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Characterisation of the Scandinavian wolf population from an ecological and forensic point of view

A skandináv farkaspopuláció jellemzése ökológiai és igazságügyi szempontból

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Abstract

The Scandinavian grey wolf, which belongs to the Eurasian wolf subspecies (*Canis lupus lupus*) of the wolf (*Canis lupus*), is a crucial apex predator in Northern Europe's ecosystems. Despite their ecological importance, these wolves face threats such as habitat loss, genetic bottlenecks, and human-wildlife conflicts. This thesis examines their population dynamics, ecological adaptations, genetic diversity, conservation status, and human-wolf interactions, focusing on the challenges posed by poaching. A review of scientific literature highlights the severe effects of inbreeding, the role of conservation efforts in population recovery, and the persistent issues of illegal poaching and societal conflicts. By integrating ecological and forensic perspectives, this research emphasises the need for balanced conservation strategies that address ecological sustainability and human interests. The challenges faced by the Scandinavian grey wolf reflect the broader difficulties of wildlife management in human-dominated landscapes.

Absztrakt

A skandináv szürke farkas, amely a farkas (Canis lupus) eurázsiai farkas alfajához (Canis lupus lupus) tartozik, kulcsfontosságú csúcsragadozó Észak-Európa ökoszisztémáiban. Ökológiai jelentőségük ellenére ezek a farkasok számos fenyegetéssel néznek szembe, például élőhelyvesztéssel, genetikai beszűküléssel, illetve az emberekkel való konfliktusokkal. Ez a dolgozat a populációdinamikájukat, ökológiai adaptációikat, genetikai diverzitásukat, védettségi státuszukat és ember-farkas interakcióikat vizsgálja, különös tekintettel az orvvadászat által jelentett kihívásokra. A tudományos irodalom áttekintése rávilágít a beltenyésztés súlyos hatásaira, a természetvédelmi erőfeszítések szerepére a populáció helyreállításában, valamint az illegális vadászat és a társadalmi konfliktusok tartós problémáira. Az ökológiai és igazságügyi szempontokat ötvözve a kutatás hangsúlyozza a kiegyensúlyozott természetvédelmi stratégiák szükségességét, amelyek figyelembe veszik az ökológiai fenntarthatóságot és az emberi érdekeket is. A skandináv szürke farkasokkal szembeni kihívások jól tükrözik a vadvilág kezelésének nehézségeit az ember által dominált tájakon.

Table of Contents

1. INTRODUCTION	1
2. LITERATURE REVIEW	2
2.1 GENERAL CHARACTERISTICS OF THE SCANDINAVIAN GREY WOLF	2
2.2 ORIGIN AND ECOLOGICAL INFLUENCES	7
2.3 GENETIC DIVERSITY AND STATUS	
2.4 CONSERVATION STATUS	14
2.5 INTERACTIONS WITH NATURAL PREY, HUMANS, AND LIVESTOCK	
2.6 THREATS AND MORTALITY	
3. OBJECTIVES	
4. MATERIALS AND METHODS	
5. RESULTS AND DISCUSSION	
ANALYSING THE ECOLOGICAL INFLUENCES OF SCANDINAVIAN WOLVES	
INVESTIGATING THEIR GENETIC DIVERSITY AND STATUS	
EXAMINING THEIR CONSERVATION STATUS AND MANAGEMENT EFFORTS	
EXPLORING THE HUMAN-WOLF AND LIVESTOCK-WOLF INTERACTIONS	
Assessing their Mortality and Prevalence of Threats	
OUTLOOK	
6. SUMMARY	
7. REFERENCES	

1. Introduction

An enigmatic and majestic apex predator, the wolf has long captured human fascination through its storied existence in myths, literature, and cultural symbolism. The Eurasian grey wolf (*Canis lupus lupus*) exists in various populations across the globe; notably, the grey wolf population from Scandinavia stands out for embodying the resilience of a species on the brink of extinction and symbolising the friction-filled relationship between humans and efforts to conserve wildlife.

Tucked into Scandinavia's vast boreal forests and rugged terrains, the Scandinavian grey wolf population has historically played a pivotal ecological role in shaping the ecosystem dynamic through their predatory roles and impact on prey demographics. Nonetheless, their coexistence has ignited intense disputes and conflicts on their biodiversity role, leading conservation advocates to find themselves against farmers, agriculturists, and social communities over livestock depredation debates and for overall public safety.

In recent decades, significant threats like habitat fragmentation, hunting pressures, and genetic isolation have plagued the Scandinavian grey wolf population, causing it to face multiple challenges for survival. Despite intense protective and conservation measures to restore and preserve their populations, this subspecies remains one of Europe's most endangered. A drastic decline in population occurred in Northern Europe during the 1960s, when Scandinavian wolves were declared virtually extinct due to extensive hunting. Fortunately, conservationists acted quickly, banning hunting to reestablish the population. Although the numbers have not returned to pre-extinction levels, a gradual recovery signals the benefits of these conservation efforts.

Characterising the Scandinavian grey wolf population highlights the interplay of ecological adaptations, forensic investigations, and human interactions in shaping the dynamics of these apex predators. From an ecological perspective, factors such as habitat availability, prey abundance, and conservation status play a critical role. Forensics complements this by focusing on issues like illegal poaching and investigating human or livestock attacks. Forensic science plays an essential role in gathering and analysing evidence, helping to enforce legal protections and providing critical insights into the threats faced by the population.

Delving deeper into the intricacies of the Scandinavian grey wolves' ecological and forensic significance reveals not only the scientific complexities of their conservation but also the ethical and cultural dimensions of human-wolf interactions.

2. Literature Review

In this literature review, the author will first characterise the Scandinavian grey wolf population, emphasising their ecological role as apex predators, traits that enable survival in the harsh northern climates, and the historical and current trends shaping their population dynamics.

Furthermore, the review will explore the origins and ecological influences of the Scandinavian wolf, including their historical migration patterns and the forensic techniques used to trace their lineage and population history. This section will provide the foundation for understanding the wolves' significance in Northern Europe's ecosystems and their challenges in balancing their ecological importance with human pressures.

Genetic analysis provides critical insights into their genetic roots and population connectivity. The discussion will then examine the population's genetic diversity, focusing on the impacts of inbreeding and genetic bottlenecks and the impact of monitoring inbreeding levels to identify new genetic inputs from immigrant wolves.

Conservation status and management efforts will follow, detailing international and national policies, their implementation, and conservation investigations, such as investigating illegal killings and monitoring compliance with its approaches.

The review will then explore human-wolf and livestock-wolf interactions, analysing the causes of conflicts and the forensic approaches used to investigate attacks on livestock and humans. These cases often involve the application of forensic science to distinguish wolf attacks from other predators, providing critical data for conflict resolution and policy decisions.

Finally, the review will assess wolves' threats and mortality, such as poaching, examining its prevalence, motivations, and impacts on population recovery. Investigating wolf carcasses will be discussed as key tool in combatting poaching and strengthening conservation enforcement.

2.1 General Characteristics of the Scandinavian Grey Wolf

The Scandinavian grey wolf, a subspecies of the wolf (*Canis lupus*), is a medium-tolarge-sized carnivorous mammal native to the Scandinavian Peninsula. It is the largest member of the Canidae family (domestic dog, coyote, foxes, etc.). The Scandinavian wolf shares several characteristics with other Eurasian grey wolves in Europe but has adapted to the northern environment [1, 2, 3]. With males weighing in approximately 35-55kg and females slightly smaller, these wolves have unique morphological characteristics, enabling them to become the top apex predator of the north. They are usually grey or brown and have darker markings on their backs, allowing them to easily camouflage with the boreal coniferous forests or snowy mountainous landscapes. Their long legs and robust bodies are specifically built to cover the vast Scandinavian distances while hunting their prey. They have a unique thick, bushy tail that helps them balance when running or jumping through the dense forests and rocky terrains and provides additional insulation to keep them warm during the harsh cold winters [4].



Figure 1: Typical appearance of the Scandinavian grey wolf (Canis lupus lupus) [5]

Grey wolves are generally known for their high intelligence, strong family bonds, and territorial behaviour. They are incredibly social animals, living in packs containing five to ten individuals. Family packs consist of an adult breeding pair (an alpha male and alpha female pair), their current offspring, and sometimes unrelated individuals. Their ability to form a solid social family bond is achieved by establishing a dominant bond to maintain order. Yet, lone wolves are also common. By using their stealth and the teamwork of their pack to bring down their prey, they are excellent apex hunters. They communicate through vocalisations like howling, scent marking, and body language within their packs or to other packs. Their diet primarily consists of large ungulates, such as deer, elk, and moose, but they may also prey on smaller animals, like hares and rodents [1, 2, 3].

Grey wolves only live up to 12 if they are kept in captivity. Most of them pass at a young age, even before age 1. It is estimated that only one out of ten wolves make it to full adulthood and can have their litter. Habitat loss and fragmentation, human-wolf conflicts, and genetic

isolation (smaller populations) challenge the successful breeding and upbringing of grey wolves, like the Scandinavian grey wolf. Conservation efforts aim to address these challenges and ensure the long-term survival of Scandinavian wolf populations. The grey wolf's reproductive capacity also enables them to withstand high mortality rates, naturally recovering from the population decline if the conditions are kept right [1, 2, 3].

Wolves live in a matriarchal society, with females typically taking control in caring for and protecting the pups, while males primarily focus on hunting and food provision. However, both sexes can actively participate in hunting and killing of their prey. During the summer, hunting is often a solitary activity due to the upbringing of their pups [2, 3].

They are monoestrous animals (having only one oestrus cycle per year) and typically breed between February and April. The gestation period is approximately 63 days (two months), resulting in a litter of five to six offspring (pups) once a year in the spring. The den is often located in a natural hole, burrow, rock crevice, hollow log, or overturned stump; any underground depression will suffice if it ensures a secure, safe spot to raise their pups. The entire pack is involved in caring for the young [2, 3].

After weaning at six to nine weeks, the pups will be fed a diet of regurgitated meat from the adults. They are the centre of attention and the pack's primary geographical focus throughout spring and summer. During the summer, the pups are relocated from the den to a secure aboveground site where they sleep and play together while the adults go hunting. As the summer season ends, the pups are relocated more frequently depending on the abundance of prey and safety from other packs, lone wolves, or threats. By October or November, most of the pups have reached nearly adult size and are expected to keep up with the pack as they resume their travels within the pack's territory [2, 3].

After spending two or more years within the pack, many young wolves depart to find a mate, form a new territory, or potentially start their pack. Those who remain may eventually become breeding animals (alphas) by replacing a parent. Larger groups often have fewer youngsters leave the pack and from litter produced by multiple females. This could pose a risk and be the cause of inbreeding depression cases. The ones who leave can travel up to 800km long in search of a new territory [2, 3].

Scandinavian wolves regularly face several challenges to breeding, including habitat loss and fragmentation, where suitable den locations and hunting prey grounds are reduced because of human activities, such as deforestation. Also, human-wolf conflicts, like livestock predation, lead to persecution of the wolves, limiting their breeding opportunities. Additionally, smaller populations face genetic isolation that can result in inbreeding and reduced genetic diversity, hindering successful reproduction. Conservation efforts are enforced to address those challenges to ensure the long-term survival of the Scandinavian grey wolf population.

Population descriptions and trends

Today, an estimated 200,000-250,000 grey wolves have been recorded globally, a distinct decrease from their previous historic abundance across North America and Europe [6, 7]. Widespread human encroachment, habitat destruction, government-sponsored eradication programs, and human-wolf conflicts have influenced the extermination of the population since the 18th and 19th centuries worldwide. Wolf reintroduction programs and conservation efforts have been implemented; due to this, the grey wolf population is now considered a minor concern for extinction, according to the International Union for Conservation of Nature (IUCN). Their protection efforts vary by country or region. Some areas have high protection standards for wolves, while others still allow hunting or resort to exterminating wolves because they are perceived as threats to public safety and livestock.

Like coyotes, wolves are called 'indicator species' because they can quickly adapt to ecoregion changes or environmental conditions. However, unlike coyotes, wolves struggle to adjust to the expanding civilisation; when the human population rises, the coyote population follows, whereas the wolf population declines [8].

The population of grey wolves is increasing within the EU. They have been detected in all EU member states except Ireland, Malta, and Cyprus in 2023, with breeding packs found in 23 EU countries [9]. Approximately 20,300 grey wolves roam the continent by 2023, which portrays an increase in the population since the previous year, where 19,400 were recorded by Boitani et al. (2022) [10] (excluding Belarus, the Russian Federation, and Ukraine) and portrayed an increase since 2012 where only 11,193 wolves were recorded. The population almost completely disappeared in central and northern Europe, and only a few survived close to extinction in the Eastern part of the European peninsulas [11].

Countries such as Belarus, Moldova, and the Russian Federation tend to be excluded from the wolf population data. However, their connectivity with them is still relevant in assessing the European populations. Ukraine's wolf population area is limited to the Carpathian mountains only, and it is also seen with Türkiye's wolf population that their area is limited to the European portion only.



Figure 2: Recorded Wolf Distribution in 2016 in Europe, reported by IUCN by Boitani et al. (2018), excluding Türkiye, Belarus, and the Russian Federation [7, 10]

The extermination of grey wolves and increased human settlement have led to wolves resettling in different areas in the EU at a much higher density. Figures 2 and 3 show that the grey wolf population is less dispersed across Europe and more confined to different parts depending on the country, often in protected areas.



Figure 3: Recorded Eurasian wolf population in 2016 in Europe by Boitani et al. (2018), excluding Italy, where the Canis lupus italicus has been recently identified as a separate subspecies compared to the Canis lupus lupus [7, 10]

The population density of Scandinavian wolves has fluctuated over time. In contrast, in the previous 50 years, wolves have presented an apparent capacity to adapt to different circumstances and changing environments by reoccupying new opportunities for suitable habitats [10]. After near extinction in the 1960s due to hunting, habitat loss, and eradication programs, the population recovered again with the help of conservation efforts in the late 20th century. Wolves could slowly repopulate, and legal protection laws at the national level were put in place to ensure their complete survival. Cimatti et al. (2021) [12] described that Europe reported an over 25% increase in the wolf range within the last decade. However, due to the low population density in the 60s, the modern Scandinavian grey wolf population was descended from only a few remaining individuals, leading to a genetic bottleneck population that wildlife conservationists aim to control.

2.2 Origin and Ecological Influences

Origins

The Scandinavian grey wolf has an extensive and complex history dating back centuries, portrayed by decades of abundance, persecution, and recovery. Their long existence can be backed up with evidence found in archaeological sites of ancient ruins from the Vikings and old folklore. They have been a prominent species across most of the Northern Hemisphere for hundreds of thousands of years, defying extinction, unlike many other large Pleistocene mammals. Genetic research of the present-day genome suggests that the current wolf population structure was formed primarily in the last 20,000 to 30,000 years ago, corresponding to the existence of the Last Glacial Maximum (LGM), estimated to be around 23,000 to 25,000 years ago [13]. With modern wolf diversity, such as the Eurasian and Siberian wolves, it's clear that they exhibit no ancestral lineages before LGM, suggesting that many of the pre-LGM wolves may have become extinct [14].

Research and evidence have made it clear that dogs are ancestry descendants of grey wolves, although the question remains as to how, when, and where the present-day dog lineage appeared [15]. With archaeological evidence [16], they aid in providing the earliest dog-like remains dating back to 14,000 years ago and concluding that with the help of genetics, researchers can estimate that the divergence of dog and wolf ancestors ranges from 14,000 to 40,000 years ago. However, to resolve the central question of the origin of dogs, a more comprehensive understanding of wolf genetic diversity is necessary since former genetic studies primarily focus only on modern wolves and dogs, disregarding the complex history of their divergence.

Nonetheless, the history of the Scandinavian grey wolves dates back centuries, with wolves once dominating the forests of Norway and Sweden [13, 17].

Habitat and Territories

Wolves are a highly adaptable species with the most extensive natural inhabitant range compared to other terrestrial mammals. It once inhabited much of the Holarctic region, a biogeographic realm encompassing the northern parts of Europe, Asia, and North America. From the High Artic in Europe to the Arabian Desert in Africa, they could accommodate the different ecosystems, especially in now human-dominated landscapes across Europe and Asia. They are native wildlife species worldwide, specifically in Eurasia and Northern America, where they aid in biodiversity and the world's natural heritage.



Figure 4: A map of the world illustrating the areas in which grey wolves are present (Green) and areas in which they have been extirpated (Red) [6]

The survival of the packs depends heavily on the availability of food per capita. The greater the abundance of prey available, the higher the chance of wolves forming a pack and inhabiting the area. Wolves can establish vast territories ranging from 500km² to 1000km², which they control and defend from other packs. They live in low densities, so the pack can disperse between one and three individuals / 100 km². They can disperse themselves hundreds of kilometres away from their natal pack, causing them sometimes to enter human-dominated landscapes (villages, cities, towns, etc.).

Nonetheless, it allows them to recolonise other regions in the country or another country from where they vanished last, giving rise to the fact that the migration of wolves across Europe occurs and the breeding of other types of wolf populations can occur. This can prominently be seen with the Russian-Finnish wolf population.



Figure 5: Representation of the range of area different wolf-packs cover in Sweden [2]

Norway and Sweden cover an area of approximately 800,000 km², forming the Scandinavian Peninsula (also known as Scandinavia). From a biological perspective, it aids in a suitable and proper habitat for grey wolves [18]. They consist of vast forests, specifically the boreal coniferous forests, which provide sufficient cover and food resources. The dense undergrowth and abundance of prey species, such as deer, elk, and hares, which also occupy the same territory, make the Scandinavian forests ideal for wolf denning and population regrowth. Additionally, Sweden's mountainous regions, such as the Scandinavian Mountains, provide rugged terrain, making it difficult for humans to access the area and allowing wolves to establish territories relatively undisturbed.

However, due to social, economic, and cultural limitations towards the establishment of the Scandinavian grey wolf population, such as in the South with agricultural plains and increasing human density population, and in the North with increasing reindeer husbandry and extensive open land sheep farming, there is only now 200,000 km² of appropriate habitat for the wolves to utilise. While human settlements and agricultural areas can pose challenges for wolves, Scandinavia's extensive wilderness areas can offer sufficient space for their populations to thrive and regrow again [19].

Role in the Ecosystem and its impacts on Society

The Eurasian grey wolf plays a significant ecological role as the largest predator in many European Northern Hemisphere ecosystems [20]. They aid in maintaining the health and balance of the ecosystems; their presence influences many aspects of biodiversity, ecosystem functioning, and even the physical environment. Large carnivore populations, in general, have seen global declines over the last century, leading to the loss of the ecological functions they sustained. The recent resurgence of large carnivores, like the wolves, in Europe could aid in restoring these functions, provided they achieve ecologically effective densities [21, 22]. After

their removal from the environment or their reintroduction, the main impact connected with wolves is the reduction in the number of herbivores and mesocarnivores populations [23].

The influence of human activity on prey's antipredator behaviour often exceeds that of natural predators. Around the world, specifically in Europe, humans have taken complete control of being the 'top predator' by regulating prey numbers and altering their behaviours [24]. The effects of human activities, like hunting, vigilance disturbances, and movement, cause more harm to herbivores than larger carnivores can [25].

Wolves are vital contributors to biodiversity and the ecosystem functioning by triggering trophic cascades, where the presence of predators indirectly affects multiple levels of the food chain. This concept is primarily supported by research conducted in relatively undisturbed, natural landscapes, where the interactions between predator and prey can occur without human interference. However, in many regions worldwide, especially in Europe, grey wolves inhabit and return to highly human-modified ecosystems, such as agriculture, urban development, and forestry. This raises the question of whether the ecological effects observed in natural environments can be applied in anthropogenic landscapes (Earth's surfaces where significant human alteration of environmental patterns and processes has occurred) [26].

Wolves and other large carnivores can help stabilise ecosystems, making them more resilient and sustainable under various environmental pressures. Primarily, they regulate prey populations and support smaller predators, known as mesopredators (e.g., foxes). This aids in maintaining the ecosystem's health and balance by keeping the herbivore populations in check and preventing overgrazing, which helps preserve plant diversity and supports a wide range of other species. Their influence can trigger trophic cascades, a ripple effect throughout the ecosystem. For example, hunting wild ungulates reduces their numbers, allowing vegetation to recover and benefit other wildlife, such as birds and insects. Furthermore, they help to maintain genetic diversity in prey populations, eliminating the weak or diseased animals through selective predation and preventing the distribution and spread of diseases [11, 26].

In addition to population control, wolves shape animal behaviour by establishing a "landscape of fear," causing prey to avoid certain areas and protecting sensitive habitats from overuse and destruction by wild ungulates. They also contribute to nutrient cycling by providing food for scavengers (e.g., bird species). The reintroduction of carnivores into ecosystems restores lost functions and enhances ecosystem resilience to environmental changes [9].

2.3 Genetic Diversity and Status

Genetic bottlenecks and low genetic diversity due to isolation exacerbate challenges for population viability. While immigrant wolves from Finland and Russia occasionally boost genetic diversity, their contributions are often limited by low immigration rates and the geographic isolation of the Scandinavian wolf population. Furthermore, the small number of breeding individuals means that genetic drift has a more pronounced effect, reducing diversity over time. Strict monitoring and collaboration between Norway and Sweden remain essential to ensure the survival of this population. Conservation programs aimed at creating pathways for wolves to migrate naturally and removing the obstacles that limit their movement could help preserve the population's genetic health. The IUCN highlights these challenges in its assessments, urging further regional cooperation and adaptive management strategies to counteract the effects of genetic isolation and improve the long-term survival of the Scandinavian wolves [7].

Inbreeding

A bottleneck population occurs when a species encounters a dramatic reduction in numbers over a short period of time, leaving only a small pool of individuals to repopulate. This limited pool significantly affects the population's genetic diversity, as there are fewer unique genes and traits available, reducing their ability to adapt to environmental changes or resist emerging threats

In the long term, even if the population size recovers, the initial loss of genetic diversity can leave the population more vulnerable to diseases, environmental changes, and inbreeding depression. In Scandinavian wolves, this has led to an accumulation of adverse mutations, as identified by researchers in Uppsala, who found around 100,000 harmful mutations in the population's genome. These mutations have manifested in physical defects, such as deformed vertebrae and cryptorchidism, underscoring the urgent need for targeted conservation strategies [27]. The management of inbreeding should focus on introducing genetic diversity through natural or assisted gene flow and careful monitoring of population dynamics to reduce the risks associated with these genetic challenges.

Genetic Status

The Scandinavian grey wolf population has shown fluctuating trends over the past decades, with a steady increase from the 1990s until 2014-2015, marked by the growth in family

groups and reproduction units. However, after 2015, this upward trend reversed, with a notable decline in family groups, particularly in Sweden. Although there was a temporary recovery in wolf numbers between 2019 and 2022, culminating in a peak population of over 500 wolves in Scandinavia, recent monitoring during the 2023-2024 winter period indicates a renewed decline. The latest estimates suggest a total population of around 440 wolves, with Sweden hosting the majority [28].



Figure 6: Documented family groups (circle) and territory-marking pairs (triangle) in Scandinavia during the winter 2023-2024 period. Wildlife management areas (red-brown line) are shown in both countries, and the shaded area indicates the Norwegian wolf zone [28]

Regular monitoring efforts track population trends, help identify new immigrant Finnish-Russian wolves, and provide vital insights into the population's genetic health. This includes estimating inbreeding coefficients, which are critical given the severe inbreeding depression that continues to threaten the long-term survival of Scandinavian wolves [28].

Finnish-Russian immigrant wolves (F0) are genetically valuable individuals for enhancing the genetic diversity in the Scandinavian grey wolf population by reducing inbreeding. Their offspring (F1) are also considered to be genetically important. During the 2023-2024 winter monitoring season, five new Finnish-Russian wolves were documented using DNA analysis from their excretes: three females (one culled in Norrbotten during a protective hunt) and two males (one GPS-collared in the Norway wolf zone after migrating from Sweden). A previously known Finnish-Russian male wolf in the Norwegian Setten territory, first seen in 2019, has established itself as a territorial wolf and has produced the only F1 litter during this period, with five new pups. Thereby, 18 F1 wolves were documented in 2023-2024: 13 older individuals and five new ones, ten primarily within Sweden. These F1s descended from three Finnish-Russian wolves, though only one remains active in the population [28].



Figure 7: Documented Scandinavian wolf family groups (Black circles) and territory-marking pairs (Black triangles) in Scandinavia during the winter 2023-2024 period. Additionally, with Finnish-Russian immigrants, sightings (Red coloured) show family groups or territory-marking pairs where an F1 is a parent or part of a territory-marking pair. F1s from Tiveden (Yellow coloured), Prästskogen/Galven (Orange coloured), and Setten (Blue coloured) [28]

The Scandinavian grey wolf population originates from six wolves that migrated from the Finnish-Russian population. In 1983, the original Nyskoga pair founded the population with their first litter. Subsequent founders and their initial years of reproduction include the Gillhov male (1991), Kynna male (2008), Galven/Prästskogen male (2008), and Tiveden female (2013). Four other Finnish-Russian immigrants have had their pups (Tiveden male, Tunturi male, Svartedalen female, Setten male) but are not considered founders since their offspring have not been reproduced. Since 1983, only eleven new parent pairs have been unrelated (e.g., Nyskoga 1, Gillhov, Galven), with all the others producing inbred pups [29].

The inbreeding coefficient (F) estimates the proportion of identical genes (alleles) inherited from both parents. It ranges from 0 to 1 and increases when parents are more closely

related (e.g., F = 0.25 for sibling offspring, ~0.13 for cousin offspring). Between 1996 and 2007, the average inbreeding coefficient in family groups increased from 0.13 to 0.30. However, from 2008 to 2016, the coefficient decreased, mainly due to immigrant wolves in Galven/Prästskogen and Kynna successfully reproducing multiple F1 offspring [29].

Annual monitoring of the population's inbreeding is based on the inbreeding coefficients of family groups documented during winter, which depends on the relatedness of wolf pairs that produced the pups in the family group. In 2023, the average inbreeding coefficient was F = 0.23 (± 0.10 standard deviations), slightly lower than in 2022 ($F = 0.24 \pm 0.10$) [29].



Graph 1: The average inbreeding coefficient (degree of inbreeding) in family groups in Scandinavia from 1983 to 2023. The dashed lines indicate the standard deviation of the inbreeding coefficient, which measures the variation within individual years [29]

2.4 Conservation Status

Scandinavian Grey wolf population status

Estimating the grey wolf population status across the Scandinavian countries can be challenging due to the varying methods used by the different countries. They all have their approach to monitoring the population, from advanced visual methods or genetic capturerecapture models to extrapolations from local surveys and habitat models. While some countries rely on counting individual wolves, others rely on estimating the reproductive units (packs or pairs), using conversion factors to assess the total number of grey wolf individuals. However, these conversion factors can have an extensive range between the nations, causing discrepancies in the population estimates and complicating the conservation assessments and comparisons.

Table I	1:	Wolf	numbers,	precision,	and	trends	in	the	Scandin	avian	countries	[1()]
												-	_

	Denmark	Finland	Norway	Sweden
Year Estimated	2021	2022 (March)	2021-2022	2022
Mean estimate of	14	290	51-52 live only in	460
wolf individuals		≈37 packs, ≈23	Norway, with 74-	
		pairs	77 in packs using	
		1	areas across the	
			border with	
			Sweden (counted	
			as 0.5)	
Measure of	13-15	275-315 (90%	No statistical	364-598 (range)
uncertainty		probability	estimate – these are	
		interval)	ranges of minimum	
			numbers	
Current	Increasing	Increasing	No obvious	Increasing
population trend			changes	
(since 2016)				
Different	1 population	1 population	1 population	1 population
European wolf				
populations in the				
country				
Conversion	None	32 packs and 21	-	The raw data is
factors		pairs fully in		number of
used to convert		Finland, the other		reproductions and
nacks/nairs to		shared with the		the conversion
numbers		Russian Federation		factor is 10
Wolf area				
monitored for				
the most recent				
the most recent	(Complete Survey (most	of the known wolf area	a)
Wolf				
abundance				
estimate				

Legal and Political Context of Scandinavian Grey Wolves

The legal protection of grey wolves in Scandinavia is governed by international agreements such as the Bern Convention, the EU Habitats Directive, and the IUCN Red List system. The Bern Convention [30], adopted in 1982, mandates that European countries implement legislative and administrative measures to protect species like the grey wolf. The Scandinavian wolf population, listed under Appendix II for strict protection, benefits from these measures, although flexibility in enforcement varies between nations [31].

The EU Habitats Directive (Council Directive 92/43/EEC) further supports wolf conservation through its Natura 2000 network, requiring strict protection for wolves in Annex IV while allowing limited management flexibility under Annex V in specific regions. Norway and Sweden maintain national conservation frameworks aligned with these directives, but challenges remain in balancing protection with the needs of reindeer husbandry and rural communities [32].

Politically, the reappearance of wolves in Scandinavia has sparked debates over livestock depredation and rural conflicts. While public opinion in the EU largely supports wolf conservation, Scandinavian countries face unique pressures due to livestock farming and cultural practices. Recent resolutions by the European Parliament emphasise balancing biodiversity goals and community livelihoods, promoting long-term solutions like damage prevention and compensation programs [21, 33, 34].

Despite its vital ecological role, the Scandinavian grey wolf population remains one of Europe's most vulnerable. Classified as "Vulnerable" by the International Union for Conservation of Nature (IUCN), this population is estimated to consist of fewer than 500 individuals, primarily in Norway and Sweden. The population has rebounded since near extinction in the 1960s, but persistent threats, including habitat fragmentation, inbreeding, and poaching, hinder their full recovery [7, 10].

	Denmark	Finland	Norway	Sweden	
EU Habitats	IV	IV and V in	Not applicable	II and IV	
Directive annex:		reindeer husbandry			
		region that covers			
		38% of Finland			
Bern Convention	II	Reservation	II	II	
appendix:					
National legal	Protected	Protected/Game	Protected/Culled	Protected with	
status		species	only in special	hunting	
			cases		
Official	Don't know/Not	No	Not relevant	Yes	
'Favorable	relevant				
conservation					
status' (FCS)					
National		Vag. mati	anal nlan		
management plan		res, nati	onai pian		
Transboundary	No	Yes	Yes	Yes	
cooperation in					
management					
Nature of the	-	Exchange of	Common monitorin	a sustam and status	
transboundary		information and	Common monitoring system and status		
agreement		expertise	report for Sweden and Norway		
Country level Red	Vulnerable 2018	Endangered 2019	Critically	Endangered 2020	
List status and			endangered 2021		
year					

Table 2: Summarizing the grey wolves legal status at country level for each Scandinavian country [10]

Wolf monitoring

Monitoring the wolf population can be difficult due to its low densities and elusive behaviour. Still, reliable data on its numbers and trends is essential for making informed science-based management decisions. This is especially vital given the polarised public debate about wolf conservation in general. The European Parliament has highlighted the lack of consistent, standardised monitoring across the EU Member States and has urged the European Commission to take action to ensure effective methods for tracking large carnivores, including the grey wolf population.

As previously highlighted by Boitani et al. (2022) [10], they emphasised that estimates of the grey wolf populations can vary across Europe, leading to significant discrepancies in the population estimates. Some EU countries rely on the standard counting of individual wolves. In contrast, others estimate the reproductive units (packs or pairs) and use conversion factors to convert that amount into individual numbers further. While this method may help monitor trends, it lacks the requirements of international conservation systems like the Red List (which assesses the species' conservation status).

Typical wolf monitoring relies on various ecological (such as population density, landscape characteristics, etc.), operational, and social aspects, including the availability of economic and scientific resources, as well as volunteers or workers to conduct such extensive fieldwork. In Scandinavian countries, adequate and regular wolf monitoring programs are in place due to substantial economic and scientific resources and a long-standing practice that began when wolves reappeared after local extinctions. Additionally, these regions consistently have winter snow, which benefits in gathering demographic and genetic information as it aids in wolf tracking and data collection.

Three monitoring methods can be used alone or combined. The data acquired from these methods are compiled and recorded in the country's national database and annual reports.

- Snow Tracking (Basic method): Over 100 field workers track wolves from October to March by finding and following their tracks in the snow.
- DNA Analysis: The wolf scat, urine, and hair collected during tracking are further analysed to confirm reproductions, identify new pairs, and distinguish the Finnish-Russian population.
- 3. Radio Telemetry: Every year, 10-20 wolves are equipped with GPS collars to track their territory boundaries and monitor their movements in the area.
- 4. Camera traps can also gather further information, reports of sightings by the public and dead wolves when available.

An evaluation study confirmed that the Scandinavian's applied monitoring approach effectively detects virtually all wolf packs, territorial pairs, and reproduction events, ensuring low uncertainty in the estimates compared to other EU member states [35]. Integrating different

field observations of snow tracking to DNA analysis and identifying scent-marking individuals in territorial pairs provides vital information on social status, reproduction, and genetic diversity. Despite snow tracking being a primary method, without it, managers would need to rely more on DNA analysis alone, causing a higher risk of discrepancies.

Snow Tracking

Wolf monitoring in Scandinavia primarily relies on three combined methods, with snow tracking being the most fundamental method [36]. The monitoring period runs from the beginning of October to the end of February, ensuring a more accurate population count before pups start dispersing. During the monitoring period, field workers actively search for tracks, with assistance from the public, and arrange to follow their tracks backwards to avoid disturbing the wolves. At least 3 km of tracks must be recorded to accurately determine their group size and retrieve data from their scent markings, oestrus bleedings, and scats for DNA analysis.

Tracking wolf packs can be challenging because they often travel in a single file, especially in deep snow, to conserve their energies, making it challenging to count individuals. To resolve this, trackers follow tracks for an extended distance (at least 3km) to reach sections where the wolves spread out, revealing the actual size of the pack. Additionally, packs may split into subgroups throughout the winter, requiring multiple revisits to the same territory for accurate counts and to avoid underestimating their size. Further complications include lone wolves joining tracks of resident packs and wolves looping back on their tracks, which can lead to overestimations.

Despite these challenges, repeated monitoring and extended tracking periods help minimise inaccuracies. If uncertainty remains, a minimum and maximum group size estimate is provided, ensuring consistency annually to detect significant changes in the wolf's status [19, 36].

DNA Analysis

DNA samples collected from Scandinavian wolves aid in determining their genetic pedigree and inbreeding levels. They can be obtained from blood (captured wolves), muscle tissue (deceased wolves), oestrus blood on snow and scats. Most samples from faecal droppings are collected during snow tracking [37]. They are vital to confirm reproduction units, identify new pairs, differentiate between neighbouring territories and detect new Finnish-Russian immigrants. The aim is to identify all territorial grey wolves each season, including marking

pairs, family packs, and lone wolves, using 30 diploid microsatellites and a haploid used as a sex marker. Genomic DNA extracted from tissue samples is isolated with a standard phenol/chloroform-isoamyl alcohol extraction protocol. While faecal samples are processed with a specific DNA isolation kit, oestrus blood samples are treated with ultraviolet light to avoid contamination.

Parentage analysis is used to determine the pedigree of the wolf population, incorporating samples from tissue (muscles or blood). Missing genotypes were reconstructed based on known parent and offspring genotypes. The analysis aids in confirming inbreeding within the population, and an inbreeding coefficient can be calculated further using a Pedigree Viewer to validate the findings.

The DNA program processes 400 samples annually for routine monitoring, with an additional 100 reserved for urgent cases, such as identifying potential immigrants. As of 2011, the program has successfully created genotype profiles for approximately 750 different wolves, representing 75-90% of the population since its founding. This conservative data has allowed the construction of a near-complete pedigree for the entire Scandinavian wolf population [19, 37].

Radio telemetry

Every winter, 10-20 wolves (primarily alphas and territorial wolves in pairs) are fitted with GPS-GSM collars as part of the Scandinavian Wolf Research Project (SKANDULV). Radio telemetry aids in distinguishing between neighbouring territories and pack territory sizes and confirming reproduction occurrences. However, the significant variation in territory sizes (ranging from 200 to 4300 km² based on data collected from GPS-collared wolves with an average of 1000 km²) poses challenges; sometimes, tracks found 100km apart can belong to the same territory. Since snow tracking can often lead to underestimations of territory sizes, telemetry data can aid in correcting the data. Additionally, track monitoring heavily relies on good snow conditions; climate change has led to warmer winters with shorter snow periods, especially in Southern Scandinavia; radio telemetry has aided during this shift [19].

2.5 Interactions with Natural Prey, Humans, and Livestock

Prey

As natural predators, the grey wolf primarily hunts wild ungulates (red deer, roe deer, wild boar, and moose) and can also prey on smaller wild animals, like hares and rodents.

However, their diet can vary depending on the availability of prey in the area. When wild prey is scarce, wolves may attack domestic animals or livestock, mainly sheep. The predatory instinct of wolves drives them to seek out the most easily accessible prey. Often, livestock are less adapted to defending themselves compared to wild prey. Such behaviour has fuelled significant human-wolf conflicts with agricultural communities, historically leading to the widespread persecution and extermination of wolves through hunting and habitat destruction in many regions to reduce its impact on livestock losses.

Protective measures, such as secure fencing, guard dogs, and compensation programs for livestock loss, can improve the efforts to mitigate human-wolf conflicts.

Wolves Predation on Wild Ungulates

Despite human influence, they cannot fully replicate the ecological effects of wolves, whose roles in nature are unique and irreplaceable. It demonstrates why human efforts often fail to control the negative impacts of the growing wild ungulate populations (deer, boar, moose), such as overgrazing, vegetation damage, and biodiversity loss. In Europe, wild ungulates like deer and wild boar populations have dramatically increased, surpassing historical times in many regions. Partly due to access to human-related food sources from agriculture, forestry, and supplementary feeding [26]. Although their expansion is vital for restoring ecosystem processes, these high-density ungulate populations can cause significant problems, such as crop and forestry damage, biodiversity loss due to overgrazing, material damage, increased risks like disease transmission to livestock and traffic collisions [38]. Wild boars, for instance, cause over 30 million euros in damage to agriculture and forestry annually, generating a substantial economic loss in Europe [39].

Forestry plays a vital part in Scandinavia's economic role. Growing moose populations lead to extensive browsing damage to young forests, creating a financial loss for forest owners. Combining and evaluating the interests of foresters, hunters, and wildlife conservationists in areas where wolves have recolonised, like Scandinavia, boosts further complexity to managing ungulate populations and their environmental impact [40].

Through trophic cascades, wolves target the most vulnerable prey, such as sick individuals, reducing transmission of diseases from wild ungulates to livestock [41]. An example is tuberculosis (TB), commonly transmitted between wild angulates and cattle. Regions with a denser population of wolves have a significantly lower TB prevalence than areas where wolves have gone extinct. Other cases show that wolves help control the spread of

African Swine Fever (ASFV) by consuming infected wild boar carcasses since the virus cannot survive the world's passage through the intestinal tract, limiting its transmission by removing infectious carrion. ASFV causes substantial economic losses to pigs, and with wolves, it can limit those losses. This demonstrates that wolf predation reduces infection rates without significantly lowering host population density, reducing disease-related mortality. The higher the density of the population of wolves, the lower the prevalence of disease transmission. Annual costs for compensation for wolf attacks on livestock are less than the yearly expenses of most disease eradication programs and treatments.

Additionally, by creating a 'landscape of fear,' wolves can reduce the number of deervehicle collisions (DVCs). Their presence has led to a significant 24% reduction in DVCs, saving €10.9 million annually. By altering the deer's behaviour, wolves highlight their unique ecological role in managing the overabundant prey populations, further minimising economic damage [42].

Since wolves and hunters target wild ungulates, hunters view wolves as competitors for the game species, claiming they impact the traditional game harvest for annual hunting. However, recent studies show that wolves kill significantly fewer wild ungulates yearly than hunters. Human hunting causes twice as much mortality towards the ungulate population than the wolves, "for most ungulate species; human harvest has a larger impact on population growth compared to predation (per capita kill) as hunters generally select adult animals at a higher rate than large carnivores" [43]. Across Europe, traditional game hunting has a higher effect on reducing wild ungulate densities than predation by wolves and other carnivores combined. Hunters tend to target adults (which have a significantly higher reproductive value), and wolves tend to target easier prey, such as calves. Therefore, countries like Sweden have had to adjust their wild ungulate management strategies for harvesting, targeting those with a lower reproductive value, like calves or modifying the age and sex compositions to compensate for the increased wolf predation and secure sustainable yields.

Wolves Predation on Livestock and Domestic Animals

Historically, grey wolf predation on livestock has been the main reason for the persecution of the population and remains a significant source of conflict between humans and wolves, both in Scandinavia and globally. While grey wolves mainly prey on wild ungulates in nature, they may also target more accessible options like unprotected domestic livestock, as it aligns with their instincts [20]. This behaviour affects not only farmers' economic concerns but

also the environment. In some regions, extensive livestock farming helps maintain biodiversityrich landscapes and prevents forest fires. Furthermore, it can carry significant emotional weight for pet owners and the public when attacks occur on domestic pets (horses, dogs, etc.).

With the non-legislative resolution adopted by the European Parliament in 2022, observing livestock predation is essential for developing policies that address human-wolf conflicts [34]. However, monitoring of livestock damage is inconsistent across Europe, partly due to varying compensation data. Each EU member state offers various compensation plans for wolf damages; some countries provide total compensation while others only partially or not, producing discrepancies in reported figures. Despite these comparison challenges, the Boitani et al. (2022) [10] study prepared an in-depth analysis of the damage caused by wolves, collecting available data from reports submitted by members of The Large Carnivore Initiative for Europe (LCIE) to the Bern Convention, providing valuable insights into the extent of wolf depredation on livestock across the Scandinavian countries and the total from all EU member states.

Wolf attacks on pets (particularly with dogs) are less common than predation on domestic livestock. Although predation on pets doesn't cause the same economic losses as on livestock, regardless, they hold a more substantial emotional impact on the public. The incidents cause increased fear and hatred in the public's attitude towards wolves since they often occur close to human civilisations. In many cultures, pets hold substantial social and emotional value for people, and their loss can trigger strong emotional responses of grief, particularly for hunting and livestock-guarding dogs, as they are more valuable and not easily replaced. Such attacks can decrease support for grey wolf conservation and strain relationships between local communities and wolf conservation efforts [9,10].

Dogs are perceived as competitors and prey for wolves, and they attack dogs under these two different circumstances. When hunting dogs roam free in known wolf territories in pursuit of hunting wild ungulates, wolves may view them as competitors for their prey. Since wolves are highly aggressive and protective when it comes to other rival wolves invading their territories, they may see hunting dogs similarly. In addition, herding dogs or livestock-guarding dogs are sometimes killed alongside the predation on livestock since wolves see them as prey, too. Dogs aren't usually the grey wolves preferred diet, so they may either partially or consume them [9, 10].

Public Safety

There has been no verified record of a fatal wolf attack on humans in Europe for the past 40 years. Only two unfortunate fatal attacks have occurred in North America [44]. However, the fear of wolves persists, primarily due to their historical negative reputation, where a wolf (Fenrir) kills Odin during Ragnarök in Norse mythology. Also, anti-wolf advocates exploit fear to challenge conservation legislation to reduce the current legal protection strategies for grey wolves [45].

Wolf attacks on the public have always been rare and often occurred due to specific conditions, such as when rabid wolves were involved or wolves preyed on unarmed children shepherds in areas with fragmented landscapes and scarce wild ungulate prey. These attacks are improbable due to the eradication of rabies in Scandinavia and changes in human activities, where children under 12 no longer work as shepherds.

The modern wolf-attack incidents nowadays involve "fearless" or food-conditioned wolves who have lost their natural wariness due to human feeding or other interactions (e.g., wolves bred and kept in captivity). It was a food-conditioned wolf responsible for one of the fatal attacks in North America. These wolves approach humans more readily, potentially causing dangerous situations. Similar cases were seen where wolves have caused injuries when being habituated to humans after prolonged exposure and feeding. Protocols have been placed to minimise such risks by encouraging the public to practice not feeding the wolves and ensuring that wolves are kept in the wild and not as household pets.

Managing the public's fear of wolves is a more significant challenge than addressing the risks of wolf attacks [45]. Misinformation from the media can exacerbate anxiety, as in cases where alleged wolf attacks were later proven to have been caused by uncontrolled and aggressive dogs. Debunking myths and spreading accurate information is critical to counteracting this fear and supporting wolf conservation globally.

Forensic Genetic Investigations

Recent advancements in molecular genetics have proven essential in distinguishing wolves from dogs in forensic investigations, helping to resolve conflicts between wildlife and human activities. With the return of wolf populations in Europe, conflicts have increased along with it, including illegal killings and livestock predation. Forensic methods, such as DNA analysis of salivary samples or physical evidence like teeth, allow researchers to identify whether wolves, dogs, or hybrids caused an attack. These investigations often rely on

determining individual genotypes using advanced techniques, such as analysing unlinked autosomal microsatellites, mitochondrial DNA (mtDNA) control-region sequences, a male-specific ZFX/ZFY restriction-site, and Y-linked microsatellites. For instance, DNA from confiscated wolf teeth provided crucial evidence in a criminal case against a serial wolf poacher, while genotyping saliva from livestock carcasses clarified that free-ranging dogs, not wolves, carried out some attacks. This distinction is critical, as false claims of wolf predation can inflate compensation requests and undermine conservation efforts [46, 47].

These forensic tools have also been used to address more unusual cases, such as a presumed wolf attack on a person. In one study, genetic analysis using the same methods revealed that the attack was carried out by a domestic dog, not a wolf, contradicting initial suspicions. This precise genetic profiling even matched the DNA to the specific dog responsible for the attack [46, 47]. Such findings highlight that wolves are often wrongly accused in conflicts, while their domestic relatives are more commonly responsible for aggression toward humans and livestock. By combining these molecular methods with veterinary field reports, researchers can provide accurate, evidence-based conclusions about predator identity, attack dynamics, and their impact on human activities.

2.6 Threats and Mortality

Grey wolves face significant pressures due to dense human populations, including legal hunting, poaching, and road mortality. Additionally, genetic issues threaten wolf populations, such as hybridisation with dogs, inbreeding, and loss of genetic diversity from habitat fragmentation and bottleneck populations. Based on expert opinions and recent scientific research, current and potential threats to wolves in the EU have been reviewed [7].

By 2015, the Large Carnivore Initiative for Europe (LCIE) identified the main threats to new biological wolf populations in Europe, including "*low acceptance, habitat loss from infrastructure development, persecution, hybridisation with dogs, poor management, and accidental mortality*" [48]. The most significant threat was the low acceptance of wolves, mainly due to widespread livestock attacks, which has, therefore, led to the primary reason for most legal and illegal killings of wolves. Later, in 2022, the LCIE highlighted additional threats based on IUCN classifications, noting that roads, illicit killings, and disturbances from tourism were other significant threat concerns to the population. Additionally, threats included disturbances from housing, industrial activities, and forestry, though the severity and persistence of these threats vary depending on local conditions and area.

Reporting under Article 17 of the EU Council Directive (92/43/EEC) identifies critical pressures (current impacts) and threats (future impacts) to wolves in Europe based on data from different biogeographic zones [49]. Nine significant issues were reported, with the most frequent being illegal shooting/killing, supported by the pressure from animal poisoning, both linked to wolf poaching. The second major issue is the impact of roads and infrastructure, which cause direct mortality from traffic accidents and lead to habitat fragmentation. The third issue conflicts with agricultural activities, primarily due to livestock predation [7].

Poaching

Wolf poaching is a significant cause of mortality in Europe, but often undetected. Studies have shown that data from an opportunistic collection of wolf carcasses typically are biased and overestimate deaths due to traffic and legal hunting while underestimating poaching and natural causes. Radiotracking studies reveal much higher rates of poaching [50].

Poaching poses a significant and often hidden threat to grey wolf populations across Europe. Much of it is "cryptic," meaning many instances go undetected, even with advanced tracking methods like radio collars. This makes it challenging to accurately assess the full extent of its impact on wolf mortality. Wolves' disappearances with no identified cause often point to illegal killings, which remain a major obstacle to conservation efforts [51].

Poaching profoundly impacts wolf populations, making it much harder for them to recover and thrive, even in areas where they are successfully reproducing. Illegal killings and unreported losses can quietly turn regions that should be safe havens for wolves into "population sinks," where deaths outnumber births. These hidden losses disrupt the balance between reproduction and survival, slowing or even reversing population growth despite conservation measures [52, 53].

Addressing poaching is essential to the recovery of wolf populations. Improved detection methods, stricter enforcement of anti-poaching laws, and enhanced public awareness are critical to reducing the effects of cryptic poaching and supporting the long-term sustainability of these apex predators.

Wolf Lethal Population Control

The European Commission's guidance on the strict protection of wolves under the Habitats Directive (Commission Notice C(2021) 7301) [54] emphasises that conflicts associated with wolf conservation in Europe cannot be resolved primarily through culling or

lethal control of the population. While lethal control was widely used in the past, current policy focuses on alternative management measures, including livestock damage prevention methods and other management measures.

Grey wolves are strictly protected under Annex IV of the Habitats Directive in most EU Member states. However, seven countries have Annex V status, allowing more management flexibility. The Directive permits derogations (exceptions to the prohibition on killing) to address severe livestock damage or public safety concerns, but their use varies by country.

In Sweden, grey wolves are strictly protected under the EU Habitats Directive, requiring the designation and management of Natura 2000 sites to ensure their conservation. However, managing this protected population presents challenges. In the northern reindeer husbandry regions, wolves are known to cause significant damage, leading to conflicts with local communities. In contrast, such conflicts are less frequent in southern areas. Licensed and protective hunting of wolves is carried out annually to address these issues and reduce socio-economic impacts. This approach aims to manage population growth and reduce the stress and economic burdens placed on affected communities [55].

Health monitoring of the Scandinavian grey wolf population is routinely conducted as part of conservation and management efforts by the County Administrative Board at SVA (Statens veterinärmedicinska anstalt). This includes investigations into infections, parasites, and congenital abnormalities found in culled wolves during licensed hunts. Findings have revealed regular cases of the dog's dwarf tapeworm (*Echinococcus granulosus*), injuries, dental anomalies, and deformed vertebrae. Notably, cryptorchidism, where one or both testicles fail to descend, has been observed frequently, therefore raising concerns about its genetic origins. After a particularly high number of cryptorchidism cases were recorded during the 2021 hunt, researchers have begun studying its link to inbreeding within the Swedish grey wolf population. The high levels of inbreeding make the population particularly vulnerable, increasing their risk of extinction. This highlights the urgent need for further research and stronger conservation efforts to protect and sustain these wolves [55, 56].

Due to the high degree of inbreeding, immigrant wolves (like the Finnish-Russian individuals) can contribute new genes of interest and help lower the threat status. The Scandinavian wolf population is one of the most well-documented in the world. DNA is collected from living and dead wolves, allowing for the identification and monitoring of genetically important wolves and providing good oversight of the dispersal patterns of other individuals [56].

3. Objectives

The primary objectives of this thesis are:

- 1. To Characterise the Scandinavian Grey Wolf Population: To provide a detailed understanding of the Scandinavian wolf population, including their traits, population trends, and their role as apex predators in Northern Europe's ecosystems.
- 2. To Analyse their Ecological Influences: To examine the ecological influences of the Scandinavian wolves and their impacts on society.
- 3. **To Investigate their Genetic Diversity and Status**: To assess the genetic diversity of the Scandinavian wolf population and analyse the impacts of genetic bottlenecks and inbreeding.
- 4. To Examine Conservation Status and Management Efforts: To evaluate the current conservation status of the Scandinavian grey wolf and assess the effectiveness of international and national policies. The role of conservation approaches and monitoring population trends will also be explored.
- 5. **To Explore Human-Wolf and Livestock-Wolf Interactions**: To investigate the causes and impacts of human-wolf and livestock-wolf conflicts, using forensic techniques to analyse cases of livestock depredation and human safety concerns.
- 6. **To Assess their Mortality and Prevalence of Threats**: To study the prevalence of legal or illegal wolf poaching and other threats, its underlying causes, and its effects on the population's recovery. Forensic methods will be emphasised to combat poaching and strengthen conservation efforts.

These objectives aim to comprehensively understand the Scandinavian grey wolf population's ecological, genetic, and forensic aspects. By integrating these perspectives, the study seeks to inform conservation strategies, address human-wolf conflicts, and promote the long-term survival of this endangered species.

4. Materials and Methods

This thesis is based on an extensive review related to the Scandinavian grey wolf. The research takes a multidisciplinary approach, combining ecological, genetic, and forensic perspectives to understand the species and its conservation challenges better.

The study analysed various sources, including peer-reviewed articles, conservation reports, case studies on human-wolf conflicts and poaching, and statistical data on population monitoring and genetic diversity. Relevant literature was identified using databases like PubMed,

ResearchGate, and Google Scholar, with keywords such as "Scandinavian grey wolf," "genetic diversity," and "human-wolf conflict." Sources were chosen based on their credibility and relevance based on recent studies.

The collected data provided insights into population trends, genetic diversity, conservation strategies, and human-wolf interactions. Forensic methods, such as DNA analysis and investigations into poaching cases, were also explored for their role in wolf management. Despite some limitations due to data availability and regional differences in monitoring methods, this thesis synthesises diverse information to offer a comprehensive understanding of the ecological and forensic aspects of the Scandinavian grey wolf.

5. Results and Discussion

The grey wolf population in Europe has recovered significantly in recent decades, largely due to legal protections, changing environmental conditions, and shifting societal dynamics. Wolves have adapted to repopulate near human-occupied landscapes, benefiting from rural-to-urban migration, natural reforestation, and increased wild ungulate populations [12, 57]. These apex predators, known for their intelligence, strong social bonds, and territorial nature, thrive in packs led by alpha pairs and primarily hunt large prey like deer and elk. Their unique physical traits, such as their robust bodies, long legs for covering vast distances, and bushy tails for insulation, make them well-suited to the boreal forests and mountainous regions of Scandinavia and beyond.

Despite these positive trends, conflicts with humans remain a persistent challenge. As wolves encroach on areas used for livestock grazing and hunting, tensions have risen among farmers, hunters, and recreational land users [12, 57]. Illegal killings of wolves, habitat fragmentation, and genetic isolation still hinder conservation efforts, even in regions with strong legal protections.

Analysing the Ecological Influences of Scandinavian Wolves

A comprehensive framework is currently lacking to accurately predict how large carnivores influence biodiversity and affect anthropogenic landscapes (areas shaped by human activity). Human presence and their activities influence the ecological roles of wolves by drastically altering their behaviour, density, and distribution of them and their prey. For instance, humans limit wolf populations through hunting or habitat fragmentation, making it difficult for these species to reach numbers high enough to exert any significant ecological influence. Furthermore, human activity has also been known to affect the populations of mesopredators (foxes, raccoons) and herbivores, disrupting the natural predator-prey dynamics [9].

Through density-mediated effects, the outcome of wolves reducing prey numbers and triggering a cascade effect throughout the ecosystem can likely be limited in human-dominated landscapes. Trophic cascades may only occur in remote areas, where small amounts of wolves can have an outsized effect on prey populations, or in the few parts of the landscape where wolves can exist in ecologically effective densities without human interference. This differs from behaviourally mediated effects, where the predators influence the behaviour of prey by altering where and when prey forage to avoid being hunted, which can occur even at lower predatory densities. This results from prey species adapting their behaviour in response to the mere presence of predators, regardless of the quantity of prey in the area [9].

The involvement of these factors illustrates that predator-prey dynamics in anthropogenic landscapes will vary significantly depending on the specific context. Factors including habitat type, land use, human activities, and the local wildlife management practice will affect how wolves impact the surrounding ecosystems. Certain human activities may weaken the predators' ecological role in some areas, reducing their ability to control prey populations or influence ecosystem processes. While wolves can exert strong effects on the ecosystem in other places, the presence of humans and human-modified environments can alter those effects.

Researching these complex dynamics is vital for wildlife conservation and management today. When wolves or other large carnivores are reintroduced in areas with high human impact, they must recognise that their ecological roles may not mirror those seen in pristine, untouched landscapes. Further investigation is needed to understand the existing gaps, specifically how human activities modify the behaviour and ecological impact of wolves and other predators. A clearer understanding of this will aid in future conservation strategies and ensure that researchers can accurately assess wolves' contribution to ecosystem health.

Investigating their Genetic Diversity and Status

46 Scandinavian wolf families were recorded during the winter of 2023-2024 (see Table 3) [58]: 38 packs were habituated in Sweden, three packs across the Swedish-Norwegian border territories, and five packs within Norway. Additionally, 30 territorial pairs were confirmed (26 in Sweden, three across the border, and one in Norway). Based on the number of reproduction

units, an estimated total wolf population is around 440; when the amount of reproduction units is multiplied by 10 (95% confidence interval (CI) = 348-572 range), this estimate includes both dead and alive wolves. The confidence intervals do not represent a minimum or maximum value but rather the uncertainty around the most likely population number. After distributing the cross-border occurrence, the number of wolves before any losses due to license hunting, protective hunting, or other mortalities during the period is indicated. The total for Sweden was 37.5 reproductions and for Norway, 6.5 reproductions. The 37.5 Swedish reproductions were distributed across the wildlife management areas, with 0 reproductions in the northern region, 29.5 reproductions in the central region, and eight reproductions in the southern area. Of the 6.5 litters in Norway, five were in Norwegian territories entirely within the Norwegian wolf zone, and three were in Swedish-Norwegian territories crossing the national border.

Table 3: Documented family packs, territory-marking pairs, and reproduction units of wolves in Sweden, in the Swedish-Norwegian border territories, in Norway, and the total during the 2023-2024 inventory period. As well as the total after the distribution of the cross-border territories (by adding half of the border wolves) [58]

	Sweden	Norway	Sweden-	Total	After
			Norway border		distributing
					the border
					territories
Total Family	38	3	5	46	39.5 (SWE)
Packs					6.5 (NOR)
Total Marking	26	3	1	30	27.5 (SWE)
Pairs					2.5 (NOR)
Sum of family	64	6	6	76	67 (SWE)
packs and					9 (NOR)
marking pairs					
Reproduction	36	3	5	44	37.5 (SWE)
units					6.5 (NOR)

The Scandinavian grey wolf population has generally increased from the 1990s until the winter monitoring period of 2014-2015, as demonstrated by the rise of family groups and reproduction units. However, this trend changed after 2014-2015, with a decline from 49 to 40 family groups by 2018-2019, equivalent to 18%. This primarily affected the Swedish population, which saw a 26% drop in family packs from 43 to 32 family groups. Afterwards, the numbers slightly inclined again from 2019-2022, peaking for the first time since the return of the population, with over 500 wolves in Scandinavia and around 460 in Sweden. The new 2023-2024 winter monitoring inventory revealed a renewed decline, with the total Scandinavian

population estimated at 440 wolves, approximately 375 in Sweden, showing a decrease in family groups and reproduction units compared to previous years [58].

Examining their Conservation Status and Management Efforts

The Scandinavian Grey wolf population is monitored annually by the Norwegian and Swedish authorities together, using joint guidelines from the Swedish Environmental Protection Agency and the Norwegian Environmental Agency. The field data is collected by the Country Administrative Boards in Sweden, the Norwegian Nature Inspectorate (SNO) and the Inland Norway University of Applied Sciences, supporting public reports of tracks and general observation. These monitoring periods have been carried out every winter since 1978 [36] across the Scandinavian peninsula under Regulation (2009:1263) § 8 "The County Administrative Board shall every year examine the population size and distribution of wolves, wolverines, loons and golden eagles in the county (predator inventory)" and § 9 "The Swedish Environmental Protection Agency must review and determine inventory results for wolves, wolverines, loons and golden eagles every year. If the weather has made it impossible to inventory a species, the Swedish Environmental Protection Agency must instead estimate the stock and its distribution." [59]. This cooperation between the two countries has resulted in a new monitoring methodology (Naturvårdsverket and Rovdata 2014), which is a shared database (Rovbase) for the recording of inventory data (www.rovbase.se) and a reporting system for the general public (www.skandobs.se), intending to ensure that both countries carry out similar methods thus being able to compare the results taken for the entire Scandinavian wolf population despite their location.

The categorisation of wolves into family groups (three or more wolves sharing a territory, usually with a litter, most common), territorial marking pairs (without a litter), and other stationary wolves and vagrants can aid in determining the annual number of productions. Both countries use the number of reproductive units, a key measure for national management goals for the population. In addition to the shared Scandinavian goals, Sweden and Norway have specific national goals. In Sweden, the goal is to document as many individual wolves per Sámi village as possible since it determines compensation for the affected Sámi villages. In Norway, all individuals in family groups are counted, and as far as possible, solitary wolves that are not part of family groups or territory-marking pairs are also inventoried.



Graph 2: Increasing trend in the territorial wolf units in Scandinavia during the winter period 1998/1999 to 2023/2024. Illustrating family packs (Dark blue bars), Marking pairs (Light blue bar), total family packs and pairs (Yellow dotted line) [58]

From May 2023 to April 2024, the population dynamics were influenced by various factors, including licensed and protective hunting, natural mortality, and human-wildlife interactions. These activities highlight the complexities of managing a vulnerable species in a region where ecological considerations intersect with political and cultural challenges. Data from this period provides critical insights into the population's status. This detailed account of wolf mortality sheds light on the delicate balance between conservation efforts, legal regulations, and how society responds to the presence of wolves. Looking at the data from this year helps conservationists better understand the current state of the Scandinavian grey wolf population and the ongoing challenges of protecting their survival while managing human-wolf conflicts and maintaining ecological balance.

The Entire Reproduction Cycle from May 1, 2023, to April 2024

During this period, 85 wolves died in Scandinavia, 59 in Sweden and 26 in Norway. Of the 59 in Sweden, 35 were culled during licensed hunts, 18 in protective hunts (including eight at the initiative of private individuals under Section 28 of the Hunting Ordinance), three died in traffic, and three from other causes. In Norway, 18 of the 26 wolves were culled during licensed hunts, six in protective hunts, one died in traffic, and one was confirmed to have been illegally killed [28].

Monitoring Inventory Period from October 1, 2023 to March 31 2024

Of the 85 known dead wolves in Scandinavia, 67 were documented during the inventory period, with 47 in Sweden and 20 in Norway. In Sweden, 35 wolves were culled during licensed hunts, seven during protective hunts (four at the initiative of private individuals under Section

28 of the Hunting Ordinance), two died in traffic, and three from other causes. In Norway, 18 of the 20 dead wolves during this period were culled during licensed hunts, one died in traffic, and one was confirmed to have been illegally killed [28].

Fifteen of the 85 wolves died before the inventory period, 67 died during it, and three died in April after the inventory period.

Licensed and Protective Hunting

During the licensed hunt in Sweden, six entirely Swedish family groups (Tjunken, Venabäcken, Villingsberg, Tångeråsa, Gryten, Ripelången) were affected. The Norwegian licensed hunt impacted one Swedish-Norwegian family group (Fjornshöjden) and a Swedish-Norwegian territorial pair (Römskog). The Norwegian family group in Rafjellet was culled during the Norwegian licensed hunt. In Norway, an uncertain territorial pair (Åsta) and three lone wolves outside of territories were culled during the licensed hunt [28].



Figure 8: Licensed wolf hunting in Sweden. Wolves are tracked, culled, and sent to laboratories for research and monitoring purposes as part of wildlife management [28]

Exploring the Human-wolf and Livestock-wolf Interactions

Based on data illustrated in Table 4, grey wolves were responsible for killing annually at least 65,500 livestock in the EU. Many of these losses were sheep and goats (73%), followed by cattle (19%). Additionally, semi-domestic reindeer are preyed upon in countries like Finland and Sweden, though exact figures for Sweden are not precise. However, these figures are significantly higher than the previous year's estimates, with only 53,530 reported livestock deaths. The rise in livestock figures could be a possibility for developing compensation plans following a more robust introduction of wolf protection measures, which, therefore, might have

led to more cases reported by the public. Alternatively, the number of attacks could have increased simultaneously with the growing wolf population. Regardless, the data indicates a growing trend in wolf-related livestock damage across the Scandinavian countries and within the EU member states. From a larger perspective, the impact of grey wolves on domestic livestock within the EU is generally relatively small; considering an estimated 60 million sheep reside in the EU, the level of sheep predation by wolves represents an annual of 0.065% killings. This data aids in understanding the need for effective management strategies to balance wolf conservation efforts with protecting agricultural livelihoods.

	Denmark	Finland	Norway	Sweden	Total within Scandinavian countries
Year of	2022	2022	2021	2022	-
depredation					
status					
Sheep and	159	518	979	255	1,911
Goats killed					
Cattle killed	2	11	0	5	18
Semi-Domestic	0	1,261	134	0	1,395
reindeer killed					
Dogs killed	0	<50	2	22	<74
Total killed	161	1,829	1,115	283	3,388
Year of	2022	2021	N.A	2022	-
compensation					
data					
Amount in	€51,093	€2,997,413	N.A	€164,000	€3,212,506
Euros of				(including	
compensation				compensation	
for losses				for the dogs)	
Rules for	Only	Only	Only a	Only	-
compensation	documented	documented	percentage of	documented	
	losses	losses	all claims are	losses	
			inspected so		
			compensation		
			is paid for more		
			documented		
Most	Walfproof	Electric fonces	Conversion	Electric fonces	
important	fences (1.20m	for sheep	from sheep	Electric fences	-
nrevention	high two	tor sheep	farming to		
measures	electric fences)		other		
measures	electric felices)		agricultural		
			activites inside		
			carnivore		
			zones electric		
			fencing		

Table 4: Wolf depredation on livestock across the Scandinavian countries [10]

Wolf-dog attacks occur more prominently in Northern European countries, where annual wild ungulate hunting is more common. In Finland, wolves killed or injured an average of 45.4 dogs annually from 2018 to 2022, while in Sweden, an average of 29.2 dogs were killed or injured annually from 2003 to 2018. Understanding the circumstances behind why wolves attack dogs can help design preventative measures to reduce the occurrence. Data from various regions indicate that the interaction between wolves and dogs depends heavily on the distance between the dog and its owner. Also, attacks on dogs weighing less than 20 kg are often fatal, whereas dogs weighing more than 25 kg (e.g., hunting hounds) are at a greater risk of injuries from these wolf attacks. Wolves are also more likely to attack certain breeds depending on their behaviour; Beagles are at much higher risk due to their energetic and sometimes aggressive behaviours, while Pointers are at lower risk because they are more vigilant [43]. Similar to the predation on domestic livestock, prey availability in the area will significantly influence the number of wolf attacks on dogs. With a lower density of wild, ungulate populations and scarce prey, wolves will tend to rely on domestic pets instead.

Assessing their Mortality and Prevalence of Threats

A review of the causes of wolf mortality in Scandinavia and across the EU demonstrates that humans are the leading cause, directly (through legal hunting, culling or poaching) or indirectly (via traffic accidents). The study method affects the causes of mortality: studies based on "found dead" wolves often highlight legal hunting and traffic as the main reasons, as they are more easily detected. In contrast, methods involving radiotracking reveal that poaching can be a significant cause of wolf deaths, even in regions where hunting is legal. Mortality rates are more accurately estimated through radiotracking studies. Rates based on "found dead" wolves are underestimated, as only some deceased wolves are discovered [7].

Cause of Death	Sweden	Finland
Legally killed (%)	66.9	3.8
Illegally killed (%)	13.0	57.2
Traffic (%)	5.2	4.4
Natural (%)	14.9	1.1
Others (%)	-	5.5
TOTAL (%)	154	91

 Table 5: Causes of wolf mortality (in percentages) in Sweden [60] and Finland [52]. The figures include data

 from "found-dead" wolf studies and radiotracking projects.

Poaching can be "cryptic," referring to how most instances go undetected, even with radio-collared wolves. For example, in Scandinavia, while 13% of the wolf deaths were verified as poaching, many radio-collared wolves disappeared with no known cause, implying that

illegal poaching could be responsible for about half of the total mortality cases. With 154 radiocollared wolves who died during this study, more than two-thirds of the total poaching remained undetected [51].

Poaching has severely impacted the grey wolf population and hinders their recovery efforts. As seen in Scandinavia, simulations estimated that without poaching, the wolf population would have been almost four times larger by 2009 [51]. Similarly, in Finland, illegal killing was the leading cause of death for wolves, with rates before being 9-13% and now up to 31-43% [52]. Furthermore, Denmark witnessed a decline in its wolf population after a female breeding a newly established pack was poached in 2018. Despite successful reproductions, the region became a "population sink" due to high levels of cryptic mortality [53]. The annual rate of mortality and disappearances in Denmark were comparable to the highest levels observed in Sweden and Finland, both of which experienced population declines due to illegal killings.

In Sweden, grey wolves are protected under the Habitats Directive as strictly protected species (Annex IV) and require the designation and management of Natura 2000 sites (Annex II). Wolves can cause significant damage in the reindeer husbandry areas in the North. However, conflicts with livestock in the South are less common. Several wolves are culled through protective and licensed hunting each year to prevent livestock damage and manage population growth, aiming to reduce socio-economic and psychosocial impacts on communities.

Table 6: Grey wolves culled through protective and licensed hunting in recent years in Sweden, along with data
on the size of the wolf population, the number of wolves found dead from other causes (Traffic, poaching, natural
causes), and the total known wolf mortality [7, 28, 36]

Year	Wolf	Number of wolves killed				
	population size	Protective hunting	Licensed hunting	Other causes (traffic, poaching etc.)	TOTAL	
2014-2015	415	21	44	12	77	
2015-2016	340	20	14	17	51	
2016-2017	355	15	25	11	51	
2017-2018	305	24	15	9	48	
2018-2019	300	9	0	7	16	
2019-2020	365	21	0	15	36	
2020-2021	395	23	27	10	60	
2021-2022	460	8	28	10	46	
2022-2023	450	23	57	8	88	

The hunting and culling of wolves are highly controversial in Sweden due to the concerns over the densely small and inbred wolf population, which has remained stable since 2014 with 400-500 individuals. Despite having a constant stable population, a relatively high number of wolves are legally allowed to be killed annually, reducing the chance for the population to grow. Due to this, Sweden's control culling practices have prompted an infringement procedure by the European Commission to review compliance with the Habitats Directive. However, Sweden regularly maintains a high standard of population monitoring and scientific knowledge, which helps detect changes in the wolf's status. Since 2020, all current and previous license hunting statistics are available to the public in 'Rovbase'. They allow hunters to get up-to-date information directly from the source, where the county administration enters information about the wolves (and other animals) killed in their county, providing an overview of the situation throughout the country [55].

Outlook

The future of the Scandinavian grey wolf depends on stronger, more innovative conservation strategies. Current population trends have remained stable for several years, showing neither significant increases nor decreases. While this stability suggests that existing measures may be preventing further decline, it raises questions about whether these efforts are sufficient to promote long-term recovery. Considering how many wolves once roamed the region, it is crucial to continue working toward restoring a more sustainable and ecologically impactful population.

Addressing public concerns about the cost of conservation programs, especially monitoring, is a significant challenge. Many people do not realize how essential wolves are for maintaining healthy ecosystems. As apex predators, they regulate prey populations, protect biodiversity, and keep ecosystems balanced. Public education is crucial for shifting perceptions and helping communities understand why investing in wolf conservation benefits both the environment and society as a whole.

Advancing technology offers exciting opportunities to improve monitoring and conservation efforts. Tools like satellite imaging and remote sensing can help provide more accurate population estimates and track wolves in real-time, reducing the reliance on less precise methods. These advancements could make monitoring more efficient and cost-effective, alleviating some concerns about funding. Combined with forensic tools like DNA analysis,

technology can play a critical role in understanding and protecting the Scandinavian grey wolf population.

Collaboration between conservationists, governments, and the public will be essential. Stable population trends should not lead to complacency but should motivate us to aim for growth and a more resilient population. By embracing new technologies, educating the public, and fostering international cooperation, we can ensure that the Scandinavian grey wolf continues to thrive and play its vital role in the ecosystem for generations to come.

6. Summary

This thesis comprehensively explores the Scandinavian grey wolf population, integrating ecological, genetic, and forensic perspectives to address key conservation challenges. The findings highlight the complex dynamics between the wolves' ecological roles, genetic challenges, and interactions with humans and livestock, all of which shape the future of their conservation.

The ecological characterisation of the Scandinavian grey wolf underscores its role as an apex predator, maintaining balance in ecosystems by regulating prey populations and contributing to biodiversity. Its ecological adaptations demonstrate resilience and the ability to thrive in Scandinavia's harsh climates and vast boreal forests. However, habitat loss and human activities continue to restrict its range, further complicating coexistence with rural communities.

The genetic analysis reveals significant concerns about inbreeding and genetic bottlenecks in populations stemming from their near extinction in the 20th century. Forensic tools like DNA analysis have been pivotal in monitoring genetic diversity, identifying immigrant wolves, and managing inbreeding depression. These findings highlight the need for transboundary collaboration between Norway and Sweden to maintain genetic health.

From a conservation perspective, international agreements like the Bern Convention and the EU Habitats Directive provide a strong legal framework for protecting wolves. However, differences in enforcement and national priorities create challenges in applying these laws. The political debate remains heated, particularly around issues like livestock attacks and public safety concerns. Forensic methods have become essential tools in tackling poaching, which continues to be a significant obstacle to wolf population recovery.

Interactions between wolves, humans, and livestock remain a key source of conflict. While wolves are essential in controlling wild prey populations, their occasional attacks on livestock often lead to tensions with farmers and rural communities. To promote coexistence, it is crucial to implement effective strategies such as fair compensation programs and better livestock protection methods.

Wolf mortality and threats, especially from poaching and human-related causes, remain a major challenge for the Scandinavian grey wolf. Despite legal protections, poaching continues due to conflicts with humans and negative perceptions, while licensed hunting further impacts population stability. Forensic tools like DNA analysis are essential for investigating illegal killings. Still, stronger enforcement, public awareness, and coexistence strategies are needed to reduce these threats and ensure the wolves' long-term survival.

While this study provides valuable insights, it also highlights several limitations. Monitoring wolf populations remains challenging due to incomplete data, inconsistent tracking methods across nations, and the elusive nature of wolves, making precise population estimates difficult. Additionally, public opinion can pose barriers to effective monitoring and conservation efforts. Debates over how much funding should go into these programs often create tension, with some arguing that resources could be better spent elsewhere. This can put conservationists in a difficult position, balancing the need for robust monitoring programs with limited budgets and competing societal priorities. Addressing these challenges will require improved data collection through standardised methods and forensic tools and stronger public support for the investment needed to protect this vulnerable species.

In summary, the Scandinavian grey wolf's story is resilient and vulnerable. While conservation efforts have led to a slow recovery, ongoing challenges like habitat loss, genetic risks, human conflicts, and poaching highlight the need for more adaptable management strategies. By combining ecological and forensic approaches, this thesis lays the groundwork for conservation policies that aim to balance ecological health with human interests. The long-term survival of this iconic species will rely on collaboration, creative solutions, and a shared commitment to coexistence.

39

7. References

- 1. Wikipedia Contributors. 2019. "Eurasian Wolf." Wikipedia. Wikimedia Foundation. November 1, 2019. https://en.wikipedia.org/wiki/Eurasian_wolf.
- 2. Gina. n.d. "Facts about Wolves." WildSweden Wildlife Adventures in Sweden. https://www.wildsweden.com/about/facts-about-wolves.
- 3. The Editors of Encyclopedia Britannica. 2018. "Gray Wolf | Size, Habitat, & Facts." In *Encyclopædia Britannica*. <u>https://www.britannica.com/animal/gray-wolf</u>.
- 4. "Factsheet: Gray Wolf (Eurasia's Carnivores > Canis Lupus)." 2015. Archive.org. 2015. https://web.archive.org/web/20150804072111/http://www.lhnet.org/gray-wolf.
- 5. "Eurasian Wolf Facts & Rewilding Significance | Rewild at Heart." 2024. Rewild at Heart. 2024. https://rewildatheart.com/pages/eurasian-wolf.
- 6. Wikipedia Contributors. 2024. "List of Gray Wolf Populations by Country." Wikipedia. Wikimedia Foundation. <u>https://en.wikipedia.org/wiki/List of gray wolf populations by country#cite_note-1</u>.
- Boitani, L.; Phillips, M.; Jhala, Y. (2020) [errata version of 2018 assessment]. <u>"Canis lupus"</u>. <u>IUCN Red</u> <u>List of Threatened Species</u>. 2018: e.T3746A163508960.
- Coppinger, Ray. 2001. "Dogs : A Startling New Understanding of Canine Origin, Behavior, and Evolution" Simon and Schuster. pp. <u>352</u>. <u>ISBN 978-0-684-85530-1</u>. https://archive.org/details/dogsstartlingnew00raym/page/10/mode/1up.
- 9. Blanco, Juan Carlos, and Kerstin Sundseth. 2023. "The Situation of the Wolf (Canis Lupus) in the European Union an In-Depth Analysis." <u>https://doi.org/10.2779/187513</u>.
- Boitani L, M Krofel, J Kutal, A Linnell, P Majic, F Mannil, D Marucco, D Melovski, et al. 2022. "Assessment of the Conservation Status of the Wolf (Canis Lupus) in Europe." <u>https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47</u>.
- Mech, L. David, and Luigi Boitani, eds. 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press. Chicago, IL: University of Chicago Press. https://press.uchicago.edu/ucp/books/book/chicago/W/bo3641392.html.
- Cimatti, Marta, Nathan Ranc, Ana Benítez-López, Luigi Maiorano, Luigi Boitani, Francesca Cagnacci, Mirza Čengić, et al. 2021. "Large Carnivore Expansion in Europe Is Associated with Human Population Density and Land Cover Changes." *Diversity and Distributions* 27 (4): 602–17. https://doi.org/10.1111/ddi.13219.
- Fan, Zhenxin, Pedro Silva, Ilan Gronau, Shuoguo Wang, Aitor Serres Armero, Rena M. Schweizer, Oscar Ramirez, et al. 2015. "Worldwide Patterns of Genomic Variation and Admixture in Gray Wolves." *Genome Research* 26 (2): 163–73. <u>https://doi.org/10.1101/gr.197517.115</u>.
- Ramos-Madrigal, Jazmín, Mikkel-Holger S. Sinding, Christian Carøe, Sarah S.T. Mak, Jonas Niemann, José A. Samaniego Castruita, Sergey Fedorov, et al. 2021. "Genomes of Pleistocene Siberian Wolves Uncover Multiple Extinct Wolf Lineages." *Current Biology* 31 (1): 198-206.e8. https://doi.org/10.1016/j.cub.2020.10.002.
- Thalmann, O, B Shapiro, P Cui, V J Schuenemann, S K Sawyer, D L Greenfield, M B Germonpré, et al. 2013. "Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs." *Science (New York, N.Y.)* 342 (6160): 871–74. <u>https://doi.org/10.1126/science.1243650</u>.
- Frantz, Laurent A. F., Victoria E. Mullin, Maud Pionnier-Capitan, Ophélie Lebrasseur, Morgane Ollivier, Angela Perri, Anna Linderholm, et al. 2016. "Genomic and Archaeological Evidence Suggest a Dual Origin of Domestic Dogs." *Science* 352 (6290): 1228–31. <u>https://doi.org/10.1126/science.aaf3161</u>.
- Bergström, A., Stanton, D.W.G., Taron, U.H. *et al.* Grey wolf genomic history reveals a dual ancestry of dogs. *Nature* 607, 313–320 (2022). <u>https://doi.org/10.1038/s41586-022-04824-9</u>
- Karlsson, J., H. Brøseth, H. Sand, and H. Andrén. 2007. "Predicting Occurrence of Wolf Territories in Scandinavia." *Journal of Zoology* 272 (3): 276–83. <u>https://doi.org/10.1111/j.1469-7998.2006.00267.x</u>.
- Liberg, Olof, Åke Aronson, Håkan Sand, Petter Wabakken, Erling Maartmann, Linn Svensson, and Mikael Åkesson. 2012. "Monitoring of Wolves in Scandinavia." *Hystrix, the Italian Journal of Mammalogy* 23 (1). <u>https://doi.org/10.4404/hystrix-23.1-4670</u>.
- 20. L David Mech. 1981. *The Wolf : The Ecology and Behavior of an Endangered Species*. Minneapolis: University Of Minnesota Press.

- Chapron, Guillaume, Petra Kaczensky, John D. C. Linnell, Manuela von Arx, Djuro Huber, Henrik Andrén, José Vicente López-Bao, et al. 2014. "Recovery of Large Carnivores in Europe's Modern Human-Dominated Landscapes." *Science* 346 (6216): 1517–19. https://doi.org/10.1126/science.1257553.
- Winnie Jr, John & Creel, Scott. (2016). The Many Effects of Carnivores on their Prey and Their Implications for Trophic Cascades, and Ecosystem Structure and Function. Food Webs. 12. 10.1016/j.fooweb.2016.09.002.
- Ripple, William J., and Robert L. Beschta. 2012. "Trophic Cascades in Yellowstone: The First 15 Years after Wolf Reintroduction." *Biological Conservation* 145 (1): 205–13. <u>https://doi.org/10.1016/j.biocon.2011.11.005</u>.
- Kuijper, D. P. J., E. Sahlén, B. Elmhagen, S. Chamaillé-Jammes, H. Sand, K. Lone, and J. P. G. M. Cromsigt. 2016. "Paws without Claws? Ecological Effects of Large Carnivores in Anthropogenic Landscapes." *Proceedings of the Royal Society B: Biological Sciences* 283 (1841): 20161625. <u>https://doi.org/10.1098/rspb.2016.1625</u>.
- Mols, Bjorn, Evert Lambers, Joris P. G. M. Cromsigt, Dries P. J. Kuijper, and Christian Smit. 2021. "Recreation and Hunting Differentially Affect Deer Behaviour and Sapling Performance." *Oikos* 2022 (1). <u>https://doi.org/10.1111/oik.08448</u>.
- Linnell, John D.C., Benjamin Cretois, Erlend B. Nilsen, Christer M. Rolandsen, Erling J. Solberg, Vebjørn Veiberg, Petra Kaczensky, et al. 2020. "The Challenges and Opportunities of Coexisting with Wild Ungulates in the Human-Dominated Landscapes of Europe's Anthropocene." *Biological Conservation* 244 (April): 108500. https://doi.org/10.1016/j.biocon.2020.108500.
- 27. Linnéa Smeds, and Hans Ellegren. 2022. "From High Masked to High Realized Genetic Load in Inbred Scandinavian Wolves." *Molecular Ecology*, December. <u>https://doi.org/10.1111/mec.16802</u>.
- Svensson, Linn, Petter Wabakken, Erling Maartmann, Kristoffer Nordli, Øystein Flagstad, Anna Danielsson, Henrike Hensel, Katarina Pöchhacker, and Mikael Åkesson. 2022. "Inventering Av Varg Vintern 2022-2023." *Nina.no.* <u>https://doi.org/978-82-426-4783-2</u>.
- 29. Åkesson, M, A Danielsson, Ö Flagstad, and L Svensson. 2023. "Sammanställning Av Släktträdet Över Den Skandinaviska Vargpopulationen Fram till 2022. Rapport På Uppdrag Av Naturvårdsverket." <u>https://www.slu.se/globalassets/ew/org/centrb/vsc/vsc-dokument/vsc-</u> publikationer/rapporter/2023/slakttrad-skand-varg-2022.pdf.
- 30. "Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) -Convention on the Conservation of European Wildlife and Natural Habitats - Www.coe.int." 2014. Convention on the Conservation of European Wildlife and Natural Habitats. 2014. <u>https://coe.int/en/web/bern-convention</u>.
- Trouwborst, Arie, and Fleurke, Floor M. 2019. "Killing Wolves Legally: Exploring the Scope for Lethal Wolf Management under European Nature Conservation Law." Ssrn.com. 2019. https://papers.ssrn.com/sol3/papers.cfm?abstract_id=3761365.
- 32. European Commission. 2024. "The Habitats Directive." Environment.ec.europa.eu. 2024. https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive_en.
- European Commission. 2023. "Wolves in Europe: Commission Urges Local Authorities to Make Full Use of Existing Derogations and Collects Data for Conservation Status Review." European Commission - European Commission. 2023. https://ec.europa.eu/commission/presscorner/detail/en/ip_23_4330.
- European Parliament. 2022. "Protection of Livestock Farming and Large Carnivores in Europe -Thursday, 24 November 2022." Europa.eu. 2022. <u>https://www.europarl.europa.eu/doceo/document/TA-9-2022-0423_EN.html</u>
- Åkesson, Mikael, Linn Svensson, Øystein Flagstad, Petter Wabakken, and Jens Frank. 2022. "Wolf Monitoring in Scandinavia: Evaluating Counts of Packs and Reproduction Events." *The Journal of Wildlife Management* 86 (4). <u>https://doi.org/10.1002/jwmg.22206</u>.
- Petter Wabakken, Håkan Sand, Olof Liberg, and Anders Bjärvall. 2001. "The Recovery, Distribution, and Population Dynamics of Wolves on the Scandinavian Peninsula, 1978-1998" 79 (4): 710–25. <u>https://doi.org/10.1139/cjz-79-4-710</u>.

- Liberg, Olof, Henrik Andrén, Hans-Christian Pedersen, Håkan Sand, Douglas Sejberg, Petter Wabakken, Mikael Åkesson, and Staffan Bensch. 2005. "Severe Inbreeding Depression in a Wild Wolf Canis Lupus Population." *Biology Letters* 1 (1): 17–20. <u>https://doi.org/10.1098/rsbl.2004.0266</u>.
- Carpio, Antonio J., Marco Apollonio, and Pelayo Acevedo. 2020. "Wild Ungulate Overabundance in Europe: Contexts, Causes, Monitoring and Management Recommendations." *Mammal Review* 51 (1): 95–108. <u>https://doi.org/10.1111/mam.12221</u>.
- 39. Apollonio, M, R Anderson, and R Putman. 2010. "European Ungulates and Their Management in the 21st Century." <u>https://www.researchgate.net/publication/292384232_European_Ungulates_and_Their_Management_in</u> the 21st Century.
- Wikenros, Camilla, Håkan Sand, Johan Månsson, Erling Maartmann, Ane Eriksen, Petter Wabakken, and Barbara Zimmermann. 2020. "Impact of a Recolonizing, Cross-Border Carnivore Population on Ungulate Harvest in Scandinavia." *Scientific Reports* 10 (1). <u>https://doi.org/10.1038/s41598-020-78585-</u><u>8</u>.
- 41. L. David Mech, Douglas W. Smith, Daniel R. MacNulty. 2015. *Wolves on the Hunt. University of Chicago Press*. <u>https://press.uchicago.edu/ucp/books/book/chicago/W/bo20145329.html</u>.
- Raynor, Jennifer L., Corbett A. Grainger, and Dominic P. Parker. 2021. "Wolves Make Roadways Safer, Generating Large Economic Returns to Predator Conservation." *Proceedings of the National Academy* of Sciences 118 (22). <u>https://doi.org/10.1073/pnas.2023251118</u>.
- Haidt, Andżelika, Radosław Gawryś, and Maciej Szewczyk. 2021. "Human Decision-Making as a Key Factor in the Risk of Wolf–Dog Interactions during Outdoor Activities." *Animals* 11 (9): 2497. <u>https://doi.org/10.3390/ani11092497</u>.
- 44. Linnell, Andersen, Andersone, and Balčiauskas. 2002. "The Fear of Wolves: A Review of Wolf Attacks on Humans." <u>https://www.researchgate.net/publication/236330045_The_fear_of_wolves_A_review_of_wolf_attacks</u> on humans.
- 45. Linnell, John D. C., and Julien Alleau. 2015. "Predators That Kill Humans: Myth, Reality, Context and the Politics of Wolf Attacks on People." *Problematic Wildlife*, December, 357–71. <u>https://doi.org/10.1007/978-3-319-22246-2_17</u>.
- 46. Caniglia, Romolo, Elena Fabbri, Claudia Greco, Marco Galaverni, and Ettore Randi. 2010. "Forensic DNA against Wildlife Poaching: Identification of a Serial Wolf Killing in Italy." Forensic Science International: Genetics 4 (5): 334–38. <u>https://doi.org/10.1016/j.fsigen.2009.10.012</u>.
- Caniglia, Romolo, Elena Fabbri, Luigi Mastrogiuseppe, and Ettore Randi. 2013. "Who Is Who? Identification of Livestock Predators Using Forensic Genetic Approaches." Forensic Science International: Genetics 7 (3): 397–404. <u>https://doi.org/10.1016/j.fsigen.2012.11.001</u>.
- Boitani L et al. 2015. Key actions for Large Carnivore populations in Europe. Institute of Applied Ecology (Rome, Italy). Report to DG Environment, European Commission, Bruxelles. Contract no. 07.0307/2013/654446/SER/B3.
- 49. European Union. 2024. "Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora." Europa.eu. 2024. <u>https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101</u>.
- Stenglein, Jennifer L., Timothy R. Van Deelen, Adrian P. Wydeven, David J. Mladenoff, Jane E. Wiedenhoeft, Nancy K. Businga, Julia A. Langenberg, Nancy J. Thomas, and Dennis M. Heisey. 2015. "Mortality Patterns and Detection Bias from Carcass Data: An Example from Wolf Recovery in Wisconsin." *The Journal of Wildlife Management* 79 (7): 1173–84. <u>https://doi.org/10.1002/jwmg.922</u>.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H (2012b). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B. <u>http://dx.doi.org/10.1098/rspb.2011.1275</u>
- Suutarinen, Johanna, and Ilpo Kojola. 2017. "Poaching Regulates the Legally Hunted Wolf Population in Finland." *Biological Conservation* 215 (November): 11–18. <u>https://doi.org/10.1016/j.biocon.2017.08.031</u>.

- Sunde P, Collet S, Nowak C, et al. (2021). Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany. Conservation Letters 14:e12812. <u>https://doi.org/10.1111/conl.12812</u>.
- European Union. 2021. "Commission Notice Guidance Document on the Strict Protection of Animal Species of Community Interest under the Habitats Directive." Europa.eu. 2021. <u>https://eurlex.europa.eu/legal-content/ES/TXT/?uri=PI_COM:C(2021)7301</u>.
- 55. Statens veterinärmedicinska anstalt. 2015. "Varg SVA." 2015. <u>https://www.sva.se/vilda-djur/rovdjur/varg/</u>.
- Linda Koffmar. 2022. "Scandinavian Wolves Carry Many Harmful Mutations Uppsala University." December 15, 2022. <u>https://www.uu.se/en/news/2022/2022-12-15-scandinavian-wolves-carry-many-harmful-mutations</u>.
- 57. Venter, Oscar, Eric W. Sanderson, Ainhoa Magrach, James R. Allan, Jutta Beher, Kendall R. Jones, Hugh P. Possingham, et al. 2016. "Sixteen Years of Change in the Global Terrestrial Human Footprint and Implications for Biodiversity Conservation." *Nature Communications* 7 (1): 1–11. <u>https://doi.org/10.1038/ncomms12558</u>.
- 58. Naturvårdsverket. 2024. "Varg, Population Skandinavien." <u>https://www.naturvardsverket.se/data-och-statistik/vilt/varg-population-skandinavien/</u>.
- Sveriges Riksdag. 2022. "Förordning (2009:1263) Om Förvaltning Av Björn, Varg, Järv, Lo Och Kungsörn." Riksdagen.se. <u>https://www.riksdagen.se/sv/dokument-och-lagar/dokument/svenskforfattningssamling/forordning-20091263-om-forvaltning-av-bjorn_sfs-2009-1263/</u>.
- Liberg, Olof, Johanna Suutarinen, Mikael Åkesson, Henrik Andrén, Petter Wabakken, Camilla Wikenros, and Håkan Sand. 2020. "Poaching-Related Disappearance Rate of Wolves in Sweden Was Positively Related to Population Size and Negatively to Legal Culling." *Biological Conservation* 243 (March): 108456. <u>https://doi.org/10.1016/j.biocon.2020.108456</u>.

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Thesis progress report for veterinary students

Name of student: Matilda Malmkvist

Neptun code of the student: DOUWYV

Name and title of the supervisor: Dr. Zenke Petra senior research fellow

Department: Animal Breeding and Genetics

Thesis title: Characterisation of the Scandinavian wolf population from an ecological and forensic point of view

Timing				Topic / Remarks of the supervisor	Circulture of the surger in the	
	year	month	day	Tople / Remarks of the supervisor	Signature of the supervisor	
1.	2023	june	02	Discussion about the topic selectionm in general	Zille	
2.	2023	dec.	12	Literature selection	full	
3.	2024	march	18	Design of the structure and the content of the thesis	Alle	
4.	2024	may	21	Literature review	BILL	
5.	2024	june	19	Discussion about the selected references	dill	

Consultation - 1st semester

Grade achieved at the end of the first semester: excellent (5)

Consultation - 2nd semester

	Timing			Topic / Remarks of the supervisor	Signature of the supervisor
	year	month	day	Tople / Remarks of the supervisor	Signatare of the supervisor
1.	2024	sept.	02	Discussion of the table of content	Sell

1

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2.	2024	oct.	09	Discussion of the abstract and summary	Lille
3.	2024	nov.	18	Evaluation of the first draft	dille
4.	2024	nov.	25	Evaluation of the second draft	Julle
5.	2024	nov.	28	Final discussion about the manuscript and approval	Diller

Grade achieved at the end of the second semester: excellent (5)

The thesis meets the requirements of the Study and Examination Rules of the University and the Guide to Thesis Writing.

I accept the thesis and find it suitable for defense,

....

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Mat.M Signature of the student:

Signature of the secretary of the department:

.

Date of handing the thesis in... November 28th, 2024

2

signature of the supervisor