplete data but as subjects whose event has no occurred yet. Data with time-varying covariates is further organized in a long format where each row represents one time interval of the exposure time of the individual with enter and exit values of the successive time steps. Covariates represent the conditions during the corresponding interval of risk.

Cox PH is quite similar to logistic regression. Logistic regression is a predictive regression analysis that explains the relationship between the binary outcome and the independent explanatory variables. Central statistical output of Cox PH is the hazard ratio (HR). It is interpreted in a similar manner as the odds ratio (OR) in logistic regression: it tells how the likelihood of the event changes if the explanatory variable changes by one unit. These ratios can be used to predict the likelihood of events with a given set of predictor values. For example, if the risk of being shot increases with the number of hunters involved, how does the risk change if the number of hunters is increased by one man? If the ratio is, for instance, 1.20, then the likelihood of being shot would increase by 20% (or by one fifth) because of the additional armed man.

Mortalities can also be surveyed in relation to their compensatory versus additive effect on the total mortality and survival at the population level. The compensatory and additive mortality models (hypotheses) have been used to examine the effects of harvesting on populations (Williams et al. 2002). The additive mortality hypothesis states that harvesting affects by adding a harvest-mortality component to the existing mortality and, therefore, causes a decrease in survival rate (Williams et al. 2002). According to the compensatory mortality hypothesis, a mortality factor does not change the overall survival rate until a compensation limit is reached, after which survival declines as harvest rate increases. Therefore, in this scenario, harvest would not reduce growth rate of the population at low or moderate levels because it is compensated by reduced rates of other causes of mortality.

The partial mortality hypothesis expresses compensatory and additive mortalities as logical extremes of population-level responses to the mortality factor. It assumes that there is a threshold for the response: below the threshold survival declines, but not as much as if there were no compensation, and above the limit mortality is additive. Mortality can be also super-additive if it affects the survival beyond the direct effect of the death of one individual; for example, if the mortality of the breeding adults affects the survival of the offspring (Creel & Rotella, 2010; Milleret et al. 2016).

2.2 Sources of uncertainty and bias in survival analysis

Observations are called censored if the information about survival time is incomplete. Censoring represents a particular type of missing data. Censored individuals are absent from the population at risk after being censored and thus affect the number of individuals entering the next time interval. To avoid negative bias in survival estimates, it is valid and necessary to retain the individuals in the population at risk as long as their detection probabilities are reasonably independent of their fates (DeCesare, Hebblewhite, Lukacs, and, Hervieux, 2016).

The most commonly encountered form is right-censored data. It means that survival times are known for some of the individuals, and for the others, survival times are only known to exceed certain values. An observation is left-censored if the event occurs before there is a chance to involve the individual in the study. Interval-censored observations are time gaps in the data after the individual has entered the study but before the event. Although it is known that the individual did not die during the period of missing observations, the whole time period cannot always be used as such in the analysis because the conditions might be unknown. Interval-censoring means that these individuals are not included in the population at risk during the intervals of missing data.

Whereas censoring can occur despite the design, truncation originates from the study design. Truncation means that individuals enter the study in steps, for instance, during different years as the study progresses. This is also called staggered-entry design (Pollock, Winterstein, Bunck, and, Curtis, 1989). Left-truncation results when individuals have been at risk before entering the study but that data is not available for the analysis because individuals have not been observed before belonging to the mathematical population at risk.

Two serious biases may arise if animals enter the population at risk as a study progresses (Heisey & Fuller, 1985). Firstly, animals that have not been marked may die early during the study period, thus being unavailable for marking in later years. This may cause an upwards bias to the estimated survival rates and underestimate the magnitude of the mortality force in question. Secondly, if survival varies seasonally, then seasons having the largest sample sizes will be most influential in determining overall survival rates, or they might be the most influential in determining annual survival rates if the sample size is largest during that season because of detection probability or marking method.

2.3 Biotelemetry in data collection for survival analysis

Detection of the individual fates in wildlife populations is highly improved when biotelemetry, i.e., positioning equipment tagged on animals, is used. Wolves are usually equipped with collars. Traditionally collars have been attached with VHF (Very High Frequency) transponders that are based on radio waves and, therefore, require manpower for locating the animals with handheld or vehicle-attached antenna. Nowadays, the solution is usually to have a satellite-based positioning system, such as GPS (Global Positioning System) together with a GSM (Global System for Mobile Communications) network component, enabling communication with the collar, i.e., scheduling the positioning frequency and receiving data from the collar.

Despite the groundbreaking data this equipment offers, it is not very durable, and the technology sometimes fails. Actively functioning tags, such as GPS-GSM-collars, are dependent on battery power and, therefore, have a limited lifespan. Collars can be destroyed along with the carrier. Collared wolves have been lost with no tracks left behind even while they have carried a brand-new collar. Unknown fates are typical in the survival data of wild animals despite the use of biotelemetry. If the contact is lost, the observations are usually treated as censored in survival analysis, a topic discussed above.

Telemetry is widely used in survival analysis of wildlife populations despite the assumptions of random and non-informative censoring (DelGiudice et al. 2002; Heisey & Fuller, 1985; López et al. 2014; Murray, 2006; Pollock et al. 1989; Tsai, Pollock, and, Brownies, 1999). In order to make population level interpretations, collared animals should constitute a representative sample of the population, and collars should not bias the cause-specific mortality risks. These assumptions might be violated directly or indirectly if the collar decreases fitness or, for example, makes the individual more attractive target for hunters. Additionally, survival times of individuals should not be correlated with each other, and animals recruited at different times (years) and ages should have the same underlying survival function. This can be challenging because of the correlation in time and space often observed in time series data. Furthermore, death times should be exact to avoid bias in survival rates. Violation of assumption(s) requires careful consideration because they might cause error or bias to the results. However, violations can shed light on the study questions if we detect them and let the data teach us.

2.4 Wolf data and analysis tools

Data becomes information when put in the correct context, and information becomes knowledge when combined with experience and interpretation. Coordinates given by the GPS collar are data; it becomes information when identified as an individual animal and mapped with the timestamps and geographical data. These movement patterns become knowledge when an expert combines the information with the expertise gained from professional experience and previous research.

In Finland, wolves have been equipped with radio and GPS collars since the year 1998. This data was used to determine the fates of individual wolves, although it was full of gaps and missing details. The original aim for the data collection has not been the detection of poaching cases. To cover the gaps, we collected all available information concerning the fates of these animals, including oral information from the wolf-research personnel. In most cases, the information remained unverified and was cumulative by nature, like a puzzle that needs time and several pieces to form a picture. In order to use such important but fragmented and imperfect information in scientific research, we classified the poaching cases according to the confidence (reliability) of information so that we could use that information in population models.

In Paper I, we used data on collared wolves that died before May 2014 to estimate cause-specific mortality rates and the possible role of cryptic poaching on population changes observed in the Finnish wolf population. The data included 130 collared wolves, 57 females and 73 males. We investigated the cause and estimated the date of death for all wolves (Table 1 in Paper I), and social status at the time of death (n=91) or censoring (n=39) was determined.

To determine the cause and date of death as accurately as possible, we surveyed the timing of the last observation of the animal being alive versus proof of its fate. In addition to positioning and snow-tracking data and the verified records of authorities, we collected above-mentioned oral, and at that point undocumented, information from research personnel on the unverified poaching cases. This so-called 'silent information' comprised both first-hand knowledge and observations of the events as well as oral information told to the research personnel by the offender or locals. We classified the information on poaching cases into four categories (Evidence, Knowledge, Hearsay and Odds) based on its quality, i.e., the confidence of the information combined with the accuracy of the event date estimate (see Table A.1 in the supplementary material of Paper I). If the information on a potential poaching case was based on less or lower quality information than in the Odds class, it was censored at the last observation.

For the Paper II, we selected collared wolves from the Finnish data to be included in the analysis on the predictors of wolf poaching with the following criteria: i) death was caused by poaching or legal hunting, ii) wolf died outside of the reindeer herding area (where the wolf hunting policy is more liberal than in the rest of Finland in order to keep the reindeer herding area free of resident wolves) (Ministry of Agriculture and Forestry, 2015), iii) was not known to be a member of the same pack as any other study animal included in the analysis, and iv) were identifiable as juvenile (< 2 years old) or adult (> 2 years old) based on social status (Kojola et al. 2006) or age defined from a tooth sample (Matson's Laboratory LLC, Montana, USA).

Following the above criteria, we had 38 illegally and 16 legally killed collared wolves that died during the calendar years 2001─2016. To obtain the same number of legally killed and poached wolves for the analysis, we randomly sampled 22 legally killed wolves from the inclusive bag record data of legal harvest from 2001─2016 that met the same criteria. Final data included 52 adults (23 females, 29 males) and 24 juveniles (13 females, 11 males).

We defined the geographic location for the kill sites. Using the kill site as the center point, we created a round-shaped range of 1000 km^2 to calculate the spatial variables. To examine the country-level predictors (Table 1 in Paper II) in more detail at the territory-level (Table 3 in Paper II), we extracted data on GPS-collared breeding adult wolves from the total data (n=30: 11 females and 19 males), of which 22 were poached and 8 were legally killed. We defined the territory area as the 100% MCP (Minimum Convex Polygon).

With the dataset from Sweden (Paper III), we examined the disappearances of adult territorial wolves by using data from the annual monitoring system of scent-marking or breeding wolf pairs from the years 2000─2017 (n=452 wolves: 217 females, 235 males). Wolf monitoring in Sweden is performed annually by authorities during the winter months from October to March. During the study period, 77 wolves (39 females, 38 males) were collared. We used the data on these collared wolves to complement our mortality analysis based on the monitoring data and, in particular, to elucidate the fates of disappeared un-collared wolves in the larger material.

We determined the status for wolves with one of the following fates from one monitoring season to the next: i) alive to next season, ii) legally shot, iii) killed in traffic or from various natural causes, iv) disappeared without known cause, or v) censored. Verified poaching cases were included in category *iv* with the disappeared wolves. Intensive genetic monitoring of the Swedish wolf population made it possible to investigate the effect of inbreeding on disappearance at individual level, by using the individual inbreeding coefficient and, at the population level, using the average of the parental inbreeding of each study year (see Åkesson et al. 2016 for details).

All statistical analyses in Papers I, II and III were performed with program R (R Core Team 2015, R Foundation for Statistical Computing, Vienna, Austria), and spatial information was handled using ArcMap 10.3.1 (ArcGIS, ESRI, Redlands, California, USA) and the Geospatial Modelling Environment (GME, Hawthorne L. Beyer, Spatial Ecology LLC). Model selection and multimodel inference were made based on Akaike's information criterion approach (Burnham & Anderson, 2002).

2.5 The unknown wolf: cause-specific mortality rates and population level effects of wolf poaching in Finland (I)

In Paper I, our goal was to examine the role of poaching on wolf population dynamics. We did this by first organizing the existing data on the fates of collared wolves in a competing risks design for survival analysis. Then, we tested random censoring assumption, which resulted in two different data sets, taking account of informative censoring in the data. Next, we categorized the data according to the confidence of information on the poaching cases by creating four different scenarios. Then, we calculated the cause-specific mortality risks for both censoring datasets including the four scenarios. Lastly, we estimated the yearly poaching rates by creating scenario-wise population size estimates and comparing them to the standardized, official population size estimates of the Finnish wolf population. These steps are described below (see Paper I for more details):

Data preparation

1. Arranged the data in time-to-event structure with one-day time interval allowing staggered entry.
2. Pooled the data over the years into an ecological year (May–April).
3. Tested if censoring was random with respect to event, sex and social status, using multinomial regression. Results indicated informative (non-random) censoring for social status. Censoring was related to dispersers and poaching to alpha wolves.
4. Informative censoring was incorporated by creating two datasets:

    a) Random censoring dataset: event dates were kept in the original form
    b) Informative censoring dataset: event dates were imputed based on social status:

        i. Alpha wolves: exact date of the last observation
        ii. Potential or actual dispersers: were assumed to be alive at the end of the study to keep them in the population at risk

Poaching scenarios

5. Created 4 scenarios based on the confidence of information categories by step-wise censoring the poaching cases in the categories resulting in 8 scenarios (2 censoring datasets both including the same 4 scenarios).

    Scenario 1: High poaching including all categories and all cases
    Scenario 2: Evidence and Knowledge cases included and cases in Odds and Hearsay categories censored
    Scenario 3: Only Evidence cases included and cases from categories Odds, Hearsay and Knowledge censored
    Scenario 4: All poaching cases censored

6. Calculated scenario-wise cause-specific mortality rates as cumulative incidences, using Cox PH with competing risk framework.

Population modelling

7. Calculated standardized population size estimates ($N_t^o(\pm)$) for the 31st of December each year, based on official reports on the wolf population size.

8. Calculated an annual dummy population ($N_{t+1}^{*}\pm = N_t^o(\pm) + R_{t+1} - M_{t+1}^l$), where N_t^o is the standardized population size estimate at year *t*, $\pm$ for calculating both lower and upper values of the estimate range the same manner, R_{t+1} is the pup recruitment and M_{t+1}^l is legal harvest at calendar year *t+1*.
9. Created scenario-specific population size estimates ($N^j\pm = N_{t+1}^{*}(\pm) \times (1 - m_{k\ldots n}^{j\ldots n})$ by combining scenario-specific mortality rates to the annual dummy population (excl. legal harvest that was included in the dummy population).
10. Defined the yearly poaching rate estimates as the smallest difference ($\bar{D}_t^j = \bar{N}_t^o - \bar{N}_t^j$) in the number of wolves between the median of the standardized population size estimates and the scenario-specific population size estimates.

2.6 Finger on the trigger: predictors of wolf poaching in Finland and how to account for cryptic poaching in management (II)

To examine the predictors of wolf poaching at the country and territory level, we analyzed the data with logistic regression using a generalized linear model (glm) with a binomial response (0=legal, 1=illegal). For the country model, we had three working hypotheses that are listed below with the covariates included in the respective a priori models (Table 1 and 2 in Paper II). We simplified the a priori full models and created a full combined model based on that simplification, which we again simplified. This procedure resulted in 15 candidate models (Table 4a in Paper II). For the territory model, we created three alternative models: one with both variables included (frequencies of road crossings and yard visits by the collared wolves) and one with both variables separately (Table 4 in Paper II). The model selection and multimodel inference procedure are described in more detail in the Paper II.

Working hypotheses 1–3 and the variables included in these a priori models:

1. "Poaching is related to unsatisfactory low levels of legal wolf hunting"
   a) Legal wolf harvest at the local area (1000 km^2 range) during the hunting year (starting 1st of August) the wolf died
   b) Legal wolf harvest within the game administration region

c) Legal wolf harvest in the whole country
d) Change in total legal wolf harvest in two consecutive hunting years

2. "Poaching is related to conflict between wolf presence and hunting in general"
   a) Annual change in moose harvest within the game administration region
   b) Proportion of hunters within the total human population in the province
   c) Number of dog damages categorized in three levels
   d) Forest road density within the 1000 km^2 range

3. "Poaching is related to conflictual coexistence of wolves and humans"
   a) Human population density per km^2 within the local area (1000 km^2)
   b) Number of livestock damages categorized in three levels
   c) Rate of total wolf population increase
   d) Life stage (adult or juvenile)
   e) Sex

We aimed to predict poaching probabilities based on odds ratios (OR) of the top-ranked-country model and to derive the estimated number of poached wolves for different scenarios of legal harvest. ORs can be used to predict a probability of an event to occur for a given set of predictor values. We calculated the predicted number of poaching cases for a hypothetical wolf population of 250 wolves with the approximate proportion of adults and juveniles as found in the Finnish wolf population (Kojola et al. unpublished data): 80 adults (32%) and 170 juveniles (68%). Finally, we calculated separately the predicted poaching probabilities for adults and juveniles. We created a new data frame representing different harvest strategies, with the local harvest ranging from 0 to 5 wolves and total legal harvest from 10 to 80 wolves at intervals of ten, with human absence and moderate human density (10 inhabitants per km^2).

2.7 Lost and never found: wolf disappearances in Sweden in relation to population size, legal harvest and inbreeding (III)

We used glm to model disappearance rate at the population level and Cox PH to model disappearance risk at the individual level, in relation to the number of territorial pairs as a proxy for population size, legal harvest and inbreeding. For the number of territorial pairs, we used the corrected monitoring data from the Wildlife Damage Center (Sweden) and Inland Norway University of Applied

Sciences (Wabakken, Svensson, Maartmann, Åkesson, and Flagstad, 2018). Legal harvest was defined as the number of legally shot wolves from October to April. To estimate the effect of inbreeding on disappearance, we used the individual inbreeding coefficient at the individual wolf level and the annual average parental inbreeding at the population level (Åkesson et al. 2016; Liberg et al. 2005).

Wolves entered the population at risk at the first monitoring season they were recorded as a territorial pair and exited it at the time of event or censoring. Individuals that lost their partner were censored but were entered again if they later appeared in a new territorial pair. All individuals alive at the end of the study period were censored. Wolves that disappeared during the first monitoring season they were recorded were kept in the analysis to avoid bias against short-lived pairs.

We calculated the annual survival and mortality rates with a Cox PH null model and estimated the overall cause-specific risks. We created the disappearance rate response variable by relating the number of disappeared wolves to the population at risk into a single response object. We created the candidate set of disappearance rate models, including all possible combinations of the three covariates and an intercept-only model, resulting in a total of eight candidate models.

For Cox PH, we constructed the survival data in a long format with each row representing one time step from one monitoring season to the next. We stratified the data based on the possible events: i) legally killed, ii) killed in traffic or from natural causes, or iii) disappeared. Finally, we pooled the data among years, resulting in enter=1 and exit=2 for all wolves. We created all possible combinations of the three covariates resulting in a total of seven candidate risk models.

To complement our mortality analysis based on the monitoring data, and especially to elucidate the fates of disappeared un-collared wolves in the larger material, we applied a Kaplan-Meier cause-specific survival analysis with staggered entry design to the 77 collared wolves. We identified three causes of mortality: i) legal harvest, ii) poaching, and iii) other mortality including traffic deaths and natural mortality. The methods are described in more detail in Paper III.

3 Results

3.1 History of intolerance: poaching regulates the legally harvested wolf population in Finland (I)

Almost all the observed deaths among the collared Finnish wolves were caused by humans. Poaching was the main cause of death and represented the fate of 40% of all collared wolves (52 of 130) and 57% of all known mortalities (52 of 91), when all poaching cases were included by using all the confidence of information categories.

Prior attempts of poaching were observed among 9 individuals during collaring or autopsy, including encapsulated lead shots in body (n=5), old injuries of being shot (n=2) and injuries caused by a snare (n=2). Poaching was the ultimate cause of death for 2 of 3 euthanized wolves: one female had severe injuries from a snare, and the other, based on the injuries, was probably run over by a snow mobile and had encapsulated lead shots in her body. The third euthanized wolf was a female who had both hind legs paralyzed because of a broken spine. Deaths from natural causes were few. Two wolves were killed by defensive prey (moose) and one by a neighboring wolf pack. Lethal diseases were not observed.

Legal hunting was the second most important cause of death, including 22% of the collared wolves and 32% of the known mortalities (n=29). The risk to die in legal hunting was substantially higher (> 0.25) among collared wolves than for an average individual in the Finnish wolf population (see also Treves et al. 2017a). In the total population, legal harvest annually represented 3.7–21% of the total population size in 2000–2016.

The annual survival ranged from 11 to 60% depending on the scenario (Table 2 in Paper I). The overall poaching risk was 0.43 in the informative censoring and 0.51 in the random censoring scenario 1; 0.25/0.31 (informative/random) in scenario 2 and 0.09/0.13 in scenario 3. Survival exhibited a clear seasonal trend in all scenarios by showing the strongest decline during winter (Figure 1 in Paper I). The median mortality was dated to the end of January and beginning of February, meaning that 50% of the annual mortality occurred before that threshold and 50% during the early spring from February to April. The risk of poaching before the annual, permanent snow cover in mid-November was less than 0.11, excluding the no-poaching scenario. Thus, the risk of poaching was 3–5 times higher in winter compared to the snow-free season. Censoring of collared individuals occurred throughout the year but peaked during winter (mid-February to late March).

Random and informative censoring scenarios showed some differences in the explanatory power to the observed population changes, with the random censoring predicting the major trends and the informative censoring giving a more detailed degree of explanation (Figure 2 and 3 in Paper I). The informative censoring procedure had a slightly better overall fit (9 years) than the random censoring procedure (7 years), measured as the smallest difference in the number of wolves between the median of the standardized population size estimate and the scenario-specific population size estimate. Scenarios 2 and 3, i.e., the scenarios with higher poaching rates, correctly predicted the years with population declines (2007, 2009, 2012 and 2016). Poaching rates in these scenarios varied between 0.9 and 0.31, and annual survival varied between 0.24 and 0.53. For the year of strongest decline (2009), scenario 1 was best supported among the informative scenarios. For all other years, scenario 4 assuming zero poaching, in which survival varied between 0.43 and 0.60, had the smallest difference (Figure 3 in Paper I). It is worth noting that survival was less than 0.60 even when assuming zero poaching. Years with poaching risk lower than 0.13 resulted in increased population size estimates. These periods of increased population size were, again, followed by increased poaching rates (Figure 2 in paper I).

3.2 One way or another: low legal harvest, adult life stage, remoteness and detectability predict poaching in Finland (II)

According to the country model of poaching predictors, the likelihood of illegal kill was related to both local and total legal harvest, human density and life stage (Table 4a in Paper II). Adult wolves had remarkably higher likelihood to be poached compared to juveniles. Higher levels of legal harvest and higher human density decreased the likelihood of poaching. The chance of being poached was three times less likely if there was another wolf shot with permission within the 1000 km^2 range during the hunting season in comparison to the absence of licensed wolf hunting. The likelihood of illegal kill decreased by an OR of 0.90 (95% CI 0.81 to 0.96) for an increase of one wolf in the total legal bag, being equal to approximately a 10% higher chance for the wolf to die in a legal hunt than to be poached.

Because the effect of forest road density in the country model was slightly unclear and human density was an important variable but dog and livestock damages were not, we examined the role of forest roads and human inhabitation to the likelihood of poaching in more detail at the territory level. According to the territory model, the likelihood of illegal kill was increased by the frequency that the wolves crossed roads, but the frequency of yard visits did not affect poaching (Table 4b in Paper II).

We used the top-ranked country model to predict poaching probabilities for different wolf harvest strategies. Assuming that we would have a harvest strategy with a constant quota of 30 wolves allocated as one permit per local area and with no human residence, the probability of being poached would be 0.46 for adult wolves and 0.05 for juveniles. For a more densely human-populated area (10 permanent inhabitants per km^2), the probabilities would be 0.14 for adults and 0.01 for juveniles. For the hypothetical population of 250 wolves, the former example would double the total loss: 36 poached adult wolves and 8 poached juveniles in addition to the quota of 30 legal kills, whereas the latter example would more than halve it: 11 poached adults and 2 poached juveniles.

3.3 Disappeared in a puff of gun smoke: population size but not legal harvest trigger wolf poaching in Sweden (III)

Of the 452 territorial wolves included in the study, 348 (77%) were recorded in one of the three classes of losses: 104 wolves were legally killed, 18 died of natural causes and 8 were traffic kills, and 218 wolves were classified as disappeared, including 19 cases of verified poaching. 104 wolves were censored. The average total annual loss rate including both known mortalities and disappearance was 0.24 (95% CI 0.21 to 0.26).

Annual disappearance rate varied between 0.04 and 0.25 with a mean of 0.14 (Table 1 in Paper III). Disappearance rate increased during the first few monitoring seasons from 0.05 up to 0.14 in 2002–2003, remained relatively stable around 0.10 (range 0.06–0.13) until the monitoring season 2010–2011 and was then followed by a new increase to approximately 0.22 (range 0.16–0.25) for the years 2011–2017.

Among the monitored territorial wolves that were lost from one year to the next, the individual risk of being legally shot for the entire study period was 0.21 (95% CI 0.13 to 0.29) and of dying of natural causes or traffic 0.15 (95% CI 0.04 to 0.24), whereas for disappearing it was 0.63 (95% CI 0.49 to 0.73). As the overall annual loss rate was 0.24, the combined annual risk to be lost due to legal harvest was 0.05 (0.24×0.21), the risk to be lost due to traffic or natural causes was 0.04 (0.24×0.15) and the individual risk of being lost due to a disappearance was 0.15 (0.24×0.63).

The Kaplan-Meier analysis of the 77 collared wolves gave similar levels of mortality as our analysis of the larger monitoring data (Table 1a and b in Paper III). Legal harvest rate over the years was 0.022, traffic-caused death rate 0.007, natural death rate 0.031, and poaching, including both verified and cryptic cases, had a rate of 0.118. Both legal harvest and verified poaching rates increased from the first part of the study (2000–2010) to the second (2011–2015), while traffic and natural death rates remained at low levels throughout the study years.

Population size and harvest both explained the disappearance rate in the models on population level and were included in the top-ranked model (Table 2 in Paper III). Population size was positively and harvest negatively related to disappearance rate. Population size was the most important variable, with high relative variable importance (RVI 1.00), followed by harvest which had RVI 0.56. Average parental inbreeding had negative effect on disappearance rate but with low relative variable importance (RVI 0.35). Confidence intervals of the model coefficients for harvest and average parental inbreeding overlapped zero.

Population size was the most important variable with a positive effect on the disappearance also at individual level (Table 3 in Paper III), but there was also a significant and negative effect of harvest (RVI 0.84). The two models with the strongest support (ΔAICc < 2, Table 3 in Paper III) included both population size and harvest. The effect and importance of individual inbreeding on disappearance risk was low, and the model coefficient overlapped zero (RVI 0.33, Table 3 in paper III).

3.4 Concluding the results per study objective

1. **The magnitude of wolf poaching as a mortality factor in the study populations**: Poaching was the major cause of death both in the Finnish and the Swedish wolf population. Most poaching cases were unverified, i.e., cryptic. Other causes of death were legal harvest, traffic and natural causes such as diseases, intraspecific conflict and killed by prey. Both populations had a relatively high number of unknown fates (censoring).
2. **The predictors of wolf poaching related to human-wolf conflict**: Poaching seems to be mainly related to wolf population size and legal harvest in both countries. Larger population size increased poaching, but annual rate of population increase had no effect on poaching likelihood in Finland. Higher levels of legal harvest decreased poaching. Inbreeding did not explain the disappearances of adult wolves in Sweden. Remoteness (low human density) and the detectability of the local wolf population from the forest roads increased the likelihood of poaching in Finland.
3. **The importance and mechanisms of poaching for wolf population dynamics**: Poaching by far outnumbered other causes of death. Adult wolves suffered from a high risk of poaching in both populations. The poaching risk was highest during the early spring in Finland, overlapping in time with the mating season. Poaching increased as a response to higher wolf population size in both countries. Increased poaching rates were followed by decreased population sizes. Cryptic poaching seemed to regulate the wolf population sizes in both countries.

4 Discussion

Poaching and inbreeding are the most critical conservation issues for the Scandinavian wolves (Åkesson et al. 2016; Liberg et al. 2005, 2012). According to the results of this thesis, it seems that the wolf populations in Finland and Sweden are more likely being limited by poaching than other factors: poaching outnumbered other causes of death (Papers I and III), targeted, in particular, adult wolves (Papers I, II and III), were particularly high during the mating season (Paper I) and seems to have intensified as a response to increased wolf presence both in detectability (Paper II) and population size (Papers I and III). Furthermore, there is no support for other explanations than poaching for the high number of lost individuals in these intensively followed populations, given the relatively low levels of legal harvest, absence of density dependence and sufficient prey resources (Gade-Jørgensen & Stagegaard, 2000; Kojola et al. 2009; Mattisson et al. 2013; Nikula, Heikkinen, and Helle, 2004; Sand et al. 2016) and the decreasing trend of inbreeding for Swedish wolves (Paper III, Åkesson et al. 2016).

Poaching rate varied considerably between the study years in Finland and seems not to be constant. Periods of increasing population size were followed by periods of higher poaching, which seemed to regulate the growth of the population (Paper I). It is worth noting that the rate of population growth in two consecutive years did not affect poaching likelihood, but the detectability of the local wolf population increased the chance of being poached (Paper II).

The wolf population in Sweden is one of the most intensively followed wolf populations in quality and quantity with a near-complete pedigree back to the founding individuals (Åkesson et al. 2016; Liberg et al. 2005, 2018) and with well-known geographical distribution over a human-inhabited landscape. Nevertheless, nearly half of the adult wolves in the scent-marking or breeding pairs that were followed over multiple monitoring seasons disappeared soon after their discovery. The Swedish wolf population has been increasing since its re-establishment in the early 1980s, but this increase has recently turned into a decrease after reaching approximately 400 wolves (Liberg et al. 2018). According to Paper III, population size was the most important variable explaining disappearances of wolves. Importantly, the positive effect of population size on disappearance was almost 5 times higher than the negative effects of legal harvest on population level and more than 4 times higher on individual level (Paper III). The increasing trend in disappearances among adult wolves in Sweden cannot be explained by undetected natural mortalities related to inbreeding depression or an unknown mortality agent.

Poaching risk was substantially higher for adult wolves in comparison to juveniles (Paper II) and was highest in January-February, i.e., during the mating season (Paper I). The loss of breeding individual(s) can lead to pack dissolution (Borg et al. 2015), and the mortality factor can act in a super-additive way, resulting in an increase in the total mortality as a consequence for the death of one individual (Creel & Rotella, 2010; Milleret et al. 2016). The in-time replacement by immigrant dispersers is essential to ensure reproduction and avoid incestuous breeding. Human-caused mortality can also have a genetic effect on both the local and population-wide scale because of the higher turnover rate (Rick et al. 2017). Wolves have high potential for population growth (Fuller et al. 2003), but given the survival rates as low as in most of the modelled poaching scenarios in Finland (Paper I), the population would need a very high recruitment rate to be able to sustain such mortality rates.

The annual survival ranged from 0.11 to 0.6 for Finnish wolves, depending on the scenario (Table 2 in Paper I), whereas the annual survival rate was, on average, 0.76 for Swedish adult wolves (Paper III). Following the censoring procedure of the poaching scenarios, survival was only 0.6 for Finnish wolves even if zero poaching was naively assumed. The population growth trajectories of the Finnish and Swedish wolf populations are different: the Finnish wolf population has been fluctuating considerably between approximately 100 and 300 wolves, whereas the Swedish wolf population has shown a relatively steady increase – although not with the full biological potential (Liberg et al. 2012) – since its re-establishment, until the recent decline (Liberg et al. 2018). Fuller et al. (2003) reviewed that the annual survival of full-grown wolves in areas without a goal to exterminate the population ranged between 0.55 and 0.85. Our results would fit into this range for most of the years if the no-poaching scenario's survival rate 0.6 would have been true in Finland, but, even then, it has been close to the lower value (0.55). The average survival in Sweden (0.76) falls into the middle of the Fuller et al. range.

Causes of mortality are competing risks, and all individuals die to some cause of death. Human-caused mortality in wolves is often assumed to be compensatory at least in low or moderate levels by increased productivity or decreased rates of natural mortality and emigration (Adams et al. 2008; Creel & Rotella, 2010; Fuller et al. 2003; Webb et al. 2011). In our study system, both poaching and legal harvest seem to target adult wolves. Partial compensatory model together with super-additive effects seems to best describe the human-caused mortality effects in these study populations that live in human-dominated landscapes.

There were only a few deaths due to natural causes, whereas human-caused mortalities were numerous, with poaching being the major cause of death. Human-caused mortalities might be compensated by a lower rate the natural causes of death until a certain threshold. Above the threshold, mortality becomes additive, and human-caused deaths decrease survival rate. Poaching as uncontrolled human-caused mortality can decrease survival rate indirectly in the form of super-additive mortality (Creel & Rotella, 2010; Milleret et al. 2016) in several ways: (i) lower pup recruitment may decrease population growth rate (Gude et al. 2011), (ii) breeder loss can decrease offspring survival (Borg et al. 2015; Brainerd et al. 2008), alter prey selection and hunting success (Sand et al. 2006), and (iii) the replacing breeders that are yet not familiar with the territory might have a higher mortality risk because of their territory use (Kojola et al. 2016).

The results of this thesis emphasize the evident intolerance towards the wolf and the law breaking in wolf issues. Poaching is an outcome of the ongoing wolf conflict. It increases unpredictability and instability in these legally harvested wolf populations. The higher poaching rates as a response to increased population size, and during the shortage of legal harvest, appear to be acts of frustration and hatred leading to the removal of the wolves in a one way or another. Wolf populations in Finland and Sweden seem to be regulated more by social intolerance than ecological carrying capacity.

Poaching was the major cause of death among alpha wolves in Finland, but the fates of the dispersers remained mostly unknown, and, consequently, they were censored in the survival analysis. The informative censoring scenario 1 was the most probable for collared wolves, as it includes all information on fates of the individuals but takes into account the lower detectability of the dispersers. Survival rate was low even in the naïve no-poaching scenario because of the large amount of unknown fates (censoring). Censored individuals are absent from the population at risk, although the time of their death is unknown.

The censoring procedure informed by the social status accounted for the two possible biases in the survival estimates. Firstly, if we would censor young wolves at the date of collar silence, we might underestimate survival. Secondly, censoring them at the end of the study might overestimate the survival rate if the deaths of dispersers were simply poorly detected. Almost one third of the Finnish collared wolves were censored due to missing data. In the Paper I, we attempted to reduce the problem of identifying cases of poaching among collared wolves for which we had lost contact, and to do that, we used what we called ‘silent information’ about the fates of these wolves. Such information without hard evidence requires critical processing of the data and following up on the possible alternative fates of the collared individuals. Lost collared wolves determined to be either censored or poached were not later detected as alive or dead because of another cause.

Poaching is a cryptic phenomenon (Liberg et al. 2012; Stenglein et al. 2015; Treves et al. 2017b) and, therefore, a tricky challenge for the conservation and management of wildlife species both from the information-gaining and practical perspective. One difficulty for management is that empirical evidence about the relationship between legal harvest and poaching is rare and difficult to obtain. The relationship between legal hunting and poaching is in the very core of the wolf conflict and was highlighted in this thesis as well.

This study increases knowledge on the relative importance of the two main drivers of the wolf conflict that escalates into poaching: the number of wolves and legal harvest. The weak decreasing effect of legal harvest on disappearance may remain hidden behind the strong positive effect of population size as discovered in the Paper III. According to the results of this thesis, the Finnish and Swedish wolf populations have been, in practice, controlled by illegal acts more than management actions. The overall poaching risk was two to three times higher than the risk to die in legal hunt in both populations (Papers I and III). Even if the disappearances would be partly explained, let us say by one third, by other causes of death than poaching, the poaching risk would still be twice as high as the risk to be legally killed.

The findings of this thesis supported the assumption that legal hunting can decrease poaching, but also reminded that legal harvest alone does not solve the problem. Despite the fact that legal harvest as management policy has been present in some form ever since the return of the wolf to Finland and Sweden, the human-wolf conflict has not led to tolerant coexistence. Legal hunting does not evidently buy goodwill (Chapron & Treves, 2016) but, instead, just washes hands from the illegal blood.

5 Further research needs and practical implications for conservation, management and law enforcement

Further research is needed on the relation between population size and poaching, both in time and space, as well as on the effects and mechanisms of breeder loss in relation to human-caused mortalities, especially when the total harvest is mostly composed of poaching. High human-caused mortality rates can have long-time effects, especially in an inbred and isolated wolf population such as the Scandinavian wolf population and the connected wolf population in Finland. Therefore, further cooperative research between the countries would be advantageous, and combined data would enhance the research possibilities.

The recent wolf-management policies in Finland and Sweden have aimed to ease the wolf conflict by legal harvest. Legal harvest decreased poaching, according to the results of this thesis. Legal hunting can act as a short-time buffer against poaching. A zero-hunting policy could be detrimental to wolves and their conservation because of the ongoing conflict. The zero-hunting policy would probably not gain public support, in particular, in countries such as Finland and Sweden where hunters, who view the wolf most negatively, represent a significant proportion of local people in rural areas (Bisi et al. 2010; Peterson et al. 2018; Pohja-Mykrä & Kurki, 2014, Skogen et al. 2017).

The local people are in key positions in anti-poaching actions worldwide (Challender & MacMillan, 2014; Dickman, 2010; Hazzah, Bath, Dolrenry, Dickman, and Frank, 2017; Mykrä, Pohja-Mykrä, and Vuorisalo, 2017; Peterson et al. 2018). Engaging local hunters to suppress poaching could stabilize the fluctuating wolf populations by enhancing the survival of breeding adults. In Paper II, we suggested a quantitative method to include the number of poached wolves in the estimate of total loss in advance, based on predicted poaching probabilities. A more stable local wolf population, through the enhanced survival of breeding adults, could be used as a measure of the absence of poaching, which could lead to an increased number of legal permits to hunt juveniles of the local packs. A concrete estimate of the number of poached wolves could diminish the acceptance of poaching through group discipline if the number of hunting permits was bound to poaching in a compensatory manner.

The likelihood of getting caught by law enforcement is low in hunting offences. This was supported by the results that cryptic poaching has been the major mortality cause for wolves in Finland and Sweden (Papers I and III), and that higher human density decreased the poaching probability (Paper II). Poaching risk has been also observed to be higher for carnivores inside remote national parks, in comparison to the areas outside them (Rauset et al. 2016).

Results of this thesis could be utilized in intelligence-led policing, for example, by mapping poaching hotspots in time and place as well as allocating resources on areas with higher poaching risk. Poaching risk in time was increased by high wolf population size (Papers I and III), during the early spring months from January to April (Paper I) and when there were only few if any legal permits nationally (Papers II and III) and locally (Paper II). The poaching risk was highest in the remote areas (Paper II) with a dense forest road network (Paper II). Poaching targeted, in particular, adult wolves with collar (Paper I) on established territories (paper I, II, III).

Reliable and quantitative measures of poaching are needed to reach credibility in wolf management and for securing viable wolf populations. Effort should be made to find solutions on how to decrease the number of unknown fates and disappearances in wolf populations. Further aftermath on wolf policy changes and multidisciplinary research are necessary. Combined forces of science and practice would be fruitful from the perspective of data availability and information sharing.

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