The return of wolves to the Netherlands

A fact-finding study

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Jansman, H.A.H.[1], J. Mergeay[2], E.A. van der Grift[1], G.A. de Groot[1], D.R. Lammertsma[1], K. Van Den Berge[2], F.G.W.A. Ottburg[1], J. Gouwy[2], R. Schuiling[1], T. van der Veken[2] & C. Nowak[3]

1 Wageningen Environmental Research
2 INBO
3 Senckenberg

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Wolves have become increasingly common in the Netherlands since 2015, and since 2019 the country has once again been home to a pack of wolves with young – the first in around 150 years. The government intends to review the current Interprovincial Wolf Plan, a process that will start in 2021. This report provides an answer to 25 research questions formulated by the government. These questions relate to five themes: (1) distribution, occurrence, origin and ecological carrying capacity; (2) behaviour and the relationship between wolves and humans; (3) policy, damage, monitoring and management; (4) ecology; (5) genetic techniques and data exchange in Europe. The latest insights from scientific research and monitoring programmes have been used to answer these questions. The knowledge presented in this report can be used to make scientifically substantiated policy choices with regard to wolves.

Keywords: wolf, Netherlands, coexistence, distribution, origin, carrying capacity, behaviour, policy, damage, monitoring, management, diet, ecology.

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Confirmation of the referee who assessed the report:

position:	Animal Ecologist
name:	Tim Visser
date:	28 July 2021

Confirmation of team leader regarding content:

name:	Marion Kluivers-Poodt
date:	28 July 2021

Foreword for the English version of this report

In the spring of 2021, the Ministry of Agriculture, Nature and Food Quality (LNV), the Association of Provincial Authorities (IPO) and BIJ12 tasked WENR to write an updated fact-finding report on wolves in The Netherlands. The previous fact-finding report, dating from 2012, focussed on the foreseeable return of wolves. In 2021 several wolves had settled in the Netherlands and had reproduced. This resulted in many questions and advancing insight, allowing for an update of the 2012 fact-finding report. The authorities formulated 25 research questions. The results were published in Dutch in October 2021 in the report ‘De wolf terug in Nederland’ (Jansman et al, 2021).

Since the Netherland is a relatively small country and wolves use large areas, it is of great importance to cooperate internationally on the conservation and management of wolves. Therefore it was decided by the Dutch authorities to have the report translated to English.

This translation was conducted by a certified translating office. The authors of the original report only checked if technical terms (jargon) were correctly translated. Further, minor errors such as incorrect references to figures in the original Dutch version were adjusted in this English version.

Currently, July 2023, 91 individual wolves have been detected in the Netherlands and the number of dead wolves has increased to 17, mainly by traffic collisions but some have been killed by poaching and management cull. At this moment there are at least 5 reproducing packs of wolves, next to some territorial individuals. Wolves are an ever increasing topic in the media and the subject of coexisting with wolves is being debated in Dutch politics. This shows that discussions about wolves, knowledge regarding wolves as well as the perception by the general public is rapidly increasing and/or dynamic. Therefore monitoring and scientific facts are of great importance in order to understand the developments and to have an scientifically sound debate.

Hugh Jansman, July 2023

Foreword

You are reading the fact-finding study ‘The Return of Wolves to the Netherlands’. The report was written by Wageningen Environmental Research, commissioned jointly by the Ministry of Agriculture, Nature and Food Quality (LNV), the twelve provinces (IPO) and BIJ12 in 2021.

The fact-finding study provides a factual and scientifically substantiated overview of the latest situation regarding wolves in the Netherlands, and has been written in part to support the policy to be formulated by central government and the provinces.

This report was published partly in order to answer the many questions that the public has regarding wolves. This includes questions from people who keep livestock, the wider population, and also nature conservationists. These questions mainly relate to the effect of wolves on humans, animals and nature. The aim of this report is to help provide an accurate framework and ways forward with respect to the doubts and questions that exist.

Due to the wide-ranging partnership between various (national and international) experts (including species-related, ecological and policy experts), it was possible to investigate and include many different aspects of the subject of wolves. The report therefore provides an important basis for the updated version of the Interprovincial Wolf Plan to be published in 2022, which has been adopted by the Association of Provincial Authorities (IPO). This update is intended to provide a direction for joint policy regarding the implementation of provincial duties related to wolves after 2021.

The provinces, jointly, and the Ministry of Agriculture, Nature and Food Quality hope to facilitate the peaceful coexistence of people and wolves.

Jolinda van der Endt, director of BIJ12, summer 2021

Acknowledgments

This report was produced in the summer of 2021 in a relatively short period of time, and we are grateful to the many people who helped, both directly and indirectly. We are very grateful to Ilka Reinhardt (ecologist at the LUPUS Institut für Wolfsmonitoring und -forschung in Germany) and Prof. Arie Trouwborst (Nature Conservation Legislation at Tilburg University) for their expertise in the fields of ecology and the law, respectively. Ilka also arranged for certain data to be made available, which has improved the quality of this report.

In addition, we would like to thank Bjorn Mols and Chris Smit (RuG) and Maurice La Haye (Dutch Mammal Society) for their contributions to ongoing studies into the diet of wolves and their effect on ecosystems. Norman Stier (TU Dresden; wildlife biologist in Mecklenburg-Vorpommern, Germany) and Jens Teubner (Landesamt für Umwelt; Brandenburg, Germany) helpfully provided information regarding the wolves coming to the Netherlands from those federal states of Germany. The telemetry data on wolves that have visited the Netherlands, fitted with a GPS collar transmitter by TU Dresden, proved particularly valuable.

We would also like to thank Gijsbert Six (Platform for Sheep and Goat Smallholders) and Wilfried Buitink (Staatsbosbeheer Shepherd working in the Veluwe area) for their knowledge and expertise regarding sheep breeds and shepherding.

Matthieu Chastel (UA & INBO) shared information regarding preventive measures and Liesbeth Bakker (WUR) shared information regarding wolves and their effect on ecosystems. We are also grateful to our partners and contact persons at BIJ12, the provinces, the IPO and the Ministry of Agriculture, Nature and Food Quality. We thank you for the constructive meetings held while working on this report and for the use of the dataset. That dataset only exists thanks to the people who provided the information that it contains. We are grateful to the many volunteers who have secured, verified and in some cases sampled DNA at the wolf reporting point (as well as the site managers and fauna managers involved).

The same applies to the constructive, wide-ranging cooperation between the organisations involved, in particular the Dutch Mammal Society and the Wolves in the Netherlands consortium. Our thanks also go to the experts who secured DNA in cases of lost livestock. Post mortems were carried out on dead wolves with the help of the DWHC. We thank Luuk Boerema for his good work regarding the legal aspects of wolves, which he and his colleagues have reported on separately. We would also like to thank our colleagues at the CEwolf consortium for exchanging knowledge and information regarding wolves, which made it possible to find out about the movements of individual wolves quickly.

Finally, we would like to thank the geneticists who contributed to the survey and the workshop with a discussion of the molecular methods used and a reflection on the future development of genetic monitoring for wolves. This report is beautifully illustrated with photos by Marielle van Uitert, www.paralleluniversum.nl, as well as Raya Strikwerda & Hans Hasper (Wolvenmeldpunt) and Eddy Ulenaers and Ernesto Zvar, Flanders.

The authors, summer 2021

Summary

Introduction
Wolves have become increasingly common in the Netherlands since 2015, and since 2019 the country has once again been home to a pack of wolves with young – the first in around 150 years. The government intends to review the current Interprovincial Wolf Plan, which dates from 2019. This report provides answers to 25 research questions formulated by the government with as much factual accuracy as possible. These questions relate to five themes: (A) distribution, occurrence, origin and ecological carrying capacity; (B) behaviour and the relationship between wolves and humans; (C) policy, damage, monitoring and management; (D) ecology; (E) genetic techniques and data exchange in Europe. The knowledge used to provide those answers is based on the latest data from ongoing monitoring and scientific research. This research uses a database created by BIJ12 detailing observations of wolves. This included all registered observations between January 2015 and April 2021. Chapter 4 of the report includes general information regarding wolves, providing some background information regarding the animals' appearance, monitoring and research, hunting behaviour, the social pack animal, population trends, some examples of wolves in the Netherlands and a section on the perception of wolves. The answers to the questions are briefly elaborated in the sections below using the original chapter and section numbering, so that it is easy to find more detailed information on a particular question.

Chapter 5 Distribution, occurrence, origin and ecological carrying capacity
5.1 The wolf has long been an endemic species in Europe. Several centuries ago wolves were distributed across the entire continent, but their numbers dwindled due to hunting and persecution. After reaching a nadir in 1950-1960, when wolves disappeared entirely from Western and Northern Europe, populations have recovered naturally in recent decades, and regions from which the species had disappeared are now being recolonised. As a striking example, a Central European wolf population has also emerged since 2000, originating in north-eastern Poland. This population is steadily spreading out in a westerly direction, and wolves from this population have recently settled in Denmark, the Netherlands and Belgium, in succession. Genetic research has shown that by far the majority of the 34 wolves observed in the Netherlands so far (as of April 2021) came from that Central European population, including the four individuals that have now settled in the Veluwe area. A majority of these wolves came from packs that have settled quite recently in the German state of Lower Saxony, some were from eastern Germany and one was from North Rhine-Westphalia. So far, two individuals have been observed that came from a different region, namely from the rapidly growing population of Alpine wolves. This includes the wolf that has now settled in the province of Noord-Brabant (Groote Heide area). Wolves originating from the Alpine population have also been found in Germany and northern France. Of the 28 wolves that were first encountered in our country at least six months ago, a quarter are known to still be alive and present in the Netherlands. Almost half (13 individuals) have left our country, either returning to German territory or moving into Belgium. Four individuals are known to have died in the Netherlands as a result of traffic accidents. The location of the four other wolves remains unknown. It seems highly likely that these individuals have died, although by what cause is unknown. They may have died of natural causes in a location where they were difficult to find, but based on research into such 'disappearances' among wolves carried out abroad, illegal prosecution also seems a realistic possibility.

5.2 There is no indication that the wolves currently present in Central Europe or the Alpine region came from the illegal introduction of the species. The genetic structure and composition of current European wolf populations can be explained adequately through the scientifically substantiated, spontaneous expansion of existing wild populations.

5.3 Just as all modern humans carry a small proportion of DNA from other human species that are now extinct, wolves also derive a very small percentage of their DNA from dogs (<5%). This is the result of occasional interbreeding between wolves and dogs over millennia. These wolves are not

considered hybrids. Occasionally, mating between wolves and dogs is observed in the Central European population. The resulting offspring are easy to recognise genetically. Although these hybrid wolves are also protected, the European Commission recommends that confirmed hybrids be removed from the population with a permit, in order to protect the genetic integrity of wolves.

5.4 In the period 2015-2021, the area of activity for wolves covered almost half of the territory of the Netherlands, if (occasional) excursions are not taken into account. Six hotspots of wolf activity have been identified within this larger area of activity: one in Drenthe, two in Overijssel, two in Gelderland and one in Noord-Brabant. Wolves entered the Netherlands mainly from Germany, via the provinces of Drenthe and Overijssel. It is expected that this route will continue to be used in the future, because there are several wolf territories in Germany at a relatively short distance from the border with the Netherlands. In the longer term, more wolves can also be expected from the south – via Limburg and North Brabant, as wolves from packs in Belgium search for new territory and/or individual animals roam northwards through the Eifel region or from the French Alps. Broadly speaking, four corridors can be designated within the Netherlands, i.e. places where there is some frequency of movements. The first corridor runs from central Drenthe through central Overijssel to the Achterhoek area. A second corridor is a branch of the first, and runs from central Overijssel towards the Veluwe area. A third corridor is an extension of the first and runs from the Achterhoek area through German territory and into North Limburg and the southeast of Noord-Brabant. The area around the Meuse, Waal and Lower Rhine rivers also shows some evidence of more frequent movements, but in an east-west direction. The expectation is that if more wolves arrive in our country or are born here, the number of corridors will increase and the location of those corridors can be described more accurately based on more systematic observation. In some hotspots many reports of damage caused by wolves may have been received, but this is not always the case. So hotspots are not necessarily linked to significant losses of livestock, and indeed there may be no such losses at all.

5.5 In recent years, the Netherlands has mainly been an area that wolves passed through. Not many have settled so far, and settlement has mainly been confined to solitary wolves settling and breeding in the Veluwe area.

5.6 Because only limited information regarding the use of habitats and territory size of wolves in the Netherlands is available, no conclusion regarding carrying capacity can currently be drawn. In 2012, preliminary models estimated that the Netherlands could support between 16 and 89 packs. However, these models do not take account of how wolves in the Netherlands use terrain.

5.7 and 5.9 It is not currently possible to predict the trend in the numbers of wolves in the Netherlands over time or in spatial terms. The data that would be required to answer that question with a reasonable degree of accuracy is not currently available. If the carrying capacity were to be reached at approximately 16-89 packs, the population in the Netherlands could reach those numbers in 8 to 18 years, in theory. It is predicted that wolves could, in principle, settle temporarily or permanently in almost all types of landscapes in the Netherlands. However, they prefer areas that have large areas of natural habitat, with enough areas to rest. The larger forested areas in the Netherlands, particularly in the Veluwe area, are expected to be important habitats for wolves. Human tolerance plays an important role here, and this factor is difficult to predict.

5.8 The average size of a territory in neighbouring countries is around 200 km^2 (ranging between 80 and 400 km^2), depending on how many daytime resting places there are, ungulate population density, competition and the social status of the wolves. A pack needs slightly more space than a solitary animal and a territory in a saturated region will be smaller than one in an empty region due to competition between packs. In a cultivated landscape that features smaller areas of natural habitat surrounded by larger areas of agricultural land and residential areas, the size of the territory may be considerably larger. This is because the territory then includes large areas of terrain that is less suitable or unsuitable, with those areas mainly being used by the wolves to move from one suitable habitat to another within the territory.

5.10 and 5.11 One thousand packs are needed for a viable isolated population of wolves. It is unlikely that a wolf population of that size could exist in the Netherlands. For this reason, it is important that enough movement is possible between the different subpopulations of wolves in Europe, in order to maintain genetic exchange and diversity.

Chapter 6 Behaviour and the relationship between wolves and humans

6.1 Wolves are very flexible animals and they adapt quickly to the presence of humans in cultural landscapes. That adaptability means that in principle they can live anywhere where there is sufficient food and they can find a safe place to rest during the day. As long as wolves see humans as a potential threat, they will avoid confronting them. The risk lies in habituation, which results in wolves becoming less shy of contact with humans. This process is often caused by human actions, such as feeding wolves. The risk of conflict can occur particularly when wolves begin to associate humans with food. In addition, they can learn that inadequately protected livestock, particularly sheep, provide an excellent source of food.

6.2 There are occasional reports of wolves displaying unusual behaviours. In many cases these behaviours are not dangerous, and involve people’s perceptions of how a wolf ‘should’ behave or wolves’ habituation to humans and human activity. If a wolf displays boldness, such as tolerating people less than 30 metres away, this is cause for concern. In most cases this means that the wolf has become highly habituated to humans and, subsequently, developed a positive association between humans and food. A wolf displaying this kind of behaviour may then actively approach humans or areas where humans are present in the expectation of obtaining food. If the wolf is not rewarded, it may become frustrated or aggressive and may bite. Other triggers that can result in problem behaviours are rabies and human provocation.

6.3 The killing of more livestock than a wolf actually consumes is largely the result of an unnatural situation. Enclosed sheep, in particular, are often unable to act on their natural flight instinct. Predators take advantage of such opportunities by killing multiple animals at once. In nature, these would be consumed, but in a human environment the wolf feels threatened and this can lead to the animal making a swift departure.

6.4 The risk of an attack on humans or dogs is an important aspect of people’s perceptions of wolves. Nevertheless, in Western settings the number of incidents is limited, and the risk of a human being bitten by a wolf is negligible. The greatest risk is posed by wolves that have little or none of their natural timidity around humans and that associate humans with food. If such a wolf approaches humans expecting food and then does not receive any, it may become aggressive. Older wolves or sick wolves that are no longer able to hunt for prey independently may also approach humans, or wolves infected with rabies. Dogs can be seen by wolves as potential mates, but also as rivals. This can lead to wolves approaching dogs to lure them out into the wild, but also to wolves attacking and killing dogs.

6.5 The direct effect of wolves on road safety in the Netherlands is currently very limited. In the period between 2015 and July 2021 there were five vehicle strikes with wolves on roads in the Netherlands. No information is available on indirect effects, such as changes in the number of vehicle strikes involving wolf prey. Although the number of vehicle strikes involving wolves will increase as the population of wolves grows, the direct effect on road safety is expected to remain limited. This is firstly because the expected number of vehicle strikes involving wolves remains relatively low compared to the number of ungulates that are hit each year, for example, and secondly because it is possible to reduce the number of vehicle strikes by using fencing and wildlife crossing points, for instance. It is not possible to draw any conclusions regarding any indirect effects of the presence of wolves on road safety, as yet. On the one hand, the presence of wolves can reduce ungulate populations, thereby reducing the number of vehicle strikes with those animals; but on the other hand, it is possible that ungulate habitat use may be affected, leading them to cross roads and railways more frequently and thus increasing the risk of vehicle strikes. Too little research has been done – either in the Netherlands or elsewhere – to reach any substantiated conclusions about this. As far as recreation is concerned, wolves may attract visitors (ecotourism) or put visitors off (out of fear). In addition, the risk of wolves becoming habituated to humans may increase as a result of the increased likelihood of interactions.

Chapter 7 Policy, damage, monitoring and management

7.1 There are two main reasons for allowing exceptions to the protected status of individual wolves: 1. high-risk, undesirable behaviour towards humans in bolder animals; or 2. significant economic damage. In the first case, human safety is the priority, and in the second case the exception is intended to limit serious economic damage if this cannot be prevented in any other way. In the first case, there is broad policy agreement between states. In the second case, there are significant differences between EU member states; these are, however, currently under legal review in the respective countries. These are discussed specifically in Boerema et al. (2021). The difference between these two exceptions is fundamental, because the associated habituation and conditioning are very different.

7.2 No research has hitherto established any causal link between the culling of wolves, as envisaged within the legal boundaries of the Habitats Directive (i.e. provided there is no deterioration in conservation status) and reducing the predation of livestock. The studies that have been carried out and that indicate a positive effect are correlative, and cannot differentiate between the effect of culling itself and the effect of the associated increased human presence in areas of significant damage. In just over half of these studies, the culling of wolves was associated with (localised) reduction in damage, while the other half found no difference or a slight increase in damage. Where culling is highly intensive and removes more animals than can be replaced through reproduction, the amount of damage will decrease, but only due to the smaller population of wolves. Depending on which individual is killed and at what time of year this occurs, the effect on the pack and on the behaviour of the pack members can range between limited to very significant. Because culling is often non-selective at the level of individual animals, there is a chance that it may actually lead to an increase in damage – the opposite effect to that intended. Providing for the option of culling through legal derogations is often also intended to increase support for wolves in conflict situations and thus indirectly also to reduce illegal hunting. However, research indicates that where culling is permitted, the illegal hunting of wolves actually increases rather than decreases.

7.3 Livestock protection measures work well in principle, but their effectiveness and practicality are highly dependent on the situation on the ground and on local circumstances (e.g. terrain profile, size of the flock or herd to be protected, livestock species, type of grazing). The most common and effective measures are the use of electric fences, livestock guard dogs and the presence of a shepherd; these measures are often combined. In Belgium, Germany and France, the government provides compensation for losses suffered and grants to put preventive measures in place. In addition, there are several other less efficient protective measures that are based primarily on neophobia (fear of the new) in wolves. These can have some temporary effect, but in the absence of a deterrent these can also lead to habituation, or even positive conditioning. In order to optimise livestock protection, it is essential to understand the natural behaviour of wolves: how wolves respond to new stimuli in their environment and the concept of neophobia, how they become accustomed to new stimuli (habituation) and may respond both positively and negatively, and how they can be conditioned to those stimuli through both the positive or negative experiences which they associate them with. Long stretches of fencing designed to keep wolves out are not desirable, as they impede the natural movement of wildlife.

7.4 The aim of repelling and deterring wolves is to discourage and eliminate the undesirable behaviour in the future, in the hope that the wolves may associate this negative experience with their own actions. However, repelling wolves from livestock is an ineffective method because the wolves actually associate this with humans, and not with the livestock. Although repelling wolves can have a localised effect, the wolves' behaviour remains unchanged. At most, they may develop an aversion to humans. This can still be beneficial if the livestock in question is kept in the vicinity of humans. Deterrence has proven valuable for wolves that are highly habituated to humans, and can reverse this habituation. In such cases, it is advisable to use the most forceful method possible, which generally means firing non-lethal ammunition. This should only be done by people who have undergone appropriate training. The distance within which rubber bullets can be fired with sufficient accuracy (without hitting vital organs) is less than 30 metres. This limits the option to deter wolves that can be approached at this distance.

7.5. The purpose of fauna management is to limit damage to crops, forestry or valuable areas of nature, and also to ensure road safety. The return of wolves means that it is important to take them into account when it comes to ungulate fauna management. For instance, it is desirable to re-examine existing fauna management strategies with respect to the effects of game hunting on the availability of prey for wolves.

Chapter 8 Ecology

8.1 It is likely that the diet of Dutch wolves is consistent with that of wolves in Germany and Flanders. Roe deer form the main component. This is supplemented by other wild ungulates, such as wild boar and red or fallow deer, depending on their availability in the wolf’s territory. Livestock, particularly sheep, make up a small proportion of the diet of settled wolves. Roaming wolves, on the other hand, can appear anywhere and are usually young, inexperienced wolves looking for a territory of their own. Livestock, particularly sheep, are also frequent prey for these roaming wolves, due to chance and convenience.

8.2 Scavengers such as raven are benefiting from the return of wolves due to the carrion they leave behind without consuming them completely. It is not known whether wolves may also have an effect on the numbers and behaviour of ungulates in the Netherlands. It is expected that the effect of wolves on the numbers of ungulates will remain limited, given the effect of the intensive human intervention on the population of ungulates in the Netherlands. The indirect effect of wolves on the behaviour of ungulates, and therefore on the ecosystem, is likely to be greater. This applies not only to wild ungulates, but possibly also to the semi-wild grazers that frequently populate Dutch nature reserves.

Chapter 9 Genetic techniques and data exchange in Europe

9. A survey and workshop were held in order to explore the extent to which improving current methods of identifying species, recognising particular individuals and detecting hybrids would be possible and useful. The results showed that the methods that have been standard in recent decades, and which are also being applied in the Netherlands, Belgium and Germany, do yield reliable results. However, if the sample numbers for periodic monitoring increase, improvements could still be made, especially in terms of lead times and cost-effectiveness. In the future, a move to analysis using alternative equipment and techniques will be important in this regard.

Photo S1 *Camera trap photo of Wolf GW1479f (Noella) of the Hechtel-Eksel pack, Flanders, August 2020. Photo: INBO-ANB.*

1 Background and objective

1.1 Introduction

In 2012, Wageningen Environmental Research (WENR), commissioned by the Ministry of Economic Affairs, the Association of Provincial Authorities (IPO) and BIJ12, carried out an initial fact-finding study on wolves (Groot Bruinderink et al., 2012). That report was written ahead of the likely return of wolves to the Netherlands. Ecologists such as Jan van Haaften and Harm van der Veen had been talking about this possibility for decades and the ecological value of wolves in the Veluwe area in particular (Van der Veen & Lardinois, 1991; Van Haaften, 1995). Van Haaften had doubts about whether wolves would be compatible with the Netherlands of the modern era. Today, in 2021, several wolves have settled in the Netherlands and have even reproduced. Due to the growing population of wolves in Europe and the more frequent occurrence of roaming wolves in the Netherlands, interaction between humans and wolves in the Netherlands is increasing. Such interaction evokes a wide range of responses in society – from enthusiastic to negative. One important factor is that most people still do not know much about these unfamiliar animals. Attitudes and reactions are therefore not always based on knowledge or experience. This is reinforced by extensive media coverage of wolves, as well as social media activity, where the accuracy of information is regularly called into question. The Interprovincial Wolf Plan (IPO, 2019) elaborated some policy principles for the way in which we handle wolves. A review of that plan will start in the autumn of 2021. The clients indicate that this revision must be based on scientific insights.

The return of wolves to a densely populated area with a high density of livestock creates a wholly new situation that does not occur anywhere else in the world. Existing knowledge from other countries cannot necessarily be applied to the situation in the Netherlands, therefore. The aim of this project is to bring together all the latest knowledge regarding wolves in the Netherlands and neighbouring countries, in order to provide a basis for updating the Wolf Plan. This knowledge consists of current facts based on ongoing monitoring and scientific research and can contribute to making scientifically substantiated policy choices. Any gaps in that knowledge are also pointed out, where applicable.

This report focuses primarily on information collected in the Netherlands in recent years, which WENR has a good overview of. In addition, data and experiences from other countries, in particular Germany, Belgium and France, are also examined, since these neighbouring countries are the most important for developments in the Netherlands. Although the situation in the Netherlands is different from that in neighbouring countries, especially in terms of the presence of humans, the fragmentation of nature and livestock density, it is very useful to learn from experiences elsewhere. For this reason, a partnership was established with the Research Institute Nature and Forest (INBO) in Flanders and the Senckenberg Gesellschaft für Naturforschung (SGN) in Germany for the purposes of this project (see Appendix 4). Both these research institutes are closely involved in research into wolves in their own countries and therefore have a great deal of factual knowledge at their disposal. Both these partners are also part of the Central European Wolf consortium (CEwolf; Appendix 3), which WENR is also a member of.

This project focuses on answering the research questions formulated by the commissioning parties. These questions are divided into five themes:

1. Distribution, occurrence, origin and ecological carrying capacity
2. Behaviour and the relationship between wolves and humans
3. Policy, damage, monitoring and management
4. Ecology
5. Genetic techniques and data exchange in Europe

Each theme generally includes several research questions, and those research questions sometimes include several sub-questions. Together, there are 25 research questions with 46 sub-questions (Appendix 1).

1.2 Reader’s guide

Given that this report covers a large number of closely related topics, it includes many references to related sections elsewhere in the report. A fixed designation is used for this, based on chapter + section (for example, section 5.1 refers to the first section of Chapter 5). References to figures and tables are made easier to find by numbering them by section. For example: Figure 5.1.1 can be found in Chapter 5, section 1 and relates to the first figure.

Chapter 2 describes the methods used to answer the research questions. Chapter 3 provides a glossary of commonly used terms and abbreviations. Uncommon terms used are sometimes also explained in the relevant chapters. Chapter 4 is an introductory chapter that provides some basic data on wolves, including the key information from the first fact-finding report from 2012. There is also an explanation of additional points concerning wolves that form the basis for answering questions, as well as themes that are not directly addressed in the answers to the questions, but which are relevant to the framework.

The research questions are addressed in Chapters 5 to 9:
- Chapter 5: Distribution, occurrence, origin and ecological carrying capacity
- Chapter 6: Behaviour and the relationship between wolves and humans
- Chapter 7: Policy, damage, monitoring and management
- Chapter 8: Ecology
- Chapter 9: Genetic techniques and data exchange in Europe

In a few cases, a question has been simplified or adjusted to make it clearer. The original research questions and sub-questions are shown in Appendix 1. Other explanatory notes are included in the appendices, as well as some information about the CEwolf consortium (Appendix 3) and the partners (Appendix 4) involved in this project.

A legal study was also set up by the clients in parallel to this ecological study. Both of these studies have some degree of overlap and also make reference to one another. For the full legal report, please refer to: Boerema L., L. Freriks. A.A. and D.B. van den Brink. 2021: *The legal protection of wolves in the Netherlands and a number of other European countries: a legal study to support the drafting of a policy on wolves in the Netherlands in light of the implementation on laws on nature [De juridische bescherming van de wolf in Nederland en in een aantal andere Europese landen; een juridisch onderzoek ter ondersteuning van het opstellen van Nederlands wolvenbeleid in het licht van de uitvoering van de natuurwetgeving.]* Boerema and Van den Brink B.V., Houwerzijl/Element Advocaten, Best.

There are numerous publications on the subject of wolves. In addition, it is becoming ever clearer that ‘wolves’ are in fact individuals with their own character traits, analogous to our own domestic pets. When it comes to this socially intelligent species, it is often the exception that proves the rule. Many of the publications that we found and considered relevant are included in this report. As authors, we do not claim to have been exhaustive and we realise that wolves are capable of doing things that simply cannot be predicted based on our existing knowledge.

2 Methodology

Three methods were used to answer the research questions:

A: Literature Review
We consulted national and international publications that were relevant to answering the research questions. The focus was primarily on scientific publications – both articles and research reports – that present the findings of monitoring and research. However, relevant non-scientific publications were also considered, especially where they provided new or additional information and it was possible to ascertain that the information was reliable. Government documents and websites presenting relevant information were reviewed for a number of the research questions, particularly those relating to policy, damage and management.

B: Data review
This study uses the BIJ12 dataset containing information about the wolves observed in the Netherlands for the period between January 2015 and April 2021. This includes data on wolf observations, data on losses to livestock and data on the origin of wolves (including genetic data). Data collected by the project partners through ongoing (but not yet published) research was also used, such as data from the dispersal movements of the tagged wolves Naya and Janka, dietary analysis of wolves in Flanders and data on hybridisation. There were occasional deviations from the time period stated above (for example, for wolves killed by vehicle strikes: a recent collision from May 2021 was included in the analysis). Any such deviations are always stated explicitly in the text.

C: Consultation with experts
Various national and international experts were consulted in order to acquire specific knowledge and/or refer to unpublished data when answering questions. These included partners within the CEwolf consortium, but also others, such as a legal expert (for questions about the national and international conservation status of wolves and the achievement of a favourable conservation status), researchers from other (academic) institutions (in relation to questions regarding diet, expectations regarding the relationship between wolves and humans) and government experts (in relation to questions about policy, regulations and experiences in the field of prevention, management and exceptional hunting permits).

In addition to a few other experts (see acknowledgments), a great deal of knowledge was gathered from the following two experts:
- Ilka Reinhardt: ecologist at the LUPUS Institute, für Wolfsmonitoring und -forschung in Deutschland
- Arie Trouwborst: Nature Conservation lawyer at Tilburg University

For the research questions regarding new developments in genetic techniques and data exchange with other European countries (Chapter 9), in addition to the above actions, an online workshop in English was also organised, to which international experts in the field of wolf genetics were invited. These were, first of all, the other partners in the CEwolf consortium (LUPUS Wildlife Consultancy, Germany; Aarhus University & Natural History Museum, Denmark; Universities of Warsaw and Gdańsk, Poland; Charles University Prague, Czech Republic; University of Veterinary Medicine Vienna, Austria; University of Liège, Belgium; Administration de la nature et des forêts, Luxembourg), but also experts from other laboratories in Europe.

Although information was gathered from many different countries, the emphasis was on France and Germany because they have more similarities with the circumstances in the Netherlands, and because a great deal of experience with wolves has been amassed there over a longer period.

3 Glossary and abbreviations

3.1 Glossary

- **Central European wolf population**: the population of wolves living mainly in Western Poland, Germany, the Netherlands, Belgium and Denmark; see sections 4.2 and 5.1).
- **Daytime resting place**: a place that wolves retreat to during the day, mainly to avoid interaction with humans.
- **Dispersion**: the departure of a young wolf from the parental territory in search of its own territory (see section 4.5).
- **Introduced species**: species that occurs in an area due to human introduction, rather than because it occurs naturally there.
- **Genotype**: a unique genetic profile that identifies an individual wolf. This profile is made up of a combination of the proven variants for multiple genetic (microsatellite) markers.
- **Habituation**: see section 6.1 for further definitions.
- **Haplotype**: a genetic variant of the mtDNA (see below) that occurs in a certain percentage of wolves and/or dogs.
- **Officially designated territory**: an area designated by the government where a wolf, pair or pack has settled and where the government facilitates coexistence with humans through policy in accordance with the IPO Wolf Plan.
- **Microsatellite**: a portion of an animal's genome whose exact length is known to vary between individuals within the same species. These differences in length make this piece of DNA useful as a genetic marker that can be used to recognise individuals.
- **mtDNA**: mitochondrial DNA, part of an animal's genome that varies between animal species, which is therefore often used as a genetic marker to identify a particular species.
- **Predator/predate**: animals that prey on other species. Predate is a verb meaning to kill other animals in order to feed on them. However, numerous non-predators also kill other animals for food, such as squirrels or blackbirds.
- **Rendez-vous site**: a safe place in a wolf's territory where young are often left while the adult wolves are out and about.
- **Pack**: group of more than two wolves, usually parents with young, possibly including several generations. As soon as a pair has young, they are known as a pack.
- **High-risk area**: see officially designated territory, but an area where instead of a settled wolf, there is an above-average risk of a conflict between wolves and livestock.
- **Territory**: habitat that wolves defend aggressively against others of the same species.
- **Wolf reporting point**: information collection point that focuses on collecting and validating reports of wolves. This has been run by BIJ12 at the Dutch Mammal Society (www.zoogdiervereniging.nl).

3.2 Abbreviations

- **BfN**: Bundesamt für Naturschutz, German Federal Agency for Nature Conservation.
- **BIJ12**: organisation that supports the provinces of the Netherlands in their work in the field of nature, including wolves (see www.bij12.nl/wolf).
- **CEwolf consortium**: international consortium of scientific institutions which focuses primarily on the genetic monitoring of the Central European wolf population, using coordinated methods to exchange information (see Appendix 3).
- **DBBW**: Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf. German Federal Documentation and Consultation Centre on Wolves, www.dbb-wolf.de.
- **DWHC**: Dutch Wildlife Health Institute. An institute affiliated with the Faculty of Veterinary Medicine of Utrecht University which carries out the veterinary part of the autopsy on dead wolves.
- **GWxxxm/f**: coding of genetically identified wolves within the Central European wolf population. GW stands for Genetically identified Wolf individual, followed by a unique serial number, and then an m (for male) or f (for female).
- **HR:** Habitats Directive.
- **INBO**: Research Institute Nature and Forest (Appendix 4).
- **IPO**: Association of Provincial Authorities.
- **LCIE**: Large Carnivore Initiative for Europe.
- **LNV**: Ministry of Agriculture, Nature and Food Quality (LNV).
- **SGN**: Senckenberg Gesellschaft für Naturforschung (Appendix 4).
- **WENR**: Wageningen Environmental Research (formerly known as Alterra and part of WUR; Appendix 4).
- **WIN**: Wolven in Nederland. A consortium of organisations that works to promote the conflict-free coexistence of humans and wolves. (www.wolveninnederland.nl).

Photo 3.1 *Pups (left, August 2021) and a yearling wolf (right, April 2021) from the Hechtel-Eksel pack, Flanders. Young wolves grow quickly and pups aged around four months old can already appear quite large. Photos: Eddy Ulenaers (left) and Ernesto Zvar (right).*

4 Basic information on wolves

4.1 Appearance

Even based purely on their appearance, it is clear that wolves are formidable predators. They look like large dogs, but wolves have a higher, narrower chest and a longer torso. The head is large with a wide forehead, slightly slanting eyes and relatively short ears. Their legs are long, and well-adapted for stamina. Wolves have bushy tails, around one third the length of their body. Their fur varies considerably in colour, but brown, grey, black and white usually predominate. Wolves in Central Europe are usually grey-brown with lighter fur in some areas, and some black fur. The ears have lighter fur inside with darker fur around the edges, and the cheeks are paler at the bottom but with a distinctive black edge along the mouth. The tail, ears and mouth are used to communicate with each other. Adult female wolves weigh around 40kg and male wolves around 45kg. Please also refer to the photos in this report.

Photo 4.1 *Compilation of shots of wolves taken with camera traps. Camera traps are an important tool for investigating the presence of wolves.*
Top left: camera trap activated with a motion sensor and infrared lamp so that night images can also be captured. Top right: night shot of a wolf in the Central Veluwe area.
Bottom left and bottom right: wolf in the North Veluwe area. The wolf in the bottom right is quite bald, almost certainly as a result of mange, a common disease affecting wolves (see section 4.5.2).
Photos: Top left and top right: H. Jansman. Bottom left and bottom right: R. Strikwerda & H. Haspers, wolf reporting point.

4.2 Monitoring & research

Studying wolves is not easy because wolves travel over large distances and, probably as a result of centuries of extensive persecution, they also tend to avoid people. When one does get the chance to see a wolf, it is often only a brief glimpse from a considerable distance. David Mech, one of the most important researchers of wolves, remarks that throughout his whole career he had almost never been able to observe an entire hunt (Mech, 2020). Usually he has only been able to see a small part of the hunt. This is echoed by the Dutch biologist Jan Hilco Frijlink, who studied the hunting behaviour of wolves in Canada at the end of the 1960s by tracking them (Frijlink, 1977). Similarly, the number of interactions between different wolf packs that had been witnessed could be counted on one hand.

All that changed when wolves were released into Yellowstone National Park in 1995. The geography of the park consists of large plateaux with hilltops, thus lending itself well to observation. In addition, the wolves in the park are not hunted, making them a little less wary of humans. As a result, the wolf population at Yellowstone is the best-studied in the world. Almost all the individuals in each pack are known, and every year a few animals in each pack are caught and fitted with a transponder tag. Between 1995 and 2020, that resulted in 52,064 wolf observations, 34,509 hours of observed wolf behaviour, including 121 pack fights, 601 wolves captured and fitted with a transponder tag, 8,173 prey carcasses examined and 85 scientific research papers written (Watters et al., 2020; Smith et al., 2020a). The reintroduction of wolves in Yellowstone National Park has, in short, generated significant new knowledge regarding wolves and their influence on each other and the ecosystem, and it has also increased the popularity of ecotourism around wolves (see section 6.5).

The options for research in the Central European population are more limited. Wolves are virtually invisible. Furthermore, there is hardly any snow in winter and there are no extensive snow-covered plains that make it easier to tranquilise wolves safely from a helicopter using a dart so that they can be fitted with a transponder tag (the most common method used in Scandinavia and North America). In addition to these major differences in terrain, the influence of humans is also very significant in Europe. Findings from Yellowstone in the US cannot therefore be translated directly to the Central European situation, but they do provide a great deal of information about wolves that would not otherwise be available.

In the Central European population of wolves, DNA testing (Photo 5.1.1) and the use of camera traps (Photo 4.1; night-vision cameras fitted with a motion sensor that captures footage whenever the motion sensor is triggered) are the main methods used. Footprints can also be tracked. In the Netherlands, the *Monitoring Wolf* report is published by the Dutch Mammal Society on behalf of BIJ12, to report on all monitoring activities (Klees et al., 2019). An important advantage in the Netherlands is the high number of volunteers who report their observations and relatively good access to natural habitats. Wolves mark their territory with droppings, among other things, and these are therefore relatively easy to find for research purposes (Photo 5.4.1). Just like the remains of wolves' prey (see section 8.1), droppings also contain DNA from the animal that produced them, and in many cases the individual, sex and possibly even origin can be identified. Occasionally other types of DNA samples are found too, such as tufts of fur on barbed wire. Predators also leave DNA traces on their prey through their saliva (see section 5.1, section 4.6 and Photos 5.1.1 and 6.2.1).

Various observation criteria are used, in accordance with the Wolf Monitoring Plan and international standards:
- C1: hard evidence (based mainly on DNA, or good photo/video footage)
- C2: confirmed sightings (e.g. droppings or footprints that are properly documented and have been judged by experts as definitely wolves)
- C3: unconfirmed sightings (observation not verified by experts)

In the Netherlands, monitoring is coordinated by BIJ12 on behalf of the provinces. Monitoring focuses on two aspects: damage and wolf monitoring. Assessors take DNA from livestock (especially sheep) that has been bitten in cases where wolf predation cannot be ruled out. If a wolf turns out to have been involved, or if this possibility cannot be excluded, the owner of the farm animal is compensated for the damage caused (IPO 2019). DNA is also collected from (a selection of) droppings found and also from deer or boar which have been predated. This is done largely by volunteers under the supervision of the wolf reporting centre (which BIJ12 has assigned to the Dutch Mammal Society). The samples are stored in the WENR laboratory. Every month, samples taken from livestock that has been attacked are analysed to identify the predator involved: was it a wolf, a dog, a golden jackal or something else? In addition, all the samples are also analysed for monitoring purposes every quarter. This includes the DNA samples from livestock that are confirmed to have been attacked by a wolf, as well as samples from droppings, fur and deer or boar that have been attacked. These samples are used to determine which wolf was involved and the sex of the animal concerned. Subsequently, based on the dataset for wolves in Central Europe, the origin of the animal can be determined in many cases (from which pack the wolf originates; see also section 4.6, section 5.1 and Chapter 9). In this way it is also possible to determine whether individual wolves have settled or are still roaming. If a wolf has been present in a particular region for six months, according to IPO 2019 the animal has settled there and the government will designate a territory and consult other parties involved regarding how to ensure coexistence.

4.2.1 Central European population

Based on research, including genetic research, we have been able to learn about the population structure of wolves in Europe (see also section 5.1). Most wolves in the Netherlands appear to have come from the Central European wolf population. The term Central European population refers to the current population of wolves that is distributed across Poland west of the River Vistula, Germany and adjacent areas in the Czech Republic, Austria, Denmark, Belgium and the Netherlands (Figure 4.2.1). In addition, wolves from the Alpine population are occasionally encountered in the Netherlands (see sections 5.1 and 4.6). There is collaboration within the CEwolf consortium for genetic research. This consortium of institutes focuses primarily on the genetic monitoring of the Central European wolf population, using coordinated methods to exchange information. A method for the mutual exchange of data has been agreed for this purpose (see Appendix 3).

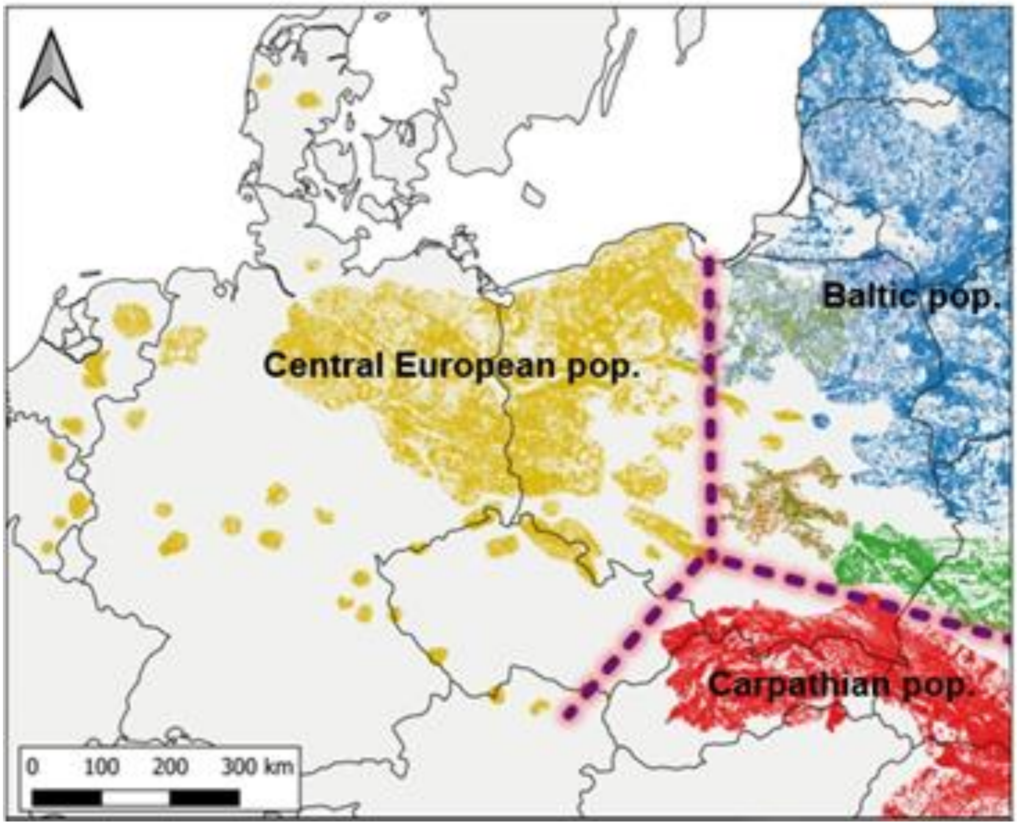

Figure 4.2.1 *The distribution of the Central European wolf population (yellow) in relation to neighbouring populations in the Baltic (blue) and the Carpathians (red). The map only shows regions with settled wolves or where wolves occur regularly. The Alpine population (not shown on map, but see section 5.1) includes isolated foothills as far as north-eastern France (Meurthe-Moselle, Vosges) and Switzerland. The map has been adapted according to Szewczyk et al. (2021).*

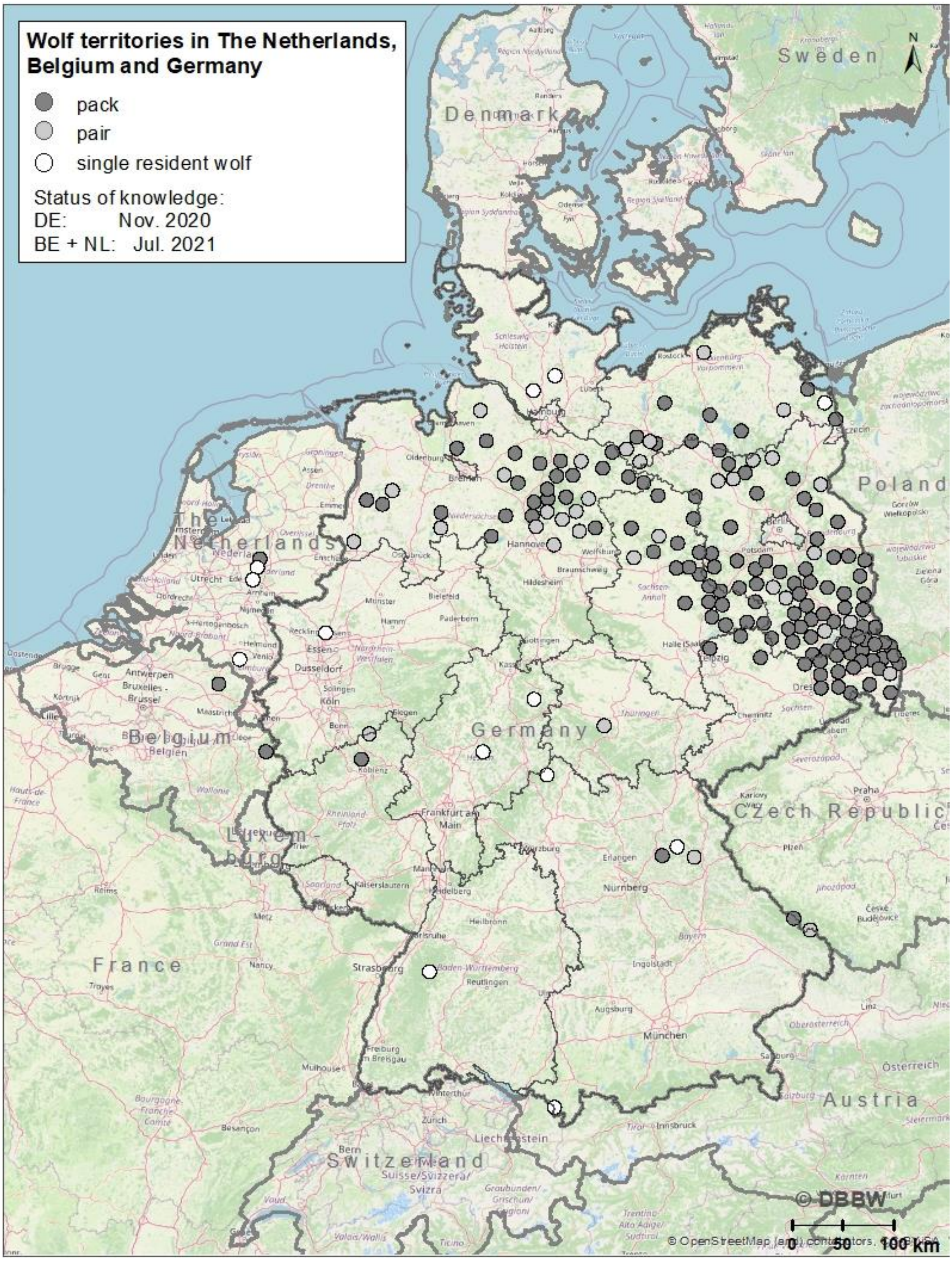

Figure 4.2.2 *Wolves settled in Germany, the Netherlands and Belgium. Dark grey: settled pack, light grey: settled pair, white: settled individual. The data regarding wolves in Germany dates from November 2020. The data regarding wolves in the Netherlands and Belgium dates from July 2021. Source: Ilka Reinhardt / DBBW.*

Figure 4.2.2 shows wolves settled in Germany, the Netherlands and Belgium. The data regarding German territory dates from November 2020. The data regarding Dutch and Belgian territory dates from July 2021. For Dutch territory (from north to south), this includes a pack in the North Veluwe area (GW998f x GW893m), a solitary wolf in the Central Veluwe area (GW960f), a solitary wolf in the Southwest Veluwe area (GW1490m) and a settled solitary wolf in the Groote Heide area, Noord-Brabant (GW1625m). The province has designated territories in all these cases (provisional for

GW1625m; see section 5.9). The officially settled female wolf in the Southwest Veluwe area, GW1729f, was killed by a car in March 2021. Her partner, GW1490m, is still in the area but has not yet formally been confirmed as settled (July 2021). Because the site manager from Natuurmonumenten indicates that there was still wolf activity in July, detected by camera trap footage among other things, this territory is shown on the map. The two packs with young located in Belgium are the pack in Hechtel-Eksel (Flanders; see also section 4.6; GW1479f x GW979m) and a recently formed pack in the High Fens (Wallonia). Although wolves also occur outside the areas mentioned, these are not shown on the map (however, see Figure 5.1.2).

4.3 Predator & hunting technique

Wolves are low-yield predators that mainly hunt wild ungulates (Mech et al., 2015). They cannot rely on great muscle strength or sharp claws and teeth (as is the case with big cats, which also prey mainly on large ungulates). Lions and tigers weigh over 100kg and have rotating ankle joints with razor-sharp claws over 3cm long that can seriously injure prey. They usually hunt by ambushing their prey after a brief chase. Wolves typically weigh less than 50kg and do not have sharp claws. They are therefore unable to inflict much damage on their prey when hunting. Instead, they use patience and stamina. Wolves travel great distances in search of safe and easy food.

If they come across a group of deer when hunting, wolves usually pursue the deer to find out whether any of the animals is weaker – maybe a younger, older, injured or sick individual. Wolves often try to exhaust their prey by pursuing them for long distances; they do not hunt by ambushing like big cats. A red deer weighs over 100 kg and could seriously injure a wolf with its hooves or antlers. Wolves prefer to hunt larger prey as a pack and in many cases they will terminate a hunt prematurely if the risks involved are too high. This explains wolves' low hunting efficiency. Wolves often kill their prey with a bite to the throat, clamping onto the animal's windpipe until it suffocates. The digestive system of wolves is built to go without food for days and then, when the situation permits, to store 10kg of food. This is also known as 'feast and famine'.

The wolf's main weapon is its long snout and extremely sensitive sense of smell. This enables them to smell potential prey and carrion from a great distance. Its long snout also allows the air to be cooled, helping keep the brain cool during a long-distance hunting, while the brain of its prey slowly overheats (MacNulty et al., 2020). These adaptations help wolves to compete with big cats in the ecosystem and are also the result of the evolutionary race between wolves and ungulates – the hunter and the hunted. (See Chapter 8 for more information on wolves' diets and their potential impact on the ecosystem.)

Photo 4.3.1 *Testing the remains of prey (see also H8.1). Left: killed red deer calf showing a typical wolf feeding pattern. Middle: remains of skin and fur from a roe deer. Wolves will ultimately eat everything, even the bones if they have to. Right: hair seen through a binocular lens to determine the species of prey from droppings or a wolf's stomach contents. Photos: H. Jansman.*

4.4 Pack & social group animal

Wolves are social group animals. A pack of wolves will generally consist of two parents and their offspring, and may include several generations. In addition, wolves from outside the pack are occasionally accepted to strengthen the pack and bring new blood into the family. The added value for wolves of living in a pack is shared defence of territory, hunting as a pack, defending food and breeding and the shared rearing of young. Injured wolves can recover from injury or illness with support from the rest of the pack in the form of food. For wolves, the value of having a territory and belonging to a pack is high enough to outweigh the cost of helping rear pups that are not their own (Stahler et al., 2020).

The wolf is a eusocial species, meaning that it is a group animal, the group consists of several generations, reproduction is restricted to a limited number of individuals, and all members of the group help to rear pups (Photo 4.6.1; Haber, 1996). These behaviours are found in only 2% of mammals (Stahler et al., 2020). Young wolves also remain dependent for longer than other species, up to 25-30% of their life expectancy. That is comparable or even longer than in most human communities. Together with their high intelligence and the fact that packs involve family bonds that normally remain intact for several generations, extended dependency forms the basis for the significant transfer of social and genetic traits from one generation to the next (Haber, 1996).

Parents and older pack members play an important role for young wolves. In addition to providing food and defending the pack’s territory, parents are also role models; this can also be viewed as imprinting or conditioning (see sections 6.1 and 6.2). The experience that parents and older pack members have accrued over their lives and which are now expressed in their behaviours are adopted by the younger pack members (Langenhof & Komdeur, 2018). This is important when individuals come to find a territory of their own: animals often choose an area that is similar to what they experienced in their parental territory in terms of environmental stimuli (Davis & Stamps, 2004). It is also important because wolves can transfer behaviours to pack mates easily, such as how to view livestock (thereby increasing or reducing the potential for conflict) (Rossler et al., 2012; also see section 7.2). In wolves, female leadership is the rule. The matriarch of the pack provides the most leadership in everyday activities throughout the year (Stahler et al., 2020).

4.5 Population dynamics of wolves

The population dynamics of wolves are complex and depend on many factors. Wolves have a strong system of territory which has a significant stabilising effect on naturally low wolf densities. Territoriality is a specific form of aggression that stems from an animal’s relationship to a particular place (Cassidy et al., 2020). Variations in population density occur as variation in territory size (with only very limited variation in the number of wolves per territory). The size of a territory is determined mainly by the availability of food and safe resting areas. An important factor is that the pressure on sources of food, or the predation pressure, also remains approximately constant (Van den Berge & Gouwy, 2021).

The size and dynamic of populations are determined by factors such as reproduction, mortality, immigration and emigration (see Figure 4.6.1). These factors depend on both internal factors (territoriality and reciprocal aggression between packs) and external factors (availability of food, climate, diseases).

In the Central European population of wolves, research has provided a good picture of population trends in terms of numbers and distribution (see, for example: Jarausch et al., 2021; Nowak & Myslajek, 2017; section 5.1 and 4.2.1). Much less is known about factors such as mortality and reproduction, because it is not easy to study these factors in nature.

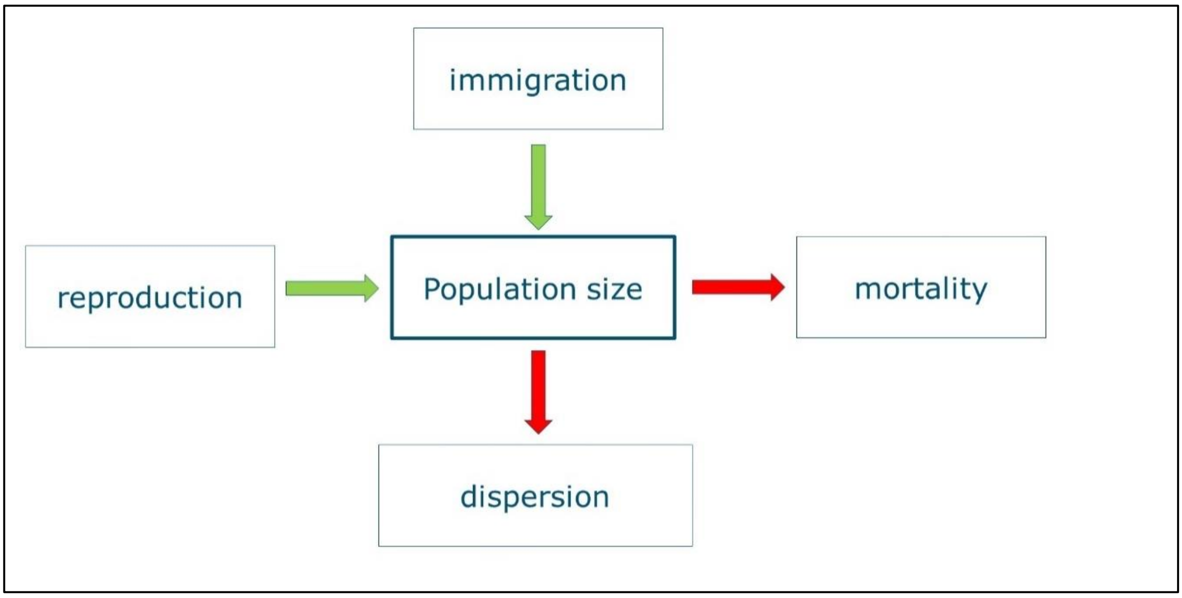

Figure 4.5.1 *The main factors that affect population size.*

4.5.1 Reproduction

Female wolves become fertile at around the age of two years. They are only fertile once a year, in around February-March. It is normally only the leaders of the pack, usually the parents, who reproduce, which means that no other female wolves become pregnant. Occasionally there may be multiple litters within a pack, usually fathered by the male leader with female subordinates (polygyny). The gestation period is approximately 63 days and most young are born in early May. The average litter size of wolves is around 4-5 pups, with a maximum of 8. The survival rate per litter (number of pups still alive on 31 December) was 1-3 pups in Yellowstone. The better the condition of the mother and the larger the pack, the larger the litter and the higher the survival rate among the pups (McNulthy et al., 2020; Stahler et al., 2020). All members of the pack help to raise the pups and keep them safe, and in a larger pack young wolves are safer and have a better supply of food. Although wolves do avoid inbreeding, this can occur, especially when no other mating partners are available (Jarausch et al., 2021). Daughters often take over the leader role from their mother (Stahler et al., 2020).

Photo 4.5.1 *Wolves are social group animals and the entire pack helps to rear the young. Photos: H. Jansman.*

Wolves can be divided into different age groups (see also Photo 3.1):

- Cub: 0-10 months old (at this stage, they are still highly dependent on the pack)
- Yearling: 10-24 months old (at this stage, young wolves often leave to start their own pack)
- Adults: 2-5 years old (at this stage, wolves are sexually mature and in the prime of their lives)
- Older adults: >5 years old (in this phase wolves have less energy and participate less in hunting, but their experience is important for the survival of the pack)

4.5.2 Mortality

The average life expectancy for wolves is 6 years (McNulthy et al., 2020) and few wolves make it to the age of 10. Wolves killed by vehicle strikes are relatively easy to observe, but natural mortality much less so (Photos 4.5.1b and 4.5.2).

Photo 4.5.1b *Investigating a wolf that has been killed by traffic. Traffic is a significant risk for wolves who share their territory with humans. Photo: M. van Uitert – www.paralleluniversum.nl.*

Extensive research in Yellowstone National Park has shown that under natural conditions, approximately 40% of adult wolves are killed by other wolves due to territorial behaviour (Smith et al., 2020b). In Europe, however, there is no evidence that wolves often kill each other. In Belarus, after tracking wolves through the snow for over 4,000 kilometres, not a single case of fatal aggression was recorded, and even after examining 700 wolf carcasses, hardly any injuries could be attributed to other wolves. Only once did the researchers come across a wolf that had been killed by another wolf (Sidorovich & Rotenko, 2019). For the Central European population, the human impact on mortality is probably much greater due to higher traffic intensity, illegal persecution and (ungulate) management. In the area surrounding Yellowstone National Park, wolf mortality caused by humans was estimated at about 80% (Smith et al., 2020b). In Germany, monitoring has also shown that human factors have a major influence on mortality, particularly traffic (see Figure 4.5.2 and Chapter 6.5.1). However, natural factors and illegal activities are almost certainly under-recorded, because they are less easy to confirm (see section 4.5.4).

Photo 4.5.2 *Post mortem on a dead wolf, being carried out by DWHC (veterinary aspects) and WENR (animal ecological aspects). Photos: H. Jansman (centre and left) & M. van Uitert (right).*

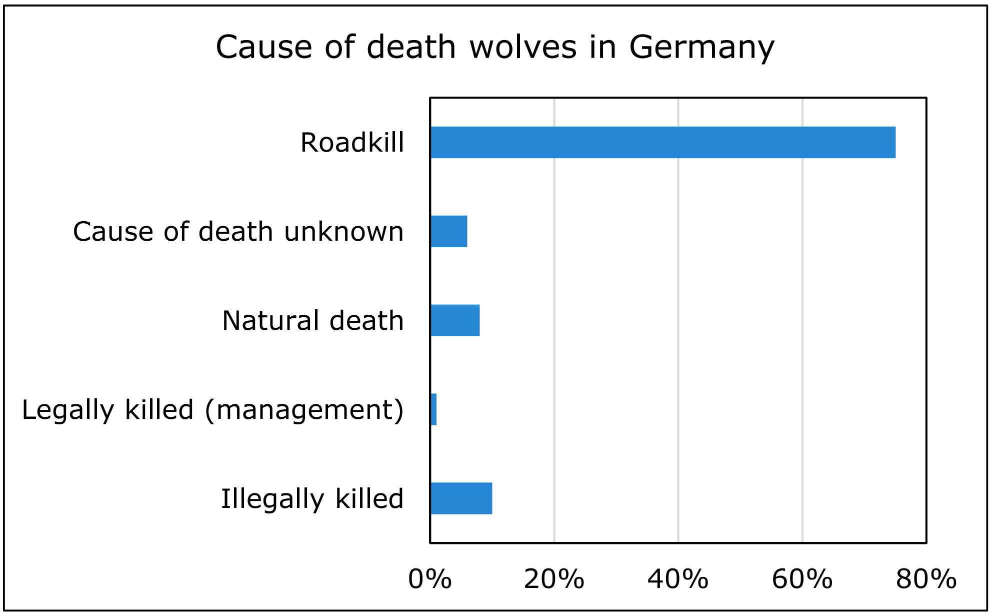

Figure 4.5.2 *Percentage distribution of the number of wolves found dead due to various causes of death in Germany (Source: https://data.dbb-wolf.de; data 1990-2020).*

Disease also plays a role in the population size and dynamics of wolves. In particular, canine distemper virus (CDV) and mange were found to have a significant effect on the population in Yellowstone National Park. CDV is also found in European wolf populations, but it is unclear what effect disease has in Europe (Francesco et al., 2020). Mange and French heartworm have already been found in Dutch wolves (BIJ12 2021a). Pseudorabies or Aujeszki’s disease is an endemic viral disease in boar that can be fatal to wolves. Many post mortems have been carried out on dead wolves by WENR in collaboration with the Dutch Wildlife Health Centre (DWHC, Utrecht), including screening for viruses, bacteria and parasites. In addition, extensive research is carried out into the cause of death, age, gender, stomach contents, reproductive status and condition. There is further analysis on veterinary aspects in Groot Bruinderink et al. (2012).

4.5.3 Dispersion (migration)

Most young wolves leave the parental pack sooner or later in order to find their own territory and reproduce. This usually happens when the young wolf is a yearling (second year of life), but it can be as early as 10 months old. A young wolf will live on its own during that phase of life – as a ‘lone wolf’. Some look for free territory in the vicinity of the parental pack, but wolves sometimes travel hundreds of kilometres (also see sections 4.6 and 6.5). We call this the dispersion phase – the phase when young wolves leave the parental pack in search of their own territory. Not all wolves leave the parental pack, however.

4.5.4 Habitat

Wolves are such generalists that they can find a niche in many different types of landscape (Kramer-Schadt et al., 2020; Chapron et al., 2014). Reinhardt et al. (2019) have looked into the characteristics of the territories that are playing a role in wolf recolonisation in Germany. Forest cover turned out to be an important feature for territories in Germany. The average forest cover in wolf territories on military sites was 52%, in nature reserves it was 50%, and in other types of territory, especially in private nature reserves, it was 47%. The density of prey – wild ungulates – was high everywhere. There were large differences in road density, especially between territories on military sites (low road density) and territories in other areas (see also section 7.5). Mortality among wolves as a result of humans (traffic accidents, legal hunting or poaching) was lower for territories in military areas than territories in other areas. Military areas in Germany therefore appear to play an important role in wolf recolonisation, particularly because of lower anthropogenic mortality rates than in other wild areas. The authors indicate that where wolf population density is low, human-induced mortality is an important factor in wolf dispersal and survival.

Wolves prefer to make their dens, where the pups are born, in remote places that are less accessible for humans. These dens are always close to water (Okarma, 2000).

4.5.5 Trends in wolf numbers

Above, we have discussed the aspects of reproduction, mortality and migration that are important to population trends. In practice, the wolf population of a particular region is largely determined by the animal’s strongly territorial way of life, which is characteristic of predators (Van Den Berge & Gouwy, 2021). This is because no outsiders are tolerated within a pack’s territory, and the number of individuals in these exclusive areas is therefore naturally – i.e. with no human intervention – always limited to a very low density, in accordance with the wolves’ position in the ecological food web. After all, a local population is limited to the parents with their young, plus a few young wolves from the previous year. The size of the pack can fluctuate over the years depending on the number of young born each year and their survival rates, but it always remains within certain bounds. The young adults will usually leave the pack at one to two years of age and occasionally a roaming lone wolf may be accepted into the pack. If the size of a pack is an average of five animals (range 2-9; Fechter & Storch, 2014) and no major incidents occur, it is possible to predict with great certainty that this will also be the number of wolves living in that area or territory next year, in three years, in ten years or (theoretically) in fifty years – in the absence of human intervention. This is an essential difference with species that are not territorial, such as wild boar. Without human intervention, the number of boar in a given area can increase significantly within a few years. This is because as long as there is food – and in our agricultural landscapes food is generally abundant – the population of boars will continue to grow in the absence of territorial restrictions. With annual percentage population growth of 100-300% in boars (Briedermann, 2009), the range of possible population growth (and fluctuations, driven by factors such as conditions during the winter) is much wider and population density is hard to predict for future years.

Due to territoriality in wolves, population changes manifest themselves in a localised spatial pattern of local presence and absence, as with other medium or large predators. Wolves’ territories can be seen as pieces in a jigsaw puzzle across the landscape, not necessarily adjacent to one another and often with intervening gaps. The variation in the size of wolf territories can sometimes be considerable and local living conditions, such as the availability of food, are a factor in this. More abundant food allows for smaller territories and vice versa. One important consequence of this is that pressure on the available food sources – in other words the predation pressure on the local wild species on which wolves prey – remains constant.

The density of a wolf population is ultimately determined primarily by the number of territories, viewed across a wider region, plus lone wolves roaming within that same area. As the density of wolves increases, negative density-dependent factors come into play. These can include smaller litter sizes, lower survival rates among young wolves, an increase in aggression between wolves and the spread of disease. Smith et al. (2020) report that population regulation in wolves is determined by density-dependent mortality as a result of aggression between packs. For the time being, there is still plenty of space for wolves in the Netherlands, since wolf numbers remain low. The population of wolves in the Netherlands remains in its growth phase and is determined mainly by immigration, reproduction and mortality. Sooner or later, numbers will increase and density-dependent factors will curb that rate of growth. Eventually the population will stabilise and fluctuate around the ecological carrying capacity of the ecosystem, a situation that has now been achieved in the Lusatia region in eastern Germany. The population in Yellowstone National Park also grew rapidly in the years following reintroduction, before stabilising, partly as a result of diseases among the wolves (Smith et al., 2020b). Wolf population growth in Idaho, Wyoming, and Montana has been approximately 25% per year over the past three decades (Wielgus & Peebles, 2014). In Germany, the wolf population grew from one pack to 67 packs between 2000 and 2015, and by 36% per year (Reinhardt et al., 2019), before falling off to around 25% per year (Reinhardt et al., 2021; also see section 5.6). The number of packs in Germany is now at about 125. Most wolves that occur in the Netherlands were born in the Central European population, particularly in German territory. The population continues to grow and it is therefore likely that more wolves will migrate to the Netherlands from Germany. In addition, due to wolves' high capacity for dispersal and growth in other subpopulations in Europe, such as the Alpine wolf population, individuals may also come from other regions in the Netherlands. Whether these newcomers can find a place to settle will depend, in turn, on the amount of suitable territory that is still available.

4.6 Wolves in the Netherlands

While the first fact-finding study (Groot Bruinderink et al., 2012) was only able to speculate about the arrival of wolves and what we might expect, today wolves have already settled in the Netherlands, including one pack with young (see section 5.1). A great deal of new information is also now available from Germany (for example), where there are more than 125 packs and approximately 500-600 wolf pups are born every year (DBBW.de). There is also information from the Netherlands itself, where wolves first reappeared in 2015. The Netherlands now has a number of wolf territories that have been officially identified and designated (see Figure 5.9.1; North Veluwe area, Central Veluwe area, Southwest Veluwe area, Groote Heide area; Jansman et al., 2019). The North Veluwe and Central Veluwe territories have been combined by the Province of Gelderland. A risk area has also been identified in Drenthe. This has not been designated as a territory, since the wolf officially established there, wolf GW 1261m, returned to German territory in the autumn of 2020 (Jansman & Sanders, 2020). In these areas, the competent authority is working actively to promote coexistence between humans and wolves, in accordance with the IPO Wolf Plan, partly because interaction with wolves is inevitable within wolf territories. A lot of detailed information is provided in the subsequent chapters, based on questions from those who commissioned this report. Below, we discuss six cases that are illustrative of wolves. They are based on the BIJ12 dataset for the period 2015-April 2021, supplemented with transponder tag data and data from CEwolf partners.

Five wolves are shown in Figure 4.6.1; each has been assigned its own colour. The round dots show location data based on monitoring. The asterisks show cases where DNA from dead livestock, particularly sheep, has been used to identify the individual animals shown in the figure. Note: The dots overlap, making it difficult to tell the individual dots apart. An attempt has also been made to keep these locations difficult to pinpoint precisely, in order to minimise any risk of disruption for the wolves. The sixth wolf is presented in Figure 4.6.2.

4.6.1 GW998f

This female wolf came from the pack in Babben in Brandenburg (Germany), over 600km from the border with the Netherlands. She appeared in Friesland on 5 May 2018 and remained in the regions of Drenthe, Friesland and Groningen until at least 31 May. Droppings were also found, implying that she may have settled in Drenthe (https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=24353). Subsequently, 31 dead sheep were found on 13 June 2018 in Laag Zuthmen/Heino, Overijssel. These appeared to have been killed by GW998f. Then it was quiet for a while, until 26 July when droppings were found in the North Veluwe area and were found to have come from GW998f. At the time of writing, summer 2021, she is still in the country and became the first wolf to have officially settled here at the end of January 2019. She had a mate in January 2019, GW893m, and three litters of pups were born in the North Veluwe pack in around May 2019, May 2020 and May 2021, the first pack in the Netherlands for about 150 years. Since GW998f was first observed in the Veluwe area, she has taken sheep on two occasions: on 19 September 2019 (Epe) and on 30 August 2020 (Epe). In both cases, the sheep had not been adequately protected within the territory of the pack, and this happened at times when the pack had larger pups to feed. GW998f has been detected 32 times from monitoring through DNA: 31 times based on DNA in droppings, and once based on DNA taken from a wild ungulate. With the exception of three observations in Drenthe (droppings), these observations were all made within the territory in the North Veluwe area.

Figure 4.6.1 *Some example wolves. The round dots show the locations where observations were made based on monitoring data (DNA or location data). The asterisks show cases where DNA from the wolf in question was recovered from attacks on livestock, particularly sheep.*

4.6.2 GW680f (Naya)

In November 2016, in the territory of the Lübthener Heide pack in Mecklenburg-Vorpommern, Germany (>500 km from the border with the Netherlands), a large cub was captured and fitted with a transponder tag. She was named Naya, and her reference number is GW680f. Her behaviour and that of the pack is part of a study by the Technical University of Dresden led by Dr Norman Stier, focusing on the effect of wolves on fallow deer. After this wolf had been part of her parental pack for a year, Naya left to search for a territory of her own on 10 October 2017. She headed west, crossing the border into the Netherlands on the night of 17 to 18 December 2017. Her path through the Netherlands was investigated further at the request of BIJ12, see also section 6.5 (Jansman et al., in prep.). During the day on 18 December, Naya was in the Hardenberg forestry area between Ommen and Hardenberg. From there, she moved northwest until the A28 motorway at De Wijk in Drenthe. Then she returned to Overijssel and the forestry area at Staphorst, the Zwarte Dennen, where she stayed between 19 and 22 December. In the early morning of 23 December, Naya headed southwards and arrived at Luttenberg. During the day she was in the Sallandse Heuvelrug National Park near Hellendoorn. She was also in the Sallandse Heuvelrug on 24 December. On 25 December, she continued southwards, crossing the A1 motorway and the Twente Canal. During the day, she was at Ruurlo in the Gelderse Achterhoek. On 26 and 27 December, Naya stayed in the woods in Montferland. On 28 December, she crossed the A12 motorway and moved back into Germany for a while, reaching Emmerich. There she crossed the River Rhine, after which she arrived in the Maasduinen National Park in Limburg on 29 December. On 30 December she crossed the Maas and crossed the A73 motorway at Venray. During the day she stayed in the Schadijkse woods near Horst. On 31 December she was in Limburg and Brabant, in the Mariapeel and the Deurnese Peel. Her route then took her south, crossing the Groote Peel National Park, the A67 motorway and the Zuid-Willemsvaart. On 1 January she was in the Weerterbos, where she crossed the A2 motorway. On 2 and 3 January 2018 she was in the Weerterbergen and Budelerbergen, where she stayed in the area of marshland near Budel-Dorplein and Loozerheide. Naya then crossed the border into Belgium and settled in Hechtel-Eksel, where she officially became the first ‘Belgian wolf’.

All in all, Naya covered at least 1,238 kilometres, and an average of 14 kilometres per day. She was particularly active between sunset and sunrise. Her chosen daytime resting places were mainly in areas of forest with a great deal of cover. All together, over her entire journey through the Netherlands, Naya spent most of the time in forest and almost none in cultivated landscapes. The average speed at which she moved through the Netherlands was the fastest in human-dominated habitats (urban and agricultural areas) and slowest in nature reserves. Naya crossed several infrastructure barriers in the Netherlands: she crossed motorways 7 times, railway lines 19 times, and waterways over 50 metres wide 3 times. These barriers do not seem to have stopped Naya on her journey. Although the tag data regularly showed that Naya was in the Netherlands, she was not seen once. Sheep were taken at five locations: on 23 December in Punthorst, on 24 and 25 December in Luttenberg, on 26 December in Nieuw Heeten and on 31 December in Helenaveen.

On 3 January 2018, Naya crossed into Belgian territory and quickly found her way to the military site in the north of Belgian Limburg (Leopoldsburg, Hechtel-Eksel, Houthalen-Helchteren). On 20 January she killed sheep for the first time in Meerhout, and on 21 March she took a sheep in Leopoldsburg. It soon became clear from her GPS transmitter that she felt at home in this military area. She lived in a territory area of approximately 250 km^2 which includes large wild areas such as nature reserves and military sites, as well as cultivated landscape. In August 2018, Naya’s DNA was found on a sheep carcass once again, but after that there were no observations until January 2019. She formed a pair with GW979m (see below), but disappeared without a trace shortly after giving birth in early May 2019 (Gouwy et al., 2019). Evidence of illegal traps intended to kill wolves was found in the area, and several poachers were caught red-handed in an inaccessible part of the military area. An inquiry into the disappearance of GW680f is still ongoing.

4.6.3 GW979m (August)

On 20 June 2018, sheep were reported killed in Oldelamer and Driesum, Friesland. DNA tests showed that they had been attacked by wolf GW979m. The animal also appeared along the German coast near Norden (Lower Saxony) in June. Subsequently, based on tests taken from the sheep, the same wolf was identified on 22 June in Rinsumageest (Friesland), on 5 July in Zeewolde (Flevoland) and on 10 July in Buren (Gelderland). The wolf just missed the Oostvaardersplassen with its many ungulates. The animal has never been seen in the Netherlands. After several months with no livestock lost to wolves in Belgium, there were suddenly six attacks in the territory of GW680f between 3 and 17 August. It soon became clear from camera trap footage that another, larger wolf was present in the area, and genetic analyses indicated that this was GW979m. In Flanders, the wolf was given the name August. It is not possible to determine the parental pack of GW979m from the CEwolf dataset. The animal may have come from a pack in western Poland. The pair that now occupy the 'Hechtel-Eksel' territory (HEK in the CEwolf database) had young at the beginning of May (Gouwy et al., 2019), but it quickly became clear that something was wrong. GW979m stopped bringing food abruptly and began roaming around within his territory once again (also see 4.6.2). In December 2019, the wolf GW1479f entered Flanders from the Netherlands and settled in August's territory at around Christmas. The environment minister Zuhal Demir gave this female wolf a name in a tweet: Noëlla (Photo S1). The pair had young in 2020 and 2021, thus forming a pack – the first in Belgium. The range of this pack also increased (also see section 5.8) occasionally bringing them across the border into the Netherlands, as evidenced by an attack on a sheep in Stramproy on 25 January 2021. DNA from August and also some other members of the pack was found.

4.6.4 GW849f (Janka)

In March 2019, after Naya, another wolf tagged by the German research project at TU Dresden crossed into the Netherlands. This was another female, almost two years old and therefore sexually mature for the first time when she left the parental pack. Janka was born in 2018 in the Ueckermünde Heide pack in Mecklenburg-Vorpommern in Germany, over 700 kilometres from the Dutch border. She entered the Netherlands at night on 24 March near Emmen – in around the same area as Naya had. She found a daytime resting place in the Gieten-Borger forestry area. Unfortunately, on 25 March, her transponder tag stopped working and it was no longer possible to track her movements. Her DNA was detected on sheep killed in Hooghalen on 29 March, but she has not been observed since, which is remarkable given her striking collar tag. Norman Stier (TU Dresden) indicates that, in contrast to the other tagged wolf Naya, Janke was more active during the day, especially in the afternoon (Photo 4.6.1).

Photo 4.6.1 *Camera trap photo of a tagged wolf GW849f (Janka) with another pack member from the parental pack in Ueckermünde Heide. Photo: N. Stier & V. Meißner-Hylanová, TU Dresden.*

4.6.5 GW1625M

On 11 February 2020, sheep were killed at Well in Limburg. DNA samples showed that they had been attacked by a wolf that had never been encountered before: GW1625m. The DNA had characteristics that were not found in wolves from the Central European population, but were consistent with the Alpine population. GW1625m turned out to be a wolf that had almost certainly come to the Netherlands from France. The animal was later observed frequently in the Groote Heide area in North Brabant, but initially traces were also found at further away in Noord-Brabant (see Figure 4.6.1) and adjacent Limburg. In the autumn of 2020, the animal was at large for more than six months and settled in the Groote Heide area, between Eindhoven and Weert. By April 2021, there had been 48 confirmed observations of the animal. Three of those were outside his territory during his roaming phase; the rest were all inside his territory. Of the 45 observations inside the territory, 5 were samples from monitoring (3x droppings, 1x game and 1x fur). The remaining 40 cases involved DNA samples from killed livestock, mainly sheep.

4.6.6 GW1554m (Billy)

GW1554m was born in the Herzlake pack in Niedersachsen near Meppen in 2019, and was first genetically identified from droppings on 1 January 2020 (Figure 4.6.2). Researchers found DNA traces of GW1554m on killed sheep and a calf in Lower Saxony and Bremen between February and April 2020. He first appeared in the east of Gelderland in the second half of April 2020 and moved further southwest at the beginning of May. He killed over forty sheep during his time in the Netherlands. The last observation in the Netherlands was on 1 June. On 3 June, video footage of the animal was captured in Oud-Turnhout (Belgium). He moved further south into the province of Antwerp, where there were frequent sightings, including photographs and video footage, and large numbers of wolf spotters were attracted to the area. Since then, the media has referred to him by the name Billy. During that time he killed a few sheep and a crippled dairy cow. He was struck by a van in Turnhout on 19 June, and thrown several metres into the verge, but he was spotted unharmed the next day. At the end of June 2020, GW1554m briefly disappeared from the radar, only to reappear a week later in the east of Belgium, close to the German border. He continued to migrate south, as evidenced by DNA traces on cattle killed in the Belgian provinces of Liège, Luxembourg, and further south in the German state of Rhineland-Palatinate. The last confirmed presence of GW1554m in Germany was on 26 July. In mid-August he appeared in the French départements of Haute-Saône and Vosges. In August and September, he regularly took sheep and calves. His DNA was identified 45 times throughout his journey.

GW1554m was quickly labelled a ‘problem wolf’ in the media, but actually he did not exhibit any behaviour that was unusual in wolves. However, he did cause considerable economic damage to unprotected livestock and was more visible than is usual among wolves. This high profile was possibly due to the fact that he ended up in a densely populated area and a cultivated landscape that was used intensively by humans and had few hiding places. However, he never approached people actively, and largely ignored them. One video clip shows how he accidentally came across a hidden wolf spotter, and quickly ran away as soon as he smelled that person. However, he clearly had no fear around human infrastructure (including stables and buildings) and made use of bridges and tunnels without any problems. He did enter open farm buildings several times, which is somewhat unusual.

GW1554m also targeted calves and was seen chasing herds of cows several times at night, in search of a weaker animal. This case demonstrated clearly that livestock protection policy focuses mainly on small livestock, fuelling a discussion on how to deal with attacks on cattle.

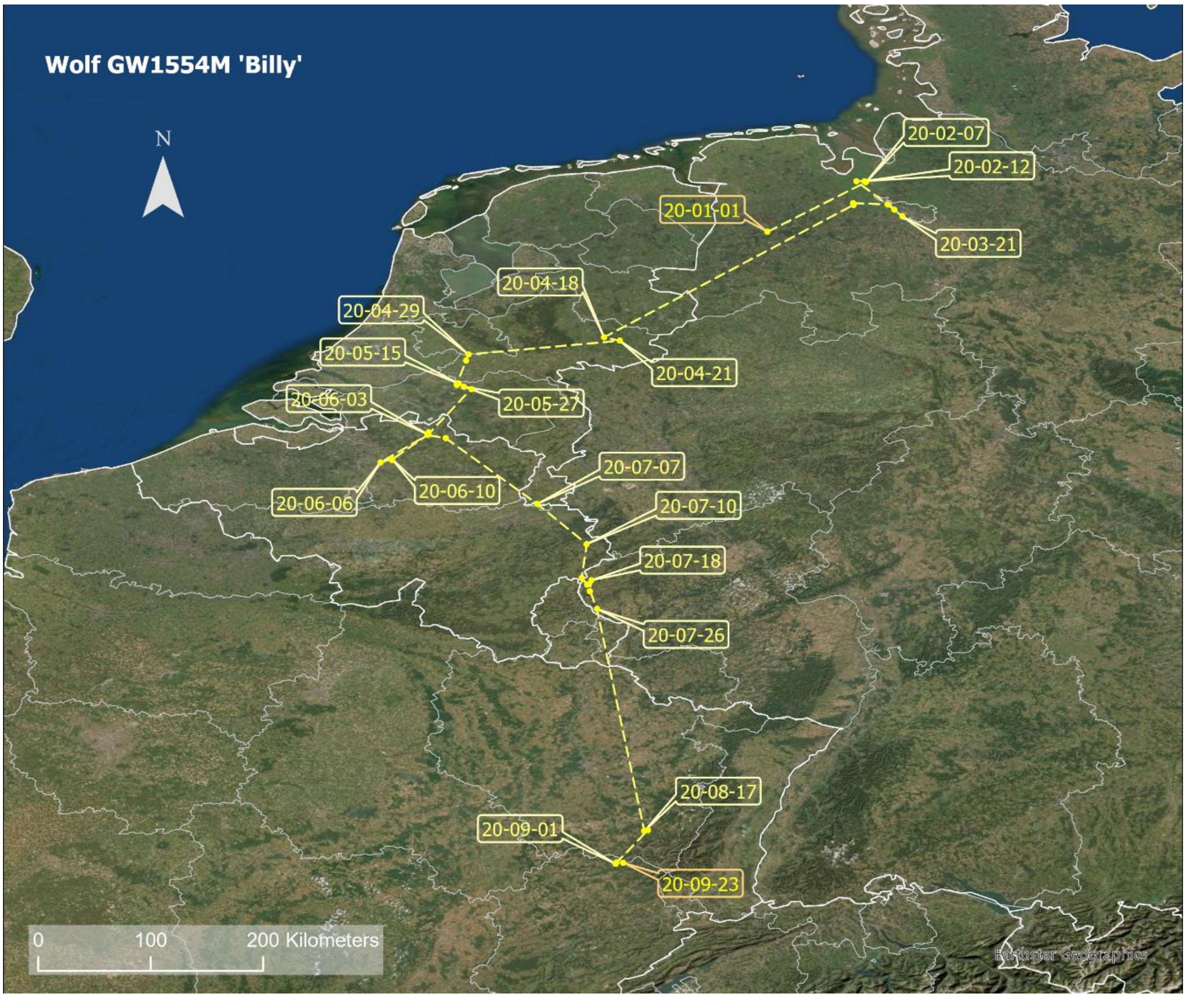

Figure 4.6.2 *Confirmed locations of Wolf GW1554m (Billy) between 1 January 2020 and 20 August 2020 (shot) and the approximate route taken between the data points (Source: INBO & CEwolf).*

In France, due to the economic damage caused, an elimination permit was quickly issued by means of a *tir de défense*, an exemption that permits the use of live ammunition during attacks on livestock (see section 7.1). Billy was shot on the night of 23 September 2020. An exchange of DNA samples between CEwolf and the French authorities confirmed that it was indeed wolf GW1554m.

4.6.7 Overview

These six portraits of individual wolves illustrate a number of relevant themes. The first of these is research. Transponder tags can be used to track the movements of wolves. However, it is not easy to catch and tag a wild wolf and then release it again (also see section 4.3). Another method, DNA tests, can also provide a good understanding of the routes taken by wolves, as illustrated here by wolf GW979m, through Germany and the Netherlands to Belgium, and wolf GW998f, who roamed in the northeast of the Netherlands for a time before eventually settling in the North Veluwe area as its territory. A transponder tag also makes it easy to spot the difference between the roaming phase and the settled phase. All the wolves mentioned above left traces across a wider region, before settling in a relatively small area – their territory. The exceptions were GW849f (Janka), who disappeared before ever settling down in a territory, and GW1554m (Billy), who was shot in France after a permit was issued. We can also see that in their roaming phase most wolves are detected by scientists sooner or later after leaving DNA on killed livestock. In the case of GW1554m (Billy), the animal even rose to a degree of fame among the public, and there was a lot of discussion about its behaviour and location. As described in more detail in section 8.1, roaming wolves in particular are inclined towards prey that is easy and safe, and in Central Europe that usually means sheep. Once settled in a territory, wild ungulates appear to be wolves' main source of food (section 8.1, and also see GW998f above; and

Naya and August). Incidentally, the female wolf GW998f was responsible for killing the highest number of sheep in one attack (31; see also section 6.3, surplus kill), and yet since she settled into a territory in August 2018 she has been responsible for only two sheep kills, and has mainly preyed on wild animals. This contrasts with wolf GW1625m in the Groote Heide area, who has also settled into a territory but continues to attack livestock with regularity. It is still unclear whether this is the result of differences in the composition of the territory and/or the supply of sheep (that are inadequately protected) or whether this particular wolf attacks sheep more frequently due to habituation, for example. Compared to the Veluwe area, the Groote Heide area and its surroundings are less contiguous in terms of nature – in other words, it is more fragmented and interspersed with farmland. In addition, the supply of wild ungulates may also be more limited, as there are no red deer there and possibly no wild boars either, in that area. Additional monitoring studies may provide us with more insight into this.

4.7 Wolves and perceptions

The social structure of wolves, which is based on family groups and in which the success of the pack members depends on protecting and feeding one another and rearing young together, is similar to that of humans (Cassidy et al., 2020). In addition, wolves epitomise the wild and the absence of controls, and as accomplished predators wolves can pose a threat to humans and domestic animals. Wolves have tremendous appeal to the human imagination and this can express itself in a range of different ways – from fascination and enthusiasm to anger and aggression. This is largely determined by innate or cultural factors, giving rise to a person's 'value orientation' with respect to wolves. The basic emotions that play a role in people's attitudes towards wolves (fear, anger, joy) are genetically determined. People whose value system with respect to animals emphasises domination tend to believe that it is fine for animals to be used and exploited by humans (also known as EGOcentrism or stewardship). People whose value system with respect to animals emphasises mutualism believe that animals deserve care and assign rights to them (also known as ECOcentrism). Mutualism is the prevalent orientation in the Netherlands. There is further background information on this in the first fact-finding study (Groot Bruinderink et al., 2012).

Bureau Motivaction was commissioned by the Ministry of Agriculture, Nature and Food Quality to carry out a study into public support for wolves in the autumn of 2020 (Griend & Kamphuis, 2020). This revealed that 53% of those surveyed welcomed wolves and 23% would rather not see wolves returning to Dutch territory. Those in favour indicated that the presence of wolves means richer and more diverse wildlife, ensuring a better natural balance. Those opposed more often cite the argument that wolves kill and eat sheep and cause damage. The Motivaction report shows that many people's perceptions of wolves include the fact that wolves often kill sheep and cause damage. They therefore recommend investing in information campaigns regarding wolves' actual eating habits. Perhaps Chapter 8 of this report could provide a basis for that.

'Damage' is a manmade concept. For wolves, there is no difference between an ungulate that is wild or one that is kept by humans. Perceptions of attacks on sheep also seems to differ depending on whether the perpetrator is a wolf or a dog, for example. In 2020, 295 sheep were reported as having been killed by wolves (BIJ12 2021a). Every year, approximately 4,000-13,000 sheep are bitten by dogs or foxes (IPO 2019), many times more than the damage caused by wolves. Of the €31 million paid out for damage caused by wild animals in the Netherlands in 2020, damage caused by wolves represented just a tiny fraction at 0.2% (BIJ12 2021a), but it received a disproportionate amount of media attention.

Lopez describes the historical relationship between humans and wolves in his book (1978). Indigenous people often speak of wolves with great respect, but wherever Western people have sought to exert their domination over the natural world, wolves have provided a scapegoat. Wolves symbolise the wild and epitomise the human desire to conquer and tame it. Christianity taught people to view wolves as 'the devil in disguise'. All this led to a campaign of persecution and extermination across Europe, and European settlers took that with them to North America. Ultimately, the species was eradicated from much of Europe and North America. These days, people's attitudes towards animals have changed, and that includes people’s attitudes towards wolves. The Council for Animal Affairs (RDA), an advisory body of the Ministry of Agriculture, Nature and Food Quality, indicates that Dutch attitudes towards animals have shifted ‘from ruler to partner’, even though ‘thorny issues’ remain around people’s perceptions of nature and nature management (Schukken et al., 2019). The RDA believes that nature benefits from the presence of wolves and that the return of wolves to the Netherlands is a positive development from an ecological point of view (Schukken et al., 2019). Our attitude towards animals is changing, which is probably due in part to better knowledge about animals’ emotional and social intelligence, including that of primates, ravens, orcas, elephants and wolves (Safina, 2015; De Waal, 2017) and also what we now know about the way entire ecosystems, including predators, fit together (Estes et al., 2011; Jepson & Blythe, 2020). Nevertheless, wolves continue to evoke an emotional response.

Norwegian sociologists have conducted extensive research on perceptions around the return of wolves, particularly in Norway, and published the results in a book entitled *Wolf Conflicts* (Skogen et al., 2017). It is likely that many of the underlying social processes that they identified also play a role in the Netherlands. One important finding of the study is that the arguments about wolves are not conflicts between humans and wolves, but *between humans about wolves*. Over the past century, according to the authors, much has changed in the relationship between the countryside and the city, the working classes, the middle classes and the elites. Among the rural working classes, there is a lot of frustration over rural depopulation and feelings of being ruled by an urban elite are strong. Wolves have ended up as a proxy for those tensions. The return of wolves is exacerbating these tensions because rural people, particularly sheep farmers, have to deal with the consequences, while – in their eyes – they are told what is and is not allowed by people from the city. This also has implications for people’s relationship with scientific knowledge, because there is a strong sense of mistrust about academic knowledge among the working classes. Indeed, science is often seen merely as ‘political opinions’ dressed up as something else. The authors conclude that it is impossible to understand conflicts between humans about wolves without considering the broader social context.

In the Netherlands, too, the societal aspects of the return of wolves have been studied. Social scientist Maarten Jacobs (WUR) indicates that it is important to take the fear around wolves seriously in order to prevent societal polarisation (Jacobs, 2019). According to the philosopher Bernice Bovenkerk (WUR), the debate about wolves not only involves facts, but also values. ‘If we want to coexist with wild animals in the Netherlands, we also have to accept that nature is more than just bees and flowers.’ She indicates that, unlike domesticated animals, wild animals want to be left alone as much as possible (Bovenkerk, 2018). According to the environmental philosopher Martin Drenthen (Radboud University, Nijmegen), the Western notion that a cultivated landscape and nature are two separate systems is flawed. He aims to consider the landscape as a multidimensional space populated by multiple sovereignties, including humans and wolves. Wild animals such as wolves are not passive organisms, but have a will of their own (*agency*). Drenthen believes that fences can be used in order to communicate clear boundaries to wolves, and this makes coexistence possible (Drenthen 2021; Photo 4.7.1). However, there are also people and organisations that are critical of the return of wolves to the Netherlands, such as NoWolves (www.nowolvesbenelux.nl/). The aim of the IPO Wolf Plan (2019) is to achieve coexistence with wolves in the Netherlands. It would be advisable to involve both sociological and philosophical expertise, as well as ecological and legal expertise, in this process.

Photo 4.7.1 *Sheep and prevention. Top left: Shepherd Daphne van Zomeren and her herd in the Veluwe area have received international media attention for the way they coexist with wolves (AON 2020). Top right: The herd enters its enclosure for the night. Inside, the sheep are protected with a wolf-proof electric fence (H. Jansman). Bottom left: A herd of sheep in the night enclosure on the heathland (drone photo taken by M. van Uitert, with permission from the municipality of Nunspeet). Bottom right: a volunteer from wolf-fencing.nl helps a sheep farmer to install electric fencing to protect the sheep from wolves (M. van Uitert).*

5 Distribution, occurrence, origin and ecological carrying capacity

5.1 The origin of wolves

The wolf has long been an endemic species in Europe. Several centuries ago, wolves were distributed across the entire continent, but their numbers dwindled due to hunting and persecution. After reaching a low point in 1950-1960, when wolves disappeared entirely from Western and Northern Europe, populations have recovered naturally in recent decades, and regions from which the species had disappeared are now being recolonised. In addition, a Central European population has also emerged, originating in north-eastern Poland. This population is steadily spreading out in a westerly direction, and wolves from this population have recently settled in Denmark, the Netherlands and Belgium. Genetic research has shown that by far the majority of the 34 wolves observed in the Netherlands so far (until April 2021) have come from that Central European population, including the four individual wolves that have now settled in the Veluwe area. A majority of these wolves came from quite recently established packs in the German state of Lower Saxony, with some also from eastern Germany and one from the state of North Rhine-Westphalia. So far, two individuals have been observed that came from a different population, namely from the rapidly expanding population of Alpine wolves. This includes wolf GW1625m that has now settled in the province of Noord-Brabant (Groote Heide area). Wolves originating from the Alpine population have also been found in Germany and northern France.

Of the 28 wolves that were first known to be in the Netherlands at least six months ago, a quarter are known to still be alive and in the country. Almost half of them (13 individuals) have left our country, either returning to German territory or continuing to Belgium. Four individuals are known to have died in the Netherlands as a result of traffic accidents. The location of the four other wolves remains unknown. It seems highly likely that these individuals have died, although by what cause is unknown. They may have died of natural causes in a location where they were difficult to find, but based on research into such ‘disappearances’ among wolves carried out abroad, illegal prosecution also seems a realistic possibility.

Detailed analysis

5.1.1 Method of genetic identification and monitoring of individuals

Genetic research is used to determine the identity and origin of wolves in the Netherlands. Material expected to contain DNA from wolves is collected for this purpose. This includes droppings, carcasses of dead animals and DNA swabs from wolf bite wounds in wild animals or livestock. For each sample, the species is first determined using what is called a PCR test. PCR stands for polymerase-chain-reaction, a biochemical procedure, whereby a specific piece of diagnostic DNA is located and then reproduced. Its exact code (the order of the base pairs that make up the DNA strand) can then be determined through a procedure known as sequencing. To distinguish between wolves and dogs, a piece of DNA from the control region of mitochondrial DNA (CR) is used that cannot be reproduced in prey species and which is indicative of canines. In this way, even when there is a great deal of DNA from the predated animal (as is the case with a swab from a bite wound) or bacterial DNA (as is the case in droppings), the predator’s DNA can still be recognised.

Different variants of that gene can then be identified based on the DNA code. Of the dozens of variants contained in that CR gene, some are found in both dogs and wolves, and some are unique to wolves. The wolves expected to be found in the Netherlands have the CR variants (also called: haplotypes) HW01, HW02 and HW22. HW01 and HW22 occur exclusively in wolves, and HW02 occurs rarely (<2%) in dogs (Pilot et al., 2010; Desmyter et al., 2012). About 95% of Central European wolves have HW01, while 5% have HW02. HW22, on the other hand, is unique to the Alpine and Apennine wolf populations. The haplotype thus enables a wolf to be distinguished from a dog with a high degree of certainty.

Every sample in which WENR has positively identified wolf DNA is then analysed once again in order to try to identify the individual wolf. A genetic profile is established for every sample, which is unique for each individual (see Chapter 6 for further details about this method). A database that includes all unique wolf profiles found by participants in the CEwolf consortium is kept by SGN. Each individual in that database is assigned its own unique code, made up of the GW-sequence number-sex (GW = genetic wolf). Whenever an unknown genetic profile is found in the Netherlands, the profile is forwarded to SGN and checks are carried out to establish whether the profile is already associated with a particular code. If so, this provides information about where the animal was previously. If, over time, a particular individual is observed by a CEwolf partner in another country, the information is passed on to the countries where the animal was previously observed.

If an individual has never been observed before, an attempt is made to trace the origin of the animal. The first question to be answered is whether the individual comes from the Central European population or from another European population. In some cases, the species test reveals a genetic variant that only occurs in one wolf population, and so this question can immediately be answered with certainty. Otherwise, a cluster analysis can be carried out using reference profiles for the ten wolf populations in Europe (Figure 5.1.1), to see which population the individual has the closest genetic similarity to. If this concerns the Central European population, an attempt will be made to identify the parental pair by checking other profiles in the database. More information about the Central European population is provided in section 4.3.

In many cases, it is possible to establish the origin of a pack in this way. In some cases, when the parents are identified, the mother and father are known to have previously belonged to different packs, which implies the formation of a new pack. In other cases, no parental pair can be identified. This is a sign that one or both parents have not yet been identified from their DNA. This may be because the wolf in question has left relatively few traces, but another factor is that the intensity of monitoring varies greatly between the various states in Germany. In some federal states, it is much easier for individuals to remain ‘under the radar’ as a result (personal communication with Gesa Kluth, LUPUS). A third possibility is that the individual concerned may come from the Central European population, but from a pack outside Germany (for example in Polish territory), in which not all the individual animals are known.

Photo 5.1.1 *DNA samples. Left: DNA samples from a sheep bite. Right: DNA sample from droppings at the WENR laboratory. Photos: Marielle van Uitert –www.paralleluniversum.nl.*

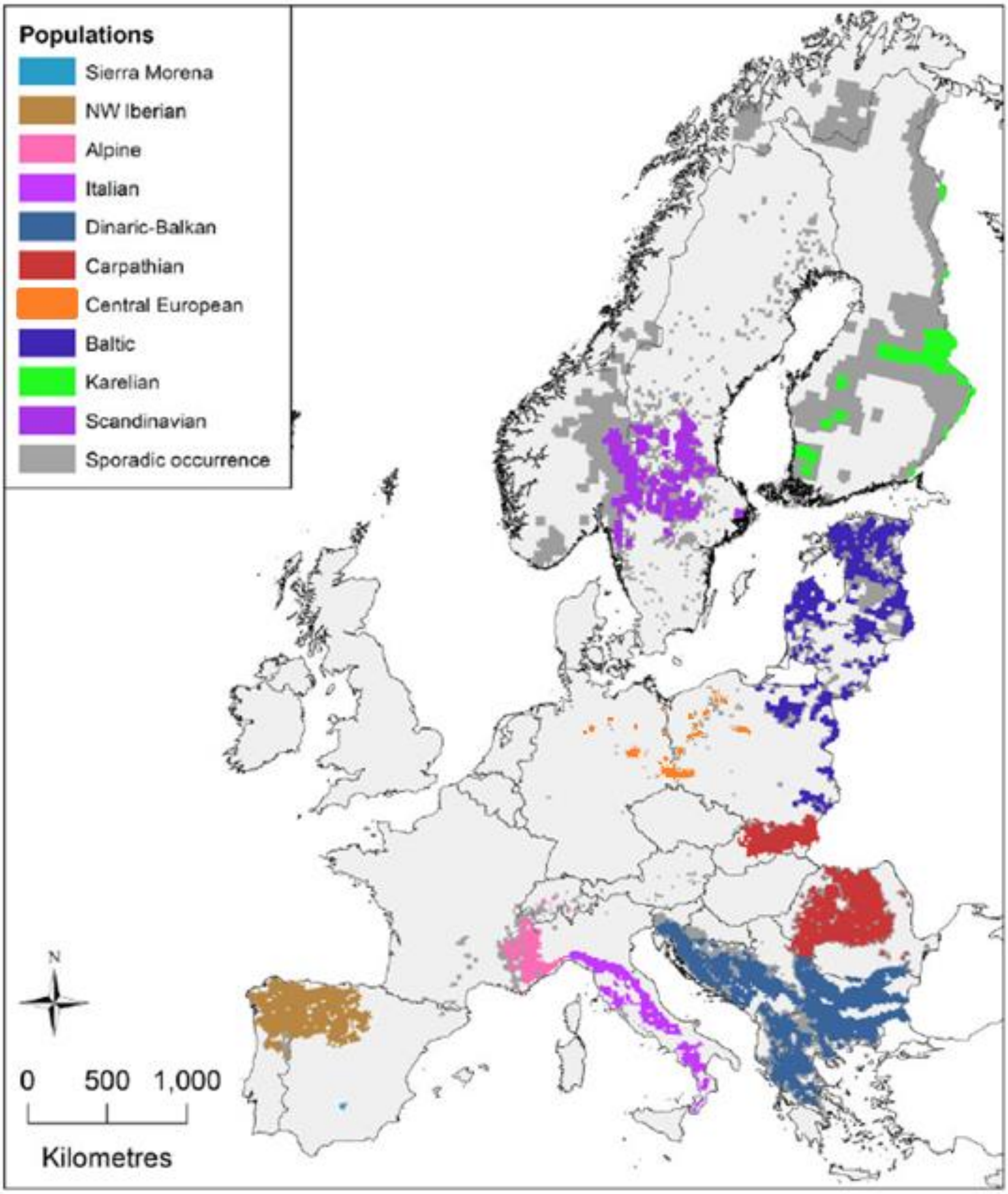

Figure 5.1.1 *Indication of the distribution areas of the ten wolf populations recognised by the LCIE, which are distinguished from one another based on their genetic make-up. The figure is taken from De Groot et al. (2016), based on the distribution area presented in Chapron et al. (2014). Since then, the distribution area of the Central European population in particular has expanded westwards, see Figure 4.2.2 and 5.1.2.*

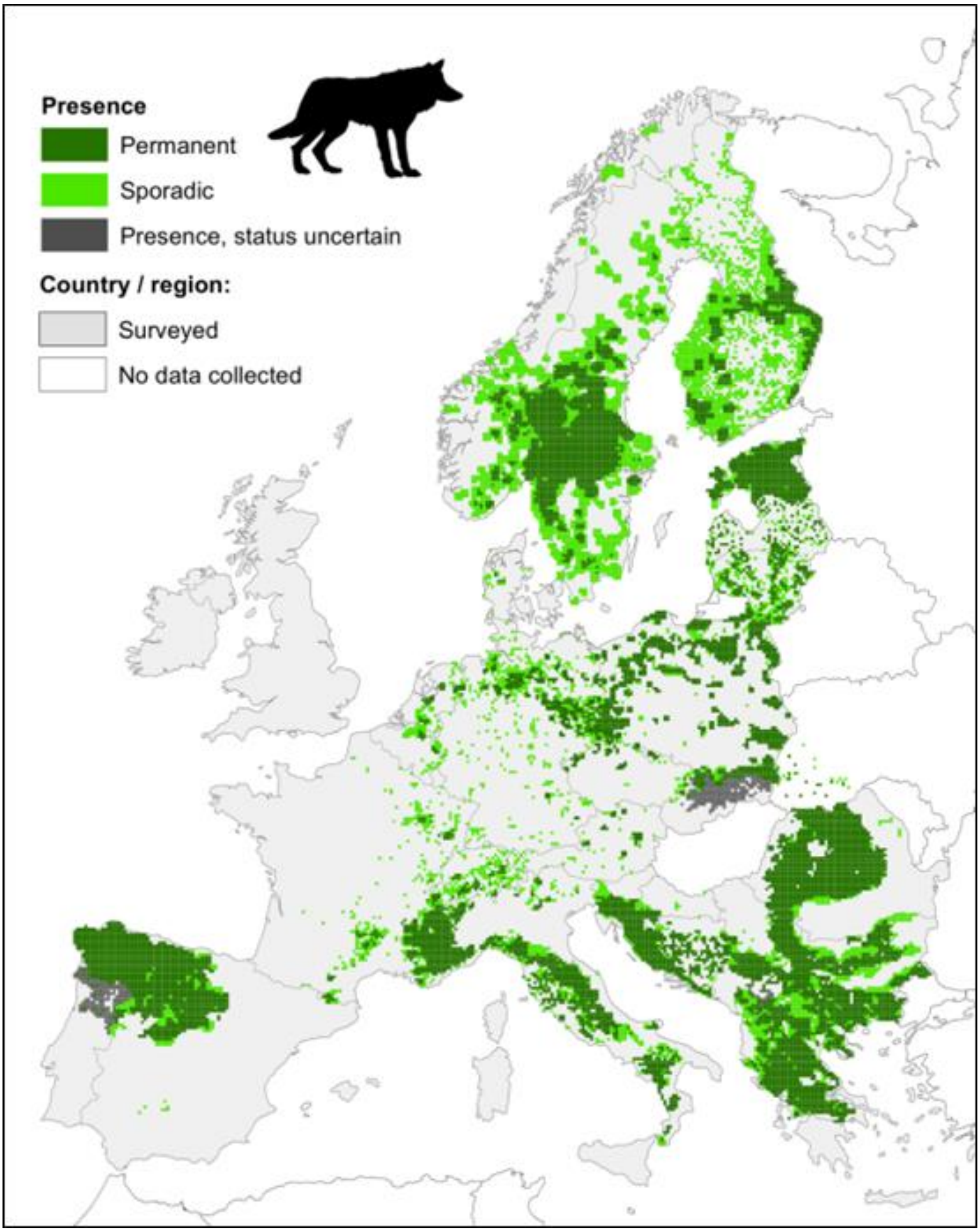

Figure 5.1.2 *Current overview of the distribution area of wolves in Europe, based on LCIE (2016) with updates of the distribution area of the CEwolf population based on information from 2020. Dark green: permanent presence. Light green: sporadic presence. Dark grey: unknown status.*

5.1.2 The origin of wolves in the Netherlands.

The first wolf (GW368m) to enter the Netherlands for 150 years did so in March 2015, and since then 34 different wolves have been observed in the Netherlands using DNA analysis (up to and including April 2021).

Based on the exchange of data in CEwolf described above, Table 5.1.1 provides as complete an overview as possible of our knowledge of the origin of each of these individuals. Quite recently (in February and November 2020), two individuals have surfaced that can be traced to the Alpine wolf population, including wolf GW1625m, now settled in Noord-Brabant in the Groote Heide area (Figure 4.6.1). All of the remaining 32 individuals are from the Central European population. For 28 of those, it was possible to identify a pack. In 21 cases that pack in question was in Germany, and in most cases (thirteen) it was in the state of Lower Saxony, which borders the Netherlands; in one case the wolf was from a pack in North Rhine-Westphalia. This makes sense, because there are many more packs in Lower Saxony than there are in North Rhine-Westphalia (Figure 4.2.2). Seven cases involved a wolf from a pack in one of the states in Eastern Germany (Mecklenburg-Vorpommern in three cases, Brandenburg in two cases and Saxony in two cases). The female wolf GW960f, now settled in the Central Veluwe area, came from Lower Saxony. The pair that has established a pack in the North Veluwe area are the male (GW893m), who also came from Lower Saxony, and the female (GW998f) from Brandenburg (see Table 5.1.1). Seven individuals have now been identified in the Netherlands who were born to this pair and raised in the Netherlands. For the remaining four individuals from the Central European population, no pack of origin has yet been established (for one of the reasons mentioned in the previous section).

5.1.3 The origin of wolves in Europe

Historical records show that wolves were common throughout Europe several centuries ago, but their numbers gradually dwindled in recent centuries. The area in which the species was found fell back to 68% of the previous native European range (Ripple et al., 2014), and wolves disappeared from large parts of Western, Central and Northern Europe (see e.g. Bouyer (2015) for a clear map of this gradual decline). However, wolves never disappeared completely from Europe. Chapron et al. (2014) provide a clear picture of the distribution of wolves in Europe at their lowest point in the 1950s-1970s. At that time there were still several thousand wolves in the Balkans and the Romanian Carpathians, several hundred in Italy, along the eastern borders of Poland, and in the Baltic States and Finland.

The 1979 Bern Convention provided the first step towards legal protection at the European level in countries where wolves still existed. In 1992, the convention was integrated into the European Habitats Directive, so that the species also enjoyed protected status in countries where wolves were no longer present, through Annex IV. As a result of this increased protection, wolf numbers have increased again and their range has now expanded in a north-westerly direction without any further intervention. For example, the westward immigration of wolves from the growing population of wolves in Finland has led to the start of a new population in the Scandinavian Peninsula (Flagstad et al., 2003). Since 1990, wolves have returned to the French, Italian and Swiss Alps, having migrated northwards from the Italian Apennines (Valière et al., 2003). In Poland, following strict protection in 1998, wolves from the Baltic population in eastern Poland began crossing the Vistula River to the western areas of the country, and a new population was established there which subsequently spread to eastern Germany and the Czech Republic (Szewczyk et al., 2019; Figure 4.2.1). This population is referred to as the Central European population and genetically it is now clearly distinct from the Baltic population and Carpathian population (Szewczyk et al., 2021). In the meantime, the Central European population has continued to push ever further west through Germany, reaching Denmark, the Netherlands and Belgium (Jarausch et al., 2021; also see Figure 4.2.2). Section 5.2 discusses the exact history of wolves in Central Europe and France, including stories about illegal introduction.

5.1.4 Settlement, new destinations and mortality among wolves observed

The current monitoring strategy in the Netherlands involves collecting DNA samples in the case of reports of damage where the involvement of a wolf cannot be ruled out, as well as volunteers who actively search for traces left by wolves in areas where a wolf has been spotted or located. This data is combined with any additional information from neighbouring countries through CEwolf. This provides a reasonably complete picture of which wolves are currently in the Netherlands (also see section 4.2). The samples are analysed once every three months and the results are published. Furthermore, even under the Dutch monitoring strategy, it is quite possible that certain wolves may not be observed for several months, only for their DNA to show up once again. Table 5.1.1 shows everything that we currently know about every individual’s movements, and Figure 5.1.3 summarises this in a number of categories. A distinction is made between individuals who are definitely known to have left the Netherlands, individuals who are definitely known to have died in the Netherlands, and individuals who were definitely alive in the Netherlands recently. Because of the chance that some individuals may 'go missing' from monitoring for a while, November 2020 was taken as the baseline (six months before the end of the last quarter for which individual genetic profiles are available). Individuals identified through DNA samples after this date are categorised as 'recently alive' unless they have been confirmed dead since that time (such as GW1729f). Individual wolves that had not been observed in the Netherlands in the past six months, but that are not known to have died or to have left the Netherlands, were categorised as 'unknown'. Six individuals that were only identified for the first time after 1 November 2020 have not been included in this overview, because the monitoring period was too brief to reach any conclusions about their recent status.

Based on feedback from CEwolf partners, it is known that over half of the 24 wolves that entered the Netherlands in the period between 2015 and 1 November 2020 left again some time later. This is a remarkably high percentage compared to the situation in Denmark, where so far not a single wolf that has entered the country has left again (Sunde et al., 2021). Five wolves are known to have moved into Belgian territory (Flanders). Two of those (GW1479f 'Noella' and GW979m 'August'; see section 4.6) are still alive and have established a pack near Hechtel-Eksel. The other three have been confirmed killed (see Table 5.1.3). Most of the animals that left the Netherlands returned to Germany (eight individuals). GW368m (the 'Wanderwolf' who was the first to enter the Netherlands in 2015) is known to have been killed in a traffic accident in Lower Saxony. The other individuals have shown up in Lower Saxony or North Rhine-Westphalia.

In Denmark, several offspring from an established pack were found to have moved into German territory within a year. Nothing similar has yet been shown for the offspring of the pack in the North Veluwe area in the Netherlands using DNA samples. However, it is true that more pups were observed on camera in both 2019 and 2020 than were detected with DNA. It is not known what became of those wolf pups. However, current analysis is limited to identifying individuals using DNA testing.

Seven wolves observed in the Netherlands were still alive recently (April 2021). In addition to the wolf that has settled in the Groote Heide area in Noord-Brabant, there are six individuals in the Veluwe area: the parents of the pack in the Veluwe area (GW998f and GW893m) and two of their offspring, the wolf that has settled in the Central Veluwe area (GW960f) and a male that has been present for some time in the Southwest Veluwe area (GW1490m). It is known that four of the 28 individual wolves were killed in the Netherlands, all as a result of traffic accidents (N.B.: the wolf that was killed by a car near Appelscha in June has not yet been included, because its identity had not yet been confirmed by DNA tests at the time of writing).

Another four individuals (14%) are categorised as 'unknown', because they were last observed in the Netherlands, but over six months ago. Table 5.1.1 shows that all four of these individuals have not been observed for over two years, which, given the intensity of monitoring, means that there is no chance that they are still alive and in the Netherlands. There are various reasons why individual wolves can fall off the radar. First, there is a real chance that the wolf has left the Netherlands and has either died in Germany, for example, or has simply not been detected using genetic testing. Another possibility is that the individual died in the Netherlands – whether from natural or unnatural causes. No further conclusions can be drawn regarding possible causes of death based on our results.

Elsewhere in Europe, some experience has been gained in determining the extent to which wolves have actually 'disappeared' and what the underlying causes may be. The information that is most relevant to the situation in the Netherlands is available from a recently published analysis on wolves in the Jutland Peninsula (mainland Denmark and the German state of Schleswig-Holstein), where, as in the Netherlands, intensive monitoring is carried out using DNA from droppings and samples taken in cases of predation (Sunde et al., 2021). The analysis showed that of the 35 individuals, nine had definitely died (of which eight had been killed in traffic accidents and one due to illegal hunting) and 14 had gone missing (40%, which is a significantly higher percentage than in the Netherlands or elsewhere in Germany). Three of these went missing in Schleswig-Holstein and may have migrated to other parts of Germany; for the other 11 individuals, this is unlikely and it is almost certain that they have died. The cause of death in these cases is unknown. It is possible that the animals died naturally in a spot where their body could not easily be found. However, the implied mortality rate is remarkably high compared with other countries, and illegal persecution seems the only realistic explanation (Sunde et al., 2021). Another recent study based on established (territorial) wolves in the Scandinavian population (Liberg et al., 2020) showed that over 42% of established wolves went missing over time. On the basis of an extensive analysis of the possible causes of this, the study concluded that the majority of these missing animals must have been killed due to illegal persecution. Another study involving 104 tagged wolves from the same population (Liberg et al., 2011) showed that over an 11-year period, 22% of the individual animals were highly likely to have died as a result of illegal persecution (23 individuals, of which five were shown to have been killed illegally) – over half of the total number of deaths.

When it comes to understanding more about the disappearance of wolves due to migration and the various causes of death, large-scale studies using transponder tags and research based only on settled wolves is the most realistic method in larger populations with a larger distribution area. At the current scale, it is not practical to monitor the fate of each individual wolf through genetic monitoring and thereby determine the percentage of wolves that go missing (let alone the causes). Datasets based on the DNA samples received are too patchy for this, almost by definition. Experience in Germany shows us that wolves sometimes fall off the radar for several years at a time and then turn up again (personal communication Ilka Reinhardt & Gesa Kluth). This makes it difficult to say after how long an individual wolf should be classified as missing. This is in part because not all the federal states of Germany monitor wolf populations equally intensively. Not all German states take DNA samples for testing every time there is an attack, and certainly not every time droppings are found. A simple check of CEwolf's full database of individuals showed that 46% of all the wolves in it (up to and including April 2021) were identified on just one date. The majority of those were dead animals that had apparently not been identified up to that time; the other animals (18% of the total number of individuals) were identified once with DNA testing and were never reported again.

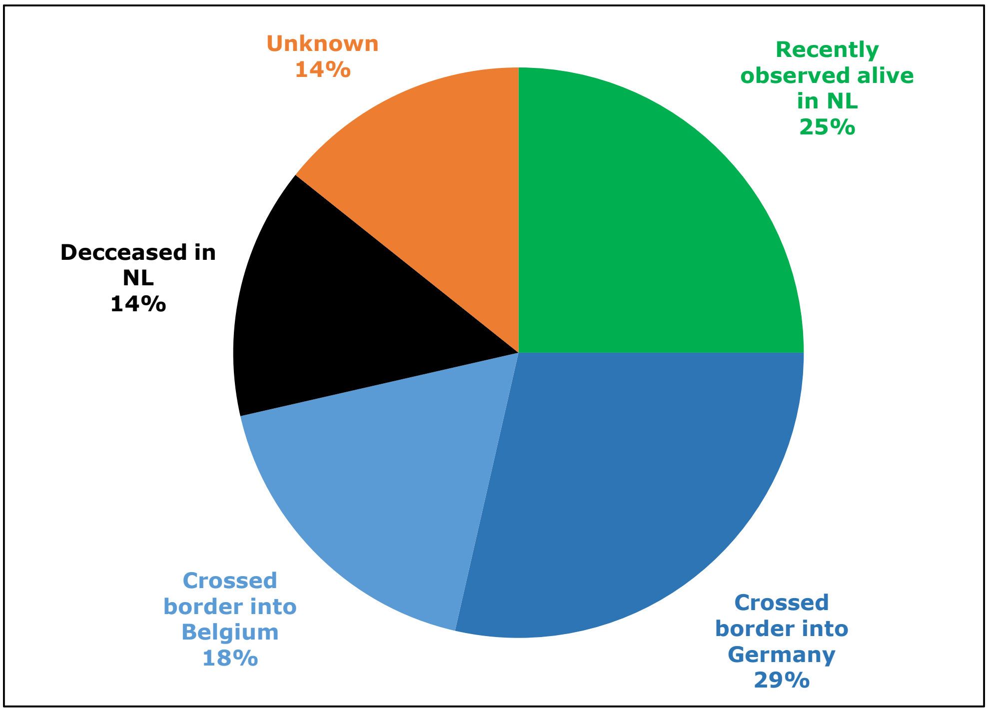

Figure 5.1.3 *Status and destination of all wolves identified for the first time in the Netherlands between 2015 and November 2020 (N=28).*

Table 5.1.1 *Overview of the origin and current status of all wolves identified in the Netherlands using DNA so far (up to April 2021). Colour coding status: grey = definitely died in the Netherlands; dark green = definitely did not die in the Netherlands (observed in the Netherlands after 1 November 2020, or definitely left the Netherlands); light green = first observed after 1 November 2020; white = missing (after 1 November 2020 no longer observed in the Netherlands or elsewhere). * = last DNA confirmation (droppings) dates from 30 October 2020, after which the animal was almost certainly seen on camera.*

Since	Individual code	Population of origin	Birth pack	first DNA in NL	Last DNA in NL	Current status
2015	GW368m 'Wanderwolf'	Central Europe	Munster (Lower Saxony)	March 2015	March 2015	Left NL; killed in traffic accident near Hannover (Germany)
2016	GW620f	Central Europe	Ueckermünde (Mecklenburg-Vorpommern)	September 2016	September 2016	Unknown
2017	GW657m	Central Europe	Cuxhaven (Lower Saxony)	March 2017	March 2017	Killed in traffic accident near Hoogeveen (NL)
	GW843m	Central Europe	Babben-Wanninchen (Brandenburg)	November 2017	November 2017	Killed in traffic accident near Kloosterhaar (NL)
	GW680f 'Naya'	Central Europe	Lübtheen (Mecklenburg-Vorpommern)	December 2017	December 2017	Left NL; settled in Leopoldsburg (Belgium), almost certainly killed there
2018	GW955m	Central Europe	Barnstorf (Lower Saxony)	February 2018	February 2018	Unknown
	GW953m	Central Europe	Unknown	February 2018	April 2018	Unknown
	GW913m 'Roger'	Central Europe	Barnstorf (Lower Saxony)	March 2018	March 2018	Left NL; killed in traffic accident near Opoeteren (Belgium)
	GW954f	Central Europe	Schneverdingen (Lower Saxony)	March 2018	April 2018	Left NL; observed in North Rhine-Westphalia (Germany) in June 2018
	GW763f	Central Europe	Daubbitz (Saxony)	April 2018	April 2018	Left NL; observed in Lower Saxony (Germany) in June 2018
	GW998f	Central Europe	Babben-Wanninchen (Brandenburg)	Mei 2018	October 2020*	Settled in North Veluwe area, recently confirmed
	GW979m 'August'	Central Europe	Unknown	June 2018	July 2018	Left NL; settled in Leopoldsburg (Belgium)
	GW1401f	Central Europe	Unknown	October 2018	October 2018	Left NL; observed in Lower Saxony (Germany) in October 2018
	GW960f	Central Europe	Göhrde (Lower Saxony)	August 2018	April 2021	Settled in Central Veluwe area, recently confirmed
	GW912f	Central Europe	Walle (Lower Saxony)	December 2018	December 2018	Left NL; observed in Lower Saxony (Germany) since February 2019
2019	GW893m	Central Europe	Eschede/Rheinmetall (Lower Saxony)	January 2019	December 2020	Settled in North Veluwe area, recently confirmed
	GW965f	Central Europe	Die Lucie (Lower Saxony)	February 2019	February 2019	Left NL; observed in North Rhine-Westphalia (Germany) in March 2019
	GW849f 'Janka'	Central Europe	Ueckermünde (Mecklenburg-Vorpommern)	March 2019	March 2019	Unknown
	GW1428m	Central Europe	North Veluwe 2019 (GW998f x GW893m)	October 2019	January 2021	Settled in North Veluwe area
	GW1261m	Central Europe	Unknown	November 2019	July 2020	Left NL; observed in Lower Saxony (Germany) in autumn 2020
	GW1479f 'Noella'	Central Europe	Gohrischheide (Saxony)	December 2019	December 2019	Left NL; settled in Leopoldsburg (Belgium)

Since	Individual code	Population of origin	Birth pack	first DNA in NL	Last DNA in NL	Current status
2020	GW1625m	French-Italian Alps	Unknown	February 2020	April 2021	Settled in Groote Heide area, Noord-Brabant
	GW1608m	Central Europe	Rodewald (Lower Saxony)	March 2020	March 2020	Left NL; via Belgium and Luxembourg to Germany (Lower Saxony; autumn 2020)
	GW1626m	Central Europe	North Veluwe 2019 (GW998f x GW893m)	March 2020	March 2020	Killed in traffic accident near Epe (NL)
	GW1554m ‘Billy’	Central Europe	Herzlake (Lower Saxony)	April 2020	May 2020	Left NL; via Belgium and Luxembourg to France, (legally) shot there
	GW1729f	Central Europe	North Veluwe 2019 (GW998f x GW893m)	June 2020	March 2021	Killed in traffic accident near Ede (NL)
	GW1889m	Central Europe	North Veluwe 2019 or 2020 (GW998f x GW893m)	September 2020	January 2021	Recently present in South Veluwe area
	GW1490m	Central Europe	Rodewald (Lower Saxony)	November 2020	April 2021	Recently present in South Veluwe area
	GW1920m	French-Italian Alps	Unknown	November 2020	November 2020	Recently observed for the first time (after 1/11/2020)
2021	GW1964m	Central Europe	North Veluwe 2019 (GW998f x GW893m)	January 2021	April 2021	Recently observed for the first time (after 1/11/2020)
	GW2088m	Central Europe	North Veluwe 2019 (GW998f x GW893m)	February 2021	February 2021	Recently observed for the first time (after 1/11/2020)
	GW2087m	Central Europe	North Veluwe 2019 (GW998f x GW893m)	March 2021	April 2021	Recently observed for the first time (after 1/11/2020)
	GW2089m	Central Europe	Schermbeck (North Rhine-Westphalia)	April 2021	April 2021	Recently observed for the first time (after 1/11/2020)
	GW2090f	Central Europe	very likely Barnstorf (Lower Saxony)	April 2021	April 2021	Recently observed for the first time (after 1/11/2020)

5.2 Wolves & illegal introduction

There is no indication that the wolves currently found in Central Europe or the Alpine region arrived there through the illegal introduction of the species. Rumours about illegal introduction are widespread across Europe and seem to stem largely from a lack of knowledge about the behaviour, ecology and distribution of wolves in Europe among certain population groups, and an underestimation of the distances which roaming wolves can travel and how long it takes them to cover significant distances. The argument sometimes used – that it is ‘simply not possible for wolves suddenly to have appeared here, and so they must have been introduced’ – does not hold water. There are isolated cases of wolves that have escaped or been released, but these have made no significant genetic contribution to current wolf populations. The genetic structure and composition of current European wolf populations can be explained adequately through the scientifically substantiated, spontaneous expansion of existing wild populations.

Detailed analysis

5.2.1 The Netherlands

In accordance with the IUCN guidelines for Reintroduction, the Ministry of Agriculture, Nature and Food Quality presented a policy for reintroductions in 2008 (Ministry of Agriculture, Nature and Food Quality, 2008). Reintroduction is defined as releasing animals into the wild with the aim of promoting or re-establishing an independently sustainable population.

Unfortunately, in the support study by Motivaction, dating from 2020 and commissioned by the Ministry of Agriculture, Nature and Food Quality, the term ‘reintroduction’ is used to indicate the spontaneous return of the wolf (Griend & Kamphuis, 2020). This occurs in sentences such as ‘Slightly more Dutch people are confident that the reintroduction of wolves is safe’ and ‘Half of people still think that wolves should be brought to the Netherlands, but the number of opponents has increased slightly’. The term ‘reintroduction’ and the above quotes also suggest that rumours of the active (and therefore illegal) reintroduction of wolves could be fuelled by an active human component. The terms ‘recolonisation’ or ‘natural return’ are a much more accurate way of describing what has happened. As explained in sections 5.1 and 4.6, the DNA of most wolves identified in the Netherlands can be traced back to their original pack. Even where this has not been possible, there is no genetic uncertainty that the animals concerned come from existing populations in the region.

5.2.2 The history of wolves in Central Europe

The existing Central European wolf population was established in the 1990s in western Poland from a small number of wolves that spread southwards from wolves that were part of the Baltic wolf population living in northern Poland (Pilot et al., 2006). Wolves have only been a protected species in Poland since 1998, and the first packs struggled to gain a foothold due to the constant threat from humans (Jędrzejewski et al., 2004). In 1996 the first wolf was observed in north-eastern Germany following an absence of 150 years, and in 2000 wolves were found to be breeding for the first time in Germany. Since then, the Central European population has grown very rapidly, with an initial annual rate of increase of 30%. By 2020, this meant there were about 130 packs in Germany and 150 packs in western Poland. Thanks to intensive genetic monitoring by the CEwolf consortium, the history of this population is well-known, and this has also allowed us to detect immigration from other wolf populations (including possible illegal introduction) (Szewczyck et al., 2019, 2020; Jarausch et al., 2021). The findings show that current migration from neighbouring populations (Baltic, Carpathians) is very limited and that no genetic mixing with the Alpine population has yet been observed. There are also no signs of the illegal introduction of wolves. However, there are occasional, genetically documented cases of wolves who have escaped from captivity: in October 2017, six wolves escaped from a wildlife park in Bavaria, but these could easily be identified as having escaped from captivity (DBBW2019) due to their different haplotype (HW13). One of these animals was recaptured shortly afterwards, two were shot (with a permit) and the other three were never found. In 2019, a wolf with HW13 also escaped from a wildlife park in Hessen, and was later killed in a traffic accident (DBBW2020). To date, despite extensive genetic monitoring, no unusual DNA profiles have been identified that could indicate that any particular wolf is of unnatural origins. In the case of every wolf identified, it has been possible to trace them back to the genealogy of the Central European wolves, attribute them to the Central European wolf population or, in exceptional cases, to neighbouring populations (Carpathian: one individual in Germany; migration from the Alpine population in several cases).

Despite excellent documentation of the spontaneous recolonisation of wolves across Europe, rumours of wolves being released have cropped up regularly (for example Von Bothmer (2014) or https://www.suedostschweiz.ch/zeitung/rueckkehr-des-wolfs-stinkt-gewaltig). Stories about 'vans with wolves in the back' abound. Deck (2015) indicates that this urban myth is rooted in the fact that many people are not aware of the great distances that wolves can cover independently. They can easily cover hundreds of kilometres within a few weeks, crossing highways, canals and major rivers. Social media and fake reports help to feed these myths, often in combination with images purporting to show wolves being released. These are usually images of wolves from a completely different region that had been struck by a vehicle and were being released after recovering. Variants of the same story are adapted to local situations, but are almost identical (Deck, 2015). In spite of all the evidence from wolf transponder tags (which shows the routes taken by roaming wolves in great detail, hour by hour), this is taken as proof that these wolves wearing tags have been 'released', or even that a person driving a van has imitated the route taken.

5.2.3 The history of wolves in France

In France, there may have been some incidental (and unverifiable) illegal attempts to reintroduce wolves in the 20th century (for an overview, see Baillon (2016) and Canteux (2019)). However, there is no indication that those attempts were successful.

During the autumn of 2020, seven Canadian and three Arctic wolves escaped from the Parc Alpha, a zoo in France, as a result of severe weather that destroyed fences. Soon afterwards, four more wolves escaped from a park that was undergoing construction work (Ecozonia). Most of these animals were recaptured or shot shortly afterwards on government orders, but three animals were never found. Most wolves kept in captivity are either American or Russian wolves. Their DNA is easy to distinguish from the Central European and Alpine populations.

Until 1992, wolves had officially disappeared from France and any roaming wolves from Italy or Spain were not protected. However, there were numerous reliable sightings of wolves in France between their official disappearance in 1934 and their official return in 1992 (for an overview, see Baillon (2016)). There are a few cases that can be traced back to escaped animals with certainty (including eight Russian wolves that escaped from a film set or one with filed teeth), but the majority of reliable observations (usually animals that were shot) were wild animals, sometimes identified by experts as 'Italian wolves' (Canteux, 2019).

France's current population of wolves is clearly derived from the Italian population. The Italian wolf is a genetically distinct lineage of the grey wolf and all traces of wolf DNA found at the time of the official recolonisation of France are attributable to this lineage (Valière et al., 2003). Genetically, this subspecies is characterised by the haplotype HW22 (a genetic type, according to the nomenclature of Pilot et al. (2006)) and wolves found in France today are almost exclusively of this type (Valière et al., 2003; Dufresnes et al., 2019), suggesting a process of natural recolonisation via northern Italy. The theory of natural recolonisation from Italy was also later confirmed in a parliamentary inquiry in France (https://www.assemblee-nationale.fr/12/rap-enq/r0825-t1.asp). The occasional wolf from the Central European population has been recorded in France, and these are clearly recognisable from their haplotypes HW01 and HW02. In France, people prefer to use the term 'Baltic' wolves because the Central European wolf population is descended from animals from the Baltic areas of Poland, and they recolonised first western Poland and later north-eastern Germany (Pilot et al., 2006). One recent example is the wolf GW1554m (Billy), which migrated from north-western Germany (Herzlake) in 2020, via the Netherlands, Belgium and southern Germany, before ending up in the Vosges region of France (see section 4.6).

Italian wolves had already been identified and shot in several regions of France earlier in the 20th century (Canteux, 2019). However, due to the lack of protection, they were never able to become established in France. Before official protection was introduced in 1992, the last wolf confirmed shot in France was in 1987. Another wolf was shot in the Alps in 1992, but was later identified as having come from the Apennines (Randi, 2011; Duchamp et al., 2017).

In Italy, the wolf population has been cautiously recovering since 1980 as a result of stronger legal protections dating from 1970. Because the roaming wolves that appeared in France were typically not identified as wolves until after they had been killed, those advocating better protections for wolves generally kept any sightings of wolves in France quiet in order not to disclose their locations and risk further hunting. The hunting of wolves remained legal until 1992, because wolves were not officially found in France and were therefore not protected under the Bern Convention. That changed in 1992 with the European Habitats Directive. Shortly after it came into effect, official confirmation of wolves' return to Mercantour National Park followed. In the neighbouring province of Italy (Cuneo), the presence of wolves had already been confirmed in 1991 (mentioned in Canteux, 2019). Wolves have been observed by park rangers in the Mercantour since at least 1989, but it was never possible to confirm these observations officially. In 1993, a settled pair with young was found in France. This 'sudden' official return kindled suspicions of the illegal introduction of wolves. All the more so because some were sceptical that wolves could move from the Apennines to the French Alps of their own accord. However, later research using tags confirmed that this is indeed possible: a wolf tagged in Italy roamed from the Apennines into the western Alps (Ciucci et al., 2009). Genetic research among Alpine wolves has also confirmed the ancestral link with the Apennine wolves (Fabbri et al., 2007). Other studies of tagged wolves in Europe and North America have confirmed that wolves can indeed cover very long distances, with the maximum being over 10,000 kilometres in a period of about 20 months (Wabakken et al., 2007).

5.2.4 Legal status of illegally released wolves

Currently in Europe, the impact of any animals that have escaped or been illegally released on the genetic make-up of populations of wild wolves would be negligible. Nonetheless, it is recommended that any non-native wolves that escape from captivity are captured or removed in other ways. Animals that have lived in captivity for a long time are habituated to humans and it seems more likely that such specimens may exhibit problematic behaviours towards humans (see sections 6.2 and 5.1).

The Nature Conservation Act prohibits the illegal release of animals. The status of illegally released wolves is less clear under European legislation. Arie Trouwborst reports that there is no absolute clarity on this yet, but that wolves should be assumed to be protected in case of doubt. 'In the case of animals that are so genetically different that they pose a threat to genetic integrity or in the case of wolves released outside their historical range, the legislation does provide for the possibility of intervention' (A. Trouwborst, personal communication).

5.3 Hybridisation between wolves and dogs

Just as all modern humans carry a small proportion of DNA from other human species that are now extinct, most wolves also derive a very small percentage of their DNA from dogs (<5%). This is the result of occasional interbreeding between wolves and dogs over millennia. These wolves are not considered hybrids.

Hybridisation due to more recent interbreeding between wolves and dogs occurs mainly in areas with large numbers of feral dogs and where wolves have almost disappeared, such as in central Italy.

In most EU Member States, wolves are subject to close genetic monitoring and hybridisation is also studied closely in order to intervene quickly in the event of interbreeding with dogs. Recent genetic studies show that hybridisation in the Alpine, Central European and Scandinavian populations is very rare (<1% of cases studied). No hybrid animals have yet been identified in the Netherlands. Many claims of hybrid wolves are likely the result of scientifically unverified, unpublished analyses that did not respect the assumptions of statistical testing.

The legal status of hybrids in the Netherlands is not entirely clear. It is likely that they should have the same protected status as pure wolves in order to prevent the illegal extermination of ‘hybrid’ wolves. The Council of Europe recommends that confirmed hybrids be eliminated from the population by government authorities in order to protect the genetic integrity of wolves.

Detailed analysis

5.3.1 Hybridisation between wolves and dogs

It is difficult to draw a definite line on hybridisation, as all European wolves have been subject to incidental hybridisation with dogs since time immemorial, ever since wolf-to-dog domestication. A distinction can be made between ancient, historical hybridisation, more recent hybridisation (dozens of generations ago) and current hybridisation (1-4 generations ago) (Donfrancesco et al., 2019; Caniglia et al., 2020). Likely all European wolves thus have a small proportion of DNA from dogs spread throughout their genome, and dogs are in turn are descended from wolves (Pilot et al., 2018). This is a case of historical introgression. We can make a comparison with humans: the genome of today’s humans (*Homo sapiens*) also includes a small proportion of DNA from at least three other human species, and this proportion varies from place to place (Sankararaman et al., 2014; Wolf & Akey, 2018). In addition to this historical introgression, more recent hybridisation has occurred in some wolf populations, particularly in areas where wolf populations were reduced to very low numbers in the 20th century and the remaining wolves came into contact with large numbers of feral dogs. This is best documented in the case of the southern Apennines in Italy (Randi et al., 2014; Galaverni et al., 2017; Salvatori et al., 2019), where some wolves have up to 20% canine DNA. In the northern Apennines, however, which is the cradle of the Alpine wolf population, this has been much less the case and the proportion of DNA from dogs is comparable to the rest of Europe (Pilot et al., 2018).

Regarding recent hybridisation (1-4 generations ago), we can further subdivide hybridisation into different categories: a first-generation hybrid (F1) consists of 50% dog DNA and 50% wolf DNA. After that, the first-generation hybrid may breed with a pure wolf (first-generation backcross), and its progeny will be 75% wolf and 25% dog. A generation further and this becomes 12.5%, etc. However, there may also be backcrosses between first, second and third generations, which can ultimately produce a whole range of different proportions of wolf DNA versus dog DNA. Using current techniques, we can distinguish the equivalent of a third-generation backcross (6% dog, 94% wolf) from a pure wolf relatively unequivocally (Harmoinen et al., 2021).

5.3.2 Genetic identification of hybrids

Claims that ‘hybrid wolves’ have been discovered or ‘wolves from a zoo’ or ‘Mongolian wolves’ regularly crop up on social media and the websites of interest groups. These claims can be traced back to DNA analysis services provided by commercial laboratories. Such claims should be regarded with the appropriate scepticism unless it is possible for third parties to verify the methods used, reference data and the conclusions that can be drawn.

In several cases, independently verified studies have concluded that there was no basis whatsoever for such claims (e.g. Smeds et al., (2021), in the context of discussions about the origin of wolves in Norway (Food&Agribusiness, 2020; Flagstad, 2020)). Since so little detail is provided by these commercial laboratories about the methodology used, it remains uncertain how they might have arrived at different conclusions. Depending on the method of analysis used, however, there are several conceivable ways in which DNA analysis might incorrectly indicate that an individual animal is a hybrid.

The first possibility is the incorrect interpretation of the mtDNA sequences that are often used to determine the species. In order to identify a random DNA sequence, it is possible to use an international database (International Nucleotide Sequence Database Collaboration) and the Basic Local Alignment Search Tool (BLAST). This compares the DNA code that is being analysed with more than 100 million DNA sequences that other researchers have added to the database, and then displays the 100 best matches. This method simply returns other DNA sequences that match the one you have entered, and indicates how close the match is. There can often be dozens of DNA sequences with a perfect match. If you enter the CR sequence of wolf GW979m ('August'), which falls under HW02 (see section 5.1.1) and occurs in wolves distributed across Eurasia, the first match in the database currently happens to be '*Canis lupus chanco* Isolate WN03 D loop'. This isolate comes from a Mongolian wolf. However, that does not mean that August is a Mongolian wolf, simply that they both share the same DNA code in those pieces of DNA. The second match gives the exact same DNA sequence and comes from '*Canis lupus* haplotype W23 D-loop'. That isolate comes from Estonia. The authors of this DNA sequence state: 'also occurs in Latvia and Poland'. There are 22 other isolates that yield a perfect match with this DNA sequence, including some dogs. As new DNA sequences are added to the database, the order in which the results are displayed changes. Focusing only on the first match ('Mongolian wolf') and using this to identify the wolf is scientifically incorrect and possibly even misleading. However, this approach does seem to be common practice among commercial labs. The laboratories that participate in the CEwolf consortium (see Appendix 3) use a reference list of known wolf haplotypes, together with a fixed naming convention in accordance with Pilot et al. (2010), also see Appendix 3. There, the European wolves have haplotypes HW01 to HW22. This is how the haplotype of GW1625m (the wolf from the Groote Heide area) was identified as HW22.

Whenever genetic markers are used to recognise individual animals, gaps in the reference database can easily lead to inaccurate conclusions. The various European wolf populations (Figure 5.1.1) differ from each other genetically to varying degrees – from slight differences to larger differences, depending on how long ago they stopped exchanging DNA (tens of generations ago, up to hundreds of generations ago) (Pilot et al., 2018). This makes it possible to assign a random DNA sample from a wolf to the correct original population with a statistically high degree of certainty. Using the same method, in principle we can also differentiate between dogs, wolf-dog hybrids and pure wolves from a particular European population. However, the validity of these results depends on the presence of sufficient reference profiles for all possible wolf populations, in addition to dogs. This is because when no reference material is available from the actual original population, the model is forced to assign an unknown genotype to an incorrect reference population, if there is no better choice. In fact, the result provided is often 'intermediate', between different source populations. Because the different wolf populations themselves have often scarcely exchanged any DNA for hundreds or thousands of generations, these populations are genetically almost as distinct from one another as they are from dogs, which also split off from wolves relatively recently. If you assign a wolf from the Central European population (without knowing its origin) and you use one set of canine genotypes on the one hand and one set of Alpine wolf genotypes on the other, there is a good chance that this individual will be misidentified as 'intermediate' – somewhere between a dog and a wolf (Harmoinen et al., 2021). In reality, the genotype is just as poor a fit for dogs as it is for Alpine wolves. When the 'wolf' reference population consists of a mix of wolves from different populations, the chance of an incorrect identification as a hybrid is also very high.

Recently, Harmoinen et al. (2021) developed an improved assignment methodology for hybrids, using genetic markers specifically identified based on the distinction between dogs and wolves. Using that method, which is publicly available, it is possible to distinguish hybrids from wolves up to the third-generation backcross with a high degree of certainty. Genotypes from the reference populations are also publicly available, which means that this method can be regarded as the gold standard when it comes to identifying recent hybridisation between dogs and wolves.

5.3.3 Cases of hybrid wolves in the Netherlands and neighbouring countries

Contemporary hybridisation between wolves and dogs is monitored closely in many places in Europe, so that swift action can be taken with respect to the composition of the population where possible. There is no evidence of hybridisation in Scandinavian wolves either (Smeds et al., 2021), and in the Central European population the extent of hybridisation is very limited (Harmoinen et al., 2021). A total of three cases of wolf-dog hybridisation have been identified in Germany. Two cases involved the same female wolf, who mated with a dog first, and with her own hybrid offspring a year later. In all cases, a permit was issued for catching the hybrid animal, and failing that to shoot the animal. Where hybrids have been detected in the Alpine and Central European population, these are removed from the population as quickly as possible, in accordance with Recommendation 173 of the Council of Europe (2014).

No cases of wolf-dog hybridisation have been identified so far in the Netherlands. All wolves registered to date in the Netherlands have been found to originate from either the Central European wolf population or (in two cases) the Alpine wolf population. In the vast majority of cases, it was also possible to assign the individual to a specific pack of origin. Since the identity of the parents was also revealed, and in many cases even the grandparents, these individuals can be identified as pure wolves and we can therefore rule out any hybridisation.

5.3.4 The protected status of hybrid wolves

The Netherlands Flora and Fauna Act grants hybrids of protected species the same status as the parent species. The Nature Conservation Act is less clear on this. The EU Regulation 2017/160 (https://eur-lex.europa.eu/eli/reg/2017/160/oj) shows that hybrids of species listed in Annexes A and B (including wolves) enjoy the same protection status as the parent species up to the fourth generation backcross (Trouwborst, 2014). However, the European Council recommends the removal of contemporary wolf-dog hybrids from the population (EC Recommendation 173, 2014), in order to avoid compromising the genetic integrity of wolves. This is the policy pursued in most European member states. In concrete terms, this requires the competent authority to provide for a selective exemption to the prohibition on disrupting or killing a confirmed hybrid. Boerema et al. (2021) also point out that in principle hybrids should be treated as protected, because confusion can easily arise regarding the hybrid status of individuals.

5.4 Hotspots/corridors in the Netherlands that are frequently used by roaming wolves

In the period 2015-2021, the area where wolves were active covered almost half of the territory of the Netherlands, excluding (incidental) excursions. Six hotspots of wolf activity have been identified within this larger area of activity: one in Drenthe, two in Overijssel, two in Gelderland and one in Noord-Brabant. Wolves entered the Netherlands mainly from Germany, via the provinces of Drenthe and Overijssel. It is expected that this route will continue to be used in the future, because there are several wolf territories in Germany at a relatively short distance from the border with the Netherlands. In the longer term, more wolves can also be expected from the south – via Limburg and North Brabant, as wolves from packs in Belgium search for new territory and/or individual animals roam northwards through the Eifel region or from the French Alps. Broadly speaking, four corridors can be designated within the Netherlands, i.e. places where there is some frequency of movements. The first corridor runs from central Drenthe through central Overijssel to the Achterhoek area. A second corridor is a branch of the first, and runs from central Overijssel towards the Veluwe area. A third corridor is an extension of the first and runs from the Achterhoek area through German territory and into North Limburg and the southeast of Noord-Brabant. The area around the Meuse, Waal and Lower Rhine rivers also shows some evidence of more frequent movements, but in an east-west direction. The expectation is that if more wolves arrive in the Netherlands or are born here, the number of corridors will increase and the location of those corridors can be described more accurately based on more systematic observations. In some hotspots many reports of damage caused by wolves may have been received, but this is not always the case. So hotspots are not necessarily linked to significant losses of livestock, and indeed there may be no such losses at all.

Detailed analysis

5.4.1 Identifying hotspots and areas of activity

An analysis of hotspots was carried out as part of this fact-finding study. The first step was to identify the areas of wolf activity in the Netherlands in broad terms. Specific hotspots were then identified within that area of activity. Two scenarios were applied here, both of which define a hotspot in different ways. In the first scenario, a hotspot was defined as a place where more intense wolf activity is recorded than elsewhere over a wider continuous area, regardless of how many different wolves are responsible for that activity. In the second scenario, the same definition of activity is used, but the number of wolves responsible for that activity is also taken into account. Two scenarios are presented here to illustrate that the chosen definition of a hotspot has a significant effect on the results of the hotspot analysis. Many alternative definitions of ‘hotspot’ are conceivable, beyond the two definitions of a hotspot applied here. Which definition is the most appropriate will depend on the goal of the hotspot analysis and the standard that is chosen. This, in turn, is a policy choice (also see *Recommendations*). The method used here is described in more detail in the inset entitled *Method of identifying area of activity and Method of identifying hotspots*.

5.4.1.1 Method of identifying area of activity and method of identifying hotspots

The area of activity of wolves in the Netherlands was determined using all wolf observations made in the period between March 2015 and April 2021 (Source: BIJ12 database, TU Dresden & WENR telemetric research database). This includes a total of 1,687 observations, of which 1,174 are classified as C1 observations and 513 as C2 observations. The observations included in the analysis were (1) livestock losses (n=191), (2) carrion from prey (wild fauna) (n=16), (3) sightings (n=345), (4) wolf paw prints and trails (n=35), (5) droppings (n=579), (6) wolves killed by vehicle strikes (n=5), (7) data from transponder tags (n=513) and other (n=8). To determine an area of activity, an MCP (Minimum Convex Polygon) was plotted around the observations. This technique takes a point cloud of observations and connects all the outer points, provided that the inner angles do not exceed 180 degrees. If the inner angle is greater than 180 degrees, the relevant observations are ‘skipped’ when drawing the outer boundary. This analysis was done firstly using all the observations (known as MCP100) and then using 95% of the observations (known as MCP95). The MCP95 excludes the 5% of observations that are furthest away from the centre of the area of activity, determined based on all the observations. The MCP95 therefore excludes (incidental) excursions into further-away locations, thus providing a better picture of the core area in which the wolves are active.

In both scenarios 1 and 2, the hotspot analysis was carried out using grid squares measuring 5km x 5km. First of all, it was determined whether any wolf observations had been made in each 5x5 grid square and an activity score was then calculated for each square. One or more observations in a square was scored as 1 point; for each adjacent square with one or more observations an extra point was added, so that each square could score between 0 and 9 points. In addition, it was determined how many different individuals had been observed in each 5x5 grid square, and in the eight adjacent squares. In the case of scenario 1, the square was categorised as a hotspot if it scored 7-9 points, regardless of the number of different wolves that had been observed. In the case of scenario 2, the square was categorised as a hotspot if it scored 7-9 points, provided at least three different wolves had been observed in that square and the adjacent squares.
The number of wolves included unknown wolves, but multiple unknown wolves were counted as one wolf. It is important to note that the analysis is based on the presence or absence of observations of wolves in the 5x5 grid squares, regardless of the number of observations inside those squares. This approach was chosen in order not to give too much weight to repeat observations of the same (settled) animal. This global analysis also fits better with the large variety of types of observations.

Wolves’ area of activity now extends to a large portion of the Netherlands. If all the observations from the database are included in the analysis (MCP100), the area of activity comprises around 76% of the land area of the country. The province of Zeeland, large parts of the provinces of Noord-Holland and Zuid-Holland, the northwest of Friesland and the north of Groningen are excluded from this area. The same applies to smaller parts in the east of the provinces of Groningen, Overijssel, Gelderland and Limburg. However, these latter areas are an artifact of the method chosen, since only wolf observations made inside the Netherlands are included. If observations in Germany had also been included in the analysis, these small areas along the eastern border would also fall within the wolf’s current area of activity. When the MCP95 method is applied and 95% of observations from the database are included in the analysis (i.e. excluding ‘outliers’), the area of activity comprises around 48% of the land surface of the country. The provinces of Zeeland, Noord-Holland and Zuid-Holland and Groningen are then excluded in their entirety. Large swathes of Noord-Brabant, Utrecht, Flevoland, Friesland and Limburg also fall outside the area of activity. This definition shows the core area of wolf activity. It is comprised largely of the provinces of Drenthe, Overijssel and Gelderland.

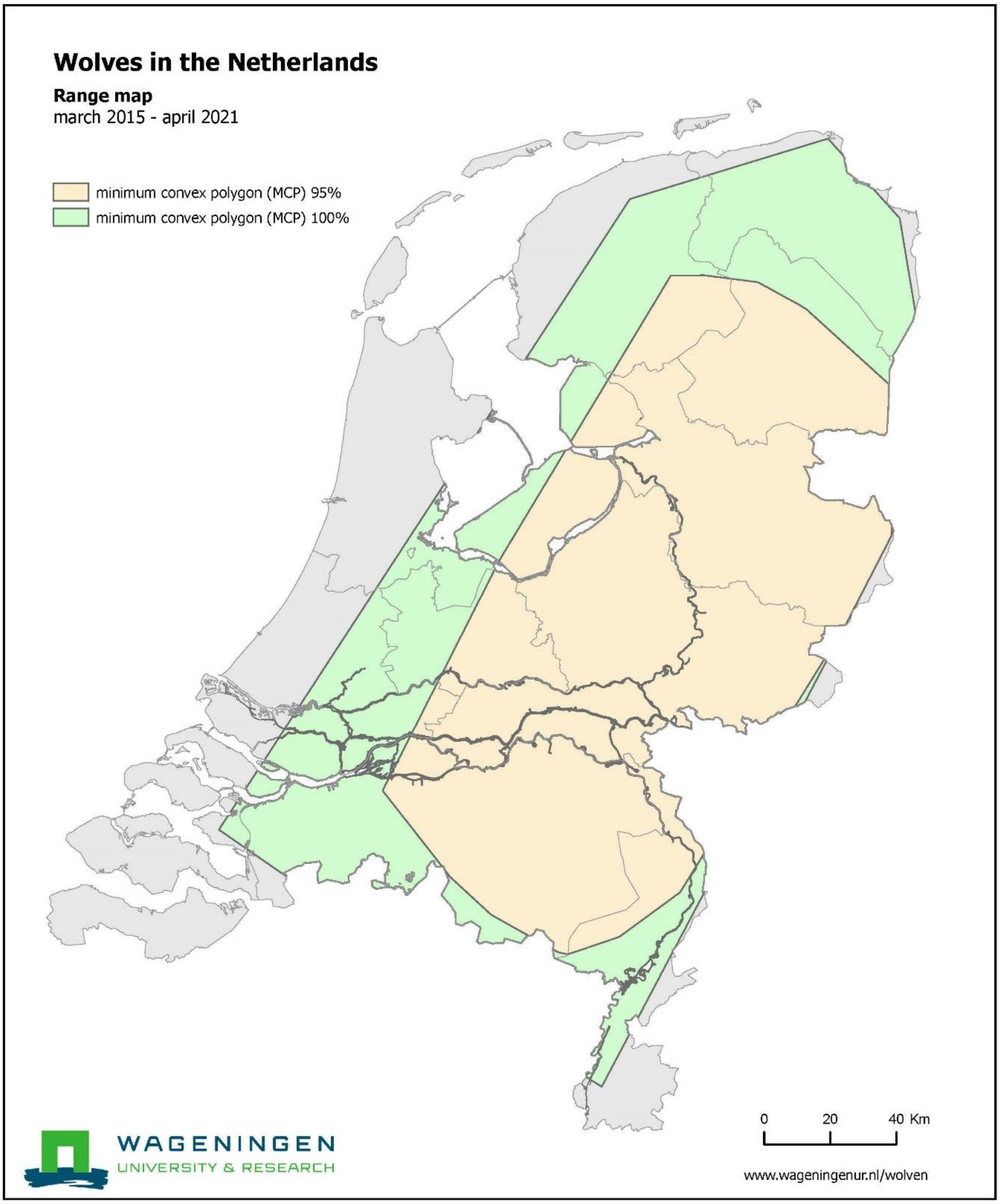

Figure 5.4.1 *Area of activity of the wolf in the Netherlands based on, respectively, 100% and 95% of all observations in the Netherlands.*

In scenario 1, based on observations made in 2015, six wolf activity hotspots can be identified in the Netherlands (Figure 5.4.2): (1) the Veluwe nature reserve in the province of Gelderland; (2) the Leenderheide and Groote Peel nature reserves and surrounding areas, southeast of Eindhoven in the province of Noord-Brabant; (3) more or less the entire area between Assen and Emmen in the centre of the province of Drenthe; (4) the Montferland nature reserve and part of the outlying area in the Oude IJsselstreek in the province of Gelderland; (5) the Lemelerberg and Sallandse Heuvelrug nature reserves and surroundings in the province of Overijssel; and (6) the Zwarte Dennen and surroundings nature reserve, to the east of Staphorst in the province of Overijssel.

Scenario 2 led to the identification of four hotspots (Figure 5.4.2): the Montferland / Oude IJsselstreek nature reserve and Lemelerberg / Sallandse Heuvelrug nature reserve and surrounding areas are not designated as hotspots in this case, because the minimum of three different wolves per 5x5km area was not reached there. For the four other hotspots listed under scenario 1, the threshold value of three wolves was achieved. Three different wolves were observed in and around hotspots 2 and 6, four different wolves were observed in and around hotspot 3, and twelve different wolves were recorded in and around hotspot 1.

The hotspots are areas which several roaming wolves passed through and/or stayed for a longer period of time and/or where wolves settled. When interpreting these maps, it should be remembered that the hotspots are based on observations over a period of six years and that some of these hotspots may no longer be hotspots. After all, observations of (roaming) wolves over a certain period of time may lead to a hotspot being identified even though the animals have since left the area. One example is the hotspot in Montferland/Oude IJsselstreek (Scenario 1), which was designated as a hotspot because wolf Naya spent some time roaming in that area before continuing her journey south. The (as yet) relatively limited number of observations in the dataset also means that new observations could easily lead to larger hotspots or the merging of two hotspots. It should also be noted that some hotspots will have been missed, since the analysis is based largely on incidental observations and not on systematic monitoring. When we compare the two scenarios, it becomes clear that the definition of a wolf hotspot and the standard chosen (threshold values) largely determine the outcome of the analysis, and a (slightly) different definition and/or standard could have a significant impact on what does or does not constitute a hotspot.

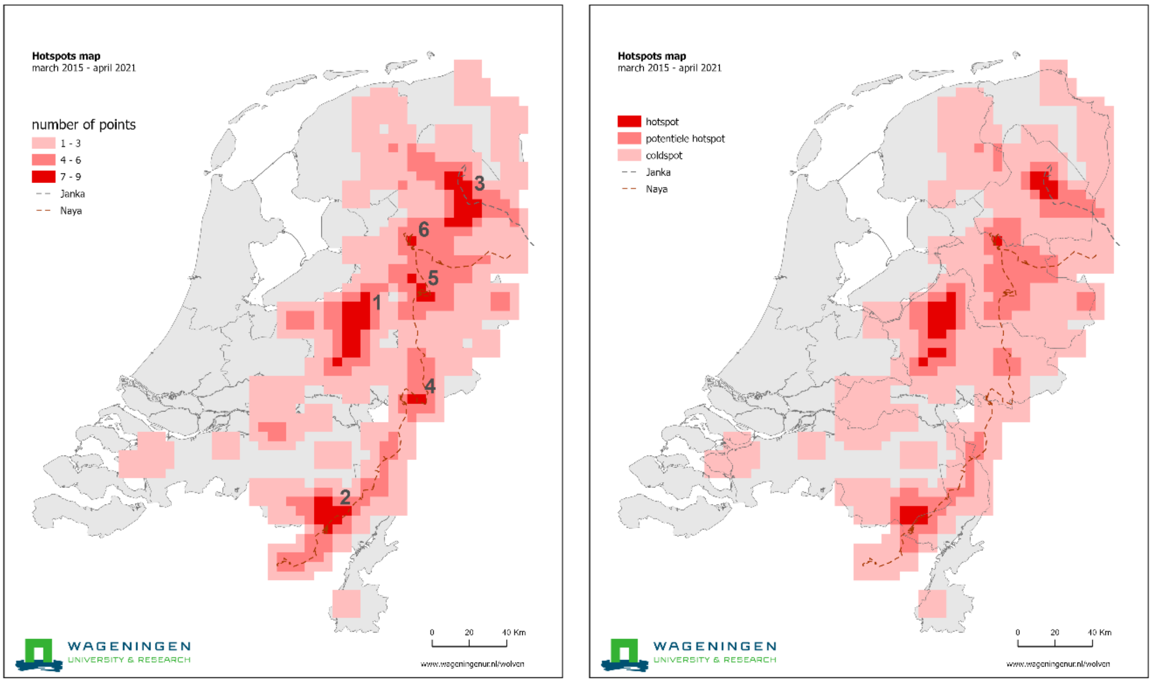

Figure 5.4.2 *Wolf hotspots in the Netherlands in the period March 2015-April 2021, based on scenario 1 (left) and scenario 2 (right).*

5.4.2 Identifying corridors

A 'corridor' is defined here as a zone or area through which wolves pass relatively frequently compared to other areas in the Netherlands. All observations that can be linked to individual animals were used in order to identify such corridors. The first step was to plot all observations of all individuals that were observed at least three times (n=22) onto a map. The second step was to link these observations in chronological order, with the direction of movement indicated by an arrow. Thirdly, any bundling of the routes taken by wolves was identified by eye. This method of global exploration was chosen here, because the dataset does not allow for a more detailed analysis. After all, most of the observations in the dataset – with the exception of those made of the two wolves fitted with a transponder tag – were incidental observations spaced quite far apart in time. The connecting lines between two observations therefore provide only limited information regarding the routes taken by wolves. Research using transponder tags would be required for that. The analysis carried out here should therefore be seen primarily as an initial exploration that only identifies potential corridors in an approximate manner.

Figure 5.4.3 gives an indication of the areas that individual wolves have crossed in the Netherlands, the direction of movement and the point of entry from neighbouring countries. Broadly speaking, four corridors can be designated within the Netherlands, i.e. places where there is some frequency of movements. The first corridor runs from central Drenthe through central Overijssel to the Achterhoek area. A second corridor is a branch of the first, and runs from central Overijssel towards the Veluwe area. A third corridor is an extension of the first and runs from the Achterhoek area through German territory and into North Limburg and the southeast of Noord-Brabant. The area around the Meuse and Waal rivers also shows some evidence of more frequent movements, but in an east-west direction. It is not possible to identify corridors much more precisely than that at present. In order to do so, we would need to know the movements of more wolves on the one hand, and be able to make more systematic observations so that the routes taken could be mapped in more detail, on the other hand. The expectation is that if more wolves arrive in our country or are born here, the number of corridors will increase and we will understand the location of those corridors better based on more systematic observations.

The majority of wolves observed in the Netherlands were first registered in the provinces of Drenthe and Overijssel, so there is clearly a northern entry route from Germany. This observation is consistent with the fact that the closest wolf territories in Germany are just to the east of these northern provinces, and the habitat in those provinces is assessed as suitable (Figure 5.6.2). Much of the area of Germany to the east of the provinces of Gelderland and Limburg, by contrast, has been assessed as unsuitable for wolves, partly due to the higher levels of urbanisation. This does not mean that wolves cannot enter the Netherlands here – see for example GW1920m and GW1625m (Figure 5.4.3) – but simply that this is expected to happen less frequently. Figure 5.6.2 also shows that the Eifel area of Germany has been assessed as a very suitable habitat, although the number of wolf territories there remains limited. The same applies to neighbouring areas of Belgium (Ardennes; Figure 5.6.3) (Schockert et al., 2020). It is therefore expected that comparable entry routes could also become established there in due course. Belgium is also in the early colonisation phase and wolves from packs that originate there will be able to cross the Dutch border. One example of this is wolf GW2089m, which was spotted in Zeeland in April 2020. The wolf entered the Netherlands from Belgium and was seen in both the west of Noord-Brabant and Zeeland over the course of several days. He then returned to Flanders (BIJ12, 2021). There is also a small, but not impossible, chance that wolves could migrate to the Netherlands from France. Wolf GW1625m, for example, settled in the Groote Heide area in the southeast of Noord-Brabant, having originated from the Alpine wolf population.

Photo 5.4.1 *Wolf droppings. Wolves mark their territory with faeces, which can be monitored relatively easily for research. Droppings can be tested for DNA (Photo 5.1.1) and for dietary research (section 8.1). Photos: H. Jansman.*

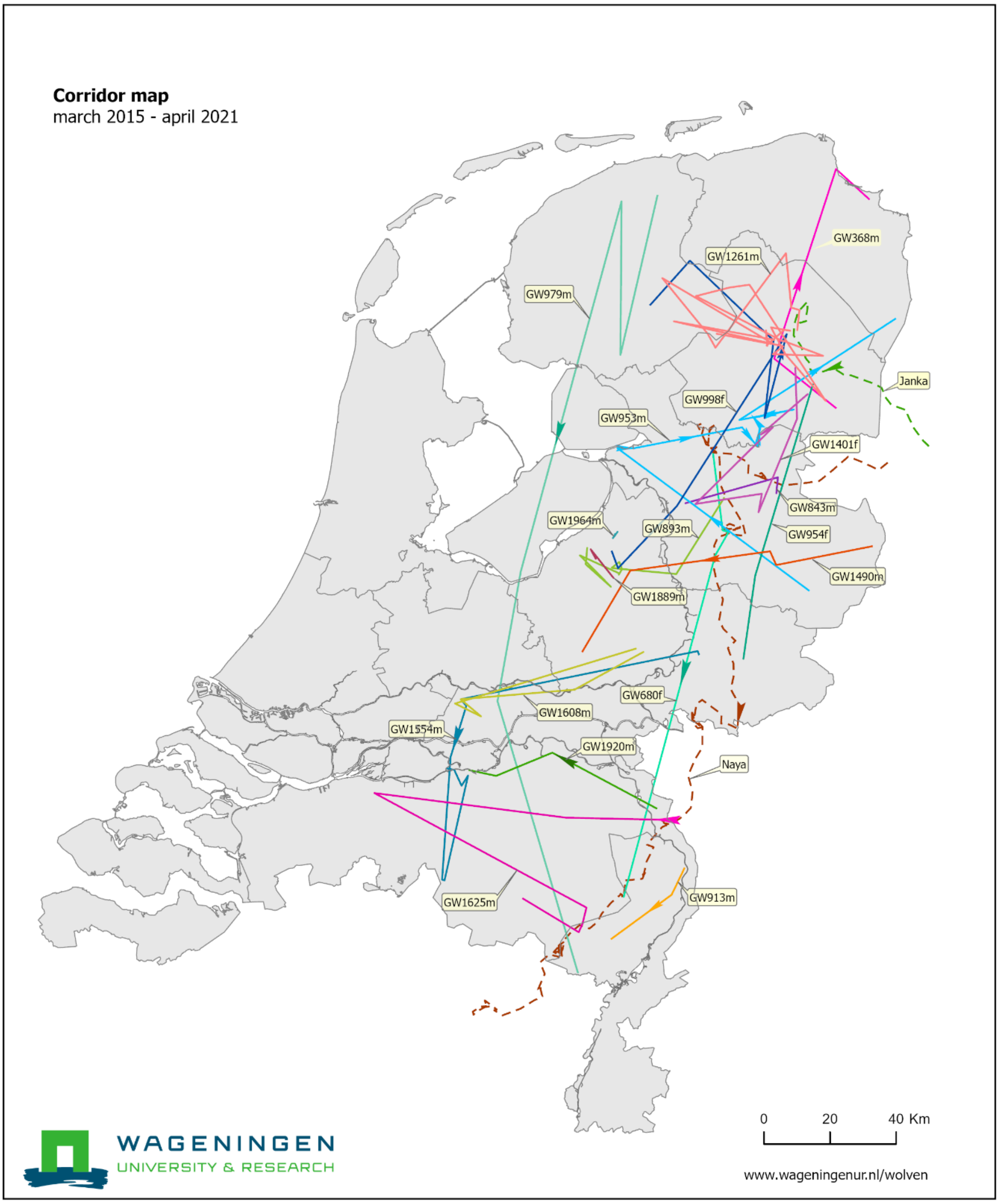

Figure 5.4.3 *Global patterns of movement for individual wolves in the Netherlands; only individuals observed at least three times.*

5.4.3 Losses to livestock within hotspots

In recent years, losses to livestock have occurred mainly in areas where roaming wolves have been passing through. Figure 5.4.4 shows an overview of the locations where livestock (mainly sheep) was killed by wolves in the period 2015-2021, in comparison with the location of hotspots according to scenarios 1 and 2. These figures illustrate that in some cases there may be many reports of damage within a hotspot, as can be seen in Noord-Brabant. But this is not always true, as can be seen for the hotspots in the Veluwe area and, in the case of scenario 1, in the Achterhoek area. So hotspots are not necessarily linked to significant losses of livestock, and indeed there may be no such losses at all.

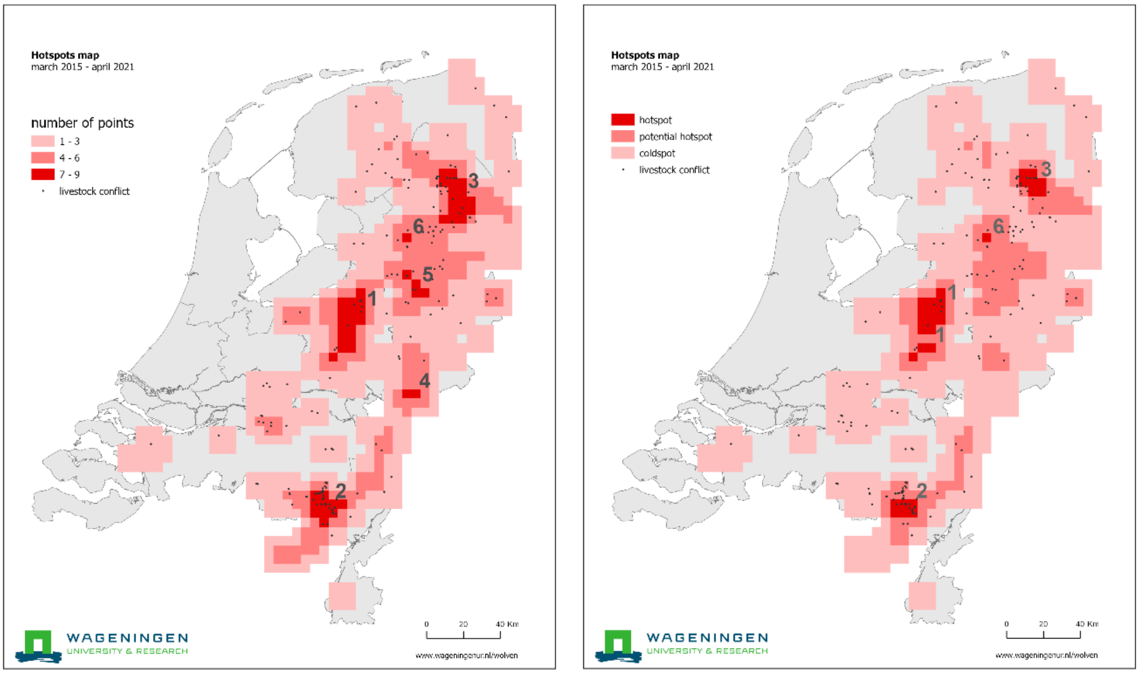

Figure 5.4.4 *Locations where livestock was lost to wolves over the period March 2015-April 2021, plotted onto the map of hotspots based on scenario 1 (left) and scenario 2 (right).*

In the Veluwe area, where wolves have now settled, the number of cases of lost livestock is relatively low. Research into the possible causes of this has not yet been initiated. One hypothesis is that wolves in the Veluwe area are able to obtain sufficient wild ungulates or other prey, but that this is not the case in other areas with settled wolves – the Groote Heide area and central Drenthe – where more frequent losses have been reported; also see section 4.6. A review of 119 articles on the diet of wolves by Janeiro-Ottero et al. (2020) found that wolves eat mainly wild ungulates where these are available in sufficient numbers, even if farm livestock is present in higher densities than wild ungulates. This applies mainly to the Central European and North American populations of wolves. In areas where wild prey is more scarce, such as in Greece, Italy and the Iberian Peninsula, livestock is the main prey of wolves. The way in which that livestock is kept also plays a role here. Wolves are less attracted to larger livestock such as cattle than to smaller livestock like sheep and goats. Smaller groups of livestock are more popular than larger ones, probably because they exhibit less antipredator behaviour. And finally, unprotected livestock is taken more often than protected livestock. A second hypothesis is that there are differences between individuals based on the behaviours prevalent in the pack in which they were born and raised (see sections 6.1 and 6.2). Van Liere et al. (2021) found an association between the behaviour of young wolves with respect to their use of areas with more human activity and the predation of livestock and the prevalent behaviours in the pack that they were born into. They suggest that wolves that are raised in packs that prey mainly on livestock will grow up to do the same themselves. This conclusion can be called into question, however, because in at least some cases it has been possible to show that the attacks on sheep studied by Van Liere et al. were not actually carried out by the pack in question (I. Reinhardt, LUPUS, personal communication). Research into wolves' use of terrain and dietary preferences in combination with parentage analysis in the various areas where wolves are settling in the Netherlands could shed more light on this.

Recommendations

- Describe in detail which (policy) decisions you wish to make using a map showing 'hotspots' or 'corridors'. What is the goal of such a map? What should the map be used for? On the basis of these goals, define what should constitute a hotspot or corridor and what should not. This should include not only the choice of variables to be included in the definition, but also the choice of the standard to be used, i.e. the chosen threshold value for each variable used to determine whether a particular area is classified as a hotspot or not.
- Design a research programme to obtain more systematic information on the distribution of wolves and wolf activity and use this as input for the future mapping of hotspots and corridors. Focus

specifically on movements and the use of terrain by both roaming and settled wolves – for example by fitting (young) wolves in various packs with a transponder tag.

- Design a research programme to gain a better understanding of the dietary preferences of both roaming and settled wolves – by analysing wolves' droppings, for example. Ideally, this would involve several different locations in the country, so that any differences between regions – such as differences in the composition and number of prey – can be identified.

5.5 The function of the Netherlands for wolves

In recent years, for wolves the Netherlands has mainly been an area that they have passed through. Not many have settled so far, and settlement has mainly been confined to solitary wolves settling and breeding in the Veluwe area. The Netherlands' limited population of wolves currently remains in the recolonisation phase, and the number of settled wolves remains small. Wolves in the Netherlands are part of a much larger cross-border population group with which there is regular exchange. It is impossible to predict whether a balance between mortality and reproduction will be achieved in the Netherlands, whether the wolf population of the Netherlands will remain dependent on the wolves coming in from neighbouring countries, or whether it will be a source of new individuals for the wolf populations of other countries. What is certain is that the regular exchange of wolves across international borders will continue. The Netherlands' wolf population will continue to be a small part of a much larger population that spans multiple national boundaries.

Detailed analysis

With the expansion of the wolf population in Germany, ever more wolves have been appearing in the Netherlands since 2015, and the annual number of sightings is also increasing (Table 5.5.1).

Table 5.5.1 *Number of verified sightings of wolves in the Netherlands and the minimum number of individuals identified based on DNA analysis for the years 2015 to 2020.*

	Number of observations	Number of individuals
2015	6	1
2016	2	1
2017	5	3
2018	78	2
2019	162	5
2020	437	10

Most wolves present in the Netherlands are roaming animals that may stay in the Netherlands for a shorter or longer period of time. By far the majority of wolves observed in the Netherlands (13 out of 22, see section 5.1) pass through the Netherlands fairly briefly without settling. Roaming wolves can travel great distances. One example of this is wolf GW1554m (Billy), which passed through the Netherlands from Germany in the period from 18 April to 1 June 2020 and later appeared in the French region of Vosges, having passed through Belgium, Luxembourg and along the German-Luxembourg border. The animal was finally shot dead in France in September 2020 (also see section 4.6 for a map showing observations). Another example is the tagged wolf Naya (GW680f), which left Mecklenburg-Vorpommern (Germany), the area she was born, in October 2017, and then passed through the Netherlands in December 2018 before reappearing in Belgium in January 2019, having covered at least 1,238 kilometres (Jansman et al., in prep.). She settled in a military training area near Hechtel-Eksel, where she found a mate and started her own pack in 2019.

Of the 28 wolves observed in the Netherlands before November 2020 (see Figure 5.1.3), seven (25%) are still in the country, eight (29%) have left the country and four (14%) were killed in a fatal accident in the Netherlands (a fifth wolf was killed in May 2021). The first wolf to settle in the Netherlands was GW998f in the North Veluwe area, in July 2018. In January 2019, she was joined by GW893m and together they formed the first pack in the Netherlands. Other wolves settled in the

Central Veluwe area from August 2018 (GW960f) and in the Groote Heide area (GW1625m) from March 2020. GW1261m had appeared to settle in Drenthe from November 2019, but eventually moved into German territory after July 2020, where the animal was later observed several times through DNA testing.

To date, reproduction in the Netherlands has only been observed in the North Veluwe pack. In addition to observations made with cameras, the resulting offspring were also identified using DNA analysis in 2019-20. Of those offspring, GW1729f has settled in the South Veluwe area since June 2020. She was killed by a car in 2021 and was found to be pregnant. Her partner was later found within the territory. Another offspring from the North Veluwe pack (GW1626m) was killed by a car near Epe in March 2020. In January 2020, eight wolves were observed in the North Veluwe pack, likely including four pups born in 2020 and two yearlings born in 2019 (WIN 2021).

Sections 5.10 and 5.11 explain why the Netherlands cannot be home to an independently viable population of wolves. Wolves in the Netherlands will always have to be part of a cross-border (meta) population in order to be sustainable. At present, the Netherlands mainly fulfils the role of a habitat that is available for recolonisation by wolves. With the increase in numbers and the distribution area of the Central European and Alpine populations, it is likely that ever more roaming wolves will visit the Netherlands. Depending on whether these roaming wolves manage to find a territory of their own and survive, they may settle in Dutch territory or move on elsewhere. Young wolves born in the Netherlands may choose to search for a territory in the Netherlands or to migrate elsewhere in the process. Important factors include the availability of a suitable territory and mortality rates. If a suitable territory is available, this will provide roaming wolves with the opportunity to establish a territory. However, once all the most suitable areas in the Netherlands have been occupied, it will become more difficult for wolves to establish territories of their own. Competition between wolves for territory, food and mates could then lead to more victims. The roaming phase is also a high-risk phase in the wolf’s life. It occurs after they leave the parental pack and have to fend for themselves. They also have to traverse unfamiliar areas, where they may encounter many new and potentially dangerous situations, such as traffic and the territories of other wolves, which they defend aggressively against intruders.

Sooner or later a growing population will reach its ecological carrying capacity: the point at which the number of animals reaches a more or less equilibrium. Mortality, reproduction and migration rates are in balance. Within the population, there may be regions where net reproduction is higher than net mortality. Equally, there may be regions where net mortality is higher than the rate of reproduction. We refer to the former situation as a source population. Young animals will often emigrate away from a source population to establish their own territory. We refer to the latter situation as a sink population. A relatively higher number of animals will need to join a sink population to compensate for the higher mortality rate (Fuller et al., 2003). Wolves in the Veluwe area currently represent a source population. More wolves are being born there than are dying, and wolves are moving into the Veluwe area from other areas.

As explained in sections 5.10 and 5.11, a viable population of wolves needs to include approximately 1,000 packs. Section 5.6 describes the carrying capacity for the Netherlands. Based on model analyses dating from 2012, the Netherlands could provide a suitable habitat for around 16 to 89 packs. Based on those numbers, the wolf population of the Netherlands could amount to around 1.6 to 8.9% of a larger cross-border population of wolves.

5.6 The ecological carrying capacity of the Netherlands for wolves

Because only limited information is available regarding the wolves living in the Netherlands, specifically with respect to their use of habitat and the size of their territories, it is not currently possible to draw any firm conclusions regarding the Netherlands' ecological carrying capacity for wolves. Two model studies dating from 2012 provide an approximate initial indication of the suitability of the Netherlands as a habitat for wolves, producing an estimate of between 16 and 89 packs. However, these estimates were not based on data on wolves that actually live in the Netherlands. Research into choice of habitat and territory size is required in order to determine the ecological carrying capacity more accurately.

Detailed analysis

5.6.1 Ecological carrying capacity

Ecological carrying capacity can be defined as the maximum population size of a species based on the food supply as well as other limited natural resources that are naturally available. In other words, the term refers to the maximum number of individuals of a particular species that can live in a given area. The carrying capacity of a given area is determined primarily by the size and quality of the habitat for the species concerned (Groot Bruinderink et al., 1999). For example, the carrying capacity of an area that has an abundant supply of food is higher than that of an area of a comparable size where less food is available. For wolves, the carrying capacity of an area is determined by factors such as (1) the presence of prey, especially ungulates, (2) the presence of parasites and pathogens, (3) the presence of other large predators which compete with wolves for food and space or leave uneaten prey behind, or which predate young wolves (such as lynxes), and (4) climatic conditions (including the amount of precipitation, temperature, snowfall and snow thickness) (Kramer et al., 2017). Under natural conditions – i.e. in the absence of population management – carrying capacity will remain more or less stable over time. Population sizes can, however, rise slightly in favourable years and fall back again as a result of disease, competition or food scarcity. In Central Europe, some of these factors are influenced or determined by humans, such as prey density and anthropogenic mortality through the hunting of either ungulates or wolves. Climate – and climatic change – is another factor that plays a role in determining the carrying capacity of an area.

5.6.2 Analysing habitat suitability

Wolves' habitat preferences are explained in more detail in Section 4.5. Following one German study into carrying capacity, the researchers concluded that wolves are such generalists that they can find a niche in many different types of landscape (Kramer-Schadt et al., 2020). It is difficult to predict the consequence of this in the Netherlands. An important factor here is not only how many wolves the ecosystem can handle (ecological carrying capacity), but also how many wolves, along with all their activity, society (i.e. public opinion) can accept. Human factors are very important in a densely populated country such as the Netherlands, and the impact is difficult to estimate in advance. In addition, public opinion can change faster than the ecological carrying capacity – as a result of an increase in the number of conflicts between humans and wolves, for example.

5.6.2.1 The Netherlands

In the Netherlands, two analyses have been carried out into how suitable Dutch territory is as a habitat for wolves (i.e. its carrying capacity). Potiek et al. (2012) carried out an analysis of carrying capacity and population dynamics in order to establish the potential for wolves in the Netherlands. The effects of fragmentation (and wildlife crossings) and climate on carrying capacity were also studied. The researchers concluded that the carrying capacity is determined in large part by the fragmentation of the landscape due to the increased risk of vehicle strikes. Climatic change is less important than fragmentation, as a factor. Climate change is actually beneficial for wolves, because the density of ungulates is likely to increase as a result of a more plentiful supply of acorns and beechnuts and fewer deaths in winter. If wildlife crossings are taken into account in the model, reducing the risk of traffic fatalities, the estimated carrying capacity is a maximum of 438 wolves. This maximum number could only be achieved if defragmentation measures were taken at traffic routes, however. The maximum number of wolves in the model ranges between 338 and 443 wolves, depending on different scenarios. This basically amounts to between 68 and 89 packs, with an average of five wolves per pack. Lelieveld (2012) carried out a habitat suitability analysis based on habitat, population density, road network and prey in particular. He concluded that there is space in the Netherlands for at least 16 packs (mainly in the Veluwe area and in the northeast of the Netherlands), but that given the adaptability of wolves, this should be viewed primarily as an indication of where wolves may choose to settle initially. However, none of these models takes account of wolves migrating to and from neighbouring regions.

Figure 5.6.1 shows Lelieveld's habitat suitability analysis (2012). 'Prime areas' are areas that are suitable for wolves, according to the model. The model inputs for this were a human population density of less than 10 per km^2, less than 400 metres of road, at least 25kg of biomass in prey and an area that is not covered by water or built-up. Based on the maximum distance that wolves travel outside their home range, an analysis was applied that shows the distance to the suitable (prime) area, with ranges between <1 km and >10 km (also see the key to the figure). Two different scenarios were then developed in more detail. Scenario 1 (B in the figure) was based on the assumption of territories of 225km^2 in suitable or prime area, with a range of 1 kilometre. Scenario 2 (C) was the same, but with a range of 2 kilometres. Figure 5.6.3 shows that with a range of 1km (B in the figure), the Veluwe area and large swathes of the north-eastern Netherlands are suitable for wolves. If a slightly more flexible criterion is used (range of 2km instead of 1km; C in the figure), the model indicates that in addition to the Veluwe area and almost the whole of the north-eastern Netherlands, large parts of Flevoland, the Utrechtse Heuvelrug, the Maasduinen and the east of Noord-Brabant are suitable areas for wolves to establish a territory.

5.6.2.2 Germany

Based on the availability of food and habitat preferences in particular, models have also been created to find out how much space there could be for wolves in Germany. The most recent study of this kind was carried out by Kramer-Schadt et al. (2020) (see Figure 5.6.2).

Using data from tagged wolves, the model was calculated based on a territorial area of at least 200km^2. Prey density in Germany is not the same everywhere, but the figures for game hunting are high compared to other European countries. The authors therefore assumed that prey density is not an obstacle for wolves in Germany. Several scenarios were calculated in the model. The results were also compared with previous analyses of habitat suitability (Fechter & Storch, 2014). Finally, confirmed distribution data was also added to the model analyses to find out whether the model corresponds to practice (Figure 5.6.2).

The study estimated the number of potential wolf territories in Germany to be 700-1,400. The study concludes that large swathes of Germany are clearly suitable as habitat for wolves. Even habitats that consist mainly of an agricultural landscape, but which also include some safe daytime resting areas, are suited to wolves. In terms of managing those wolves, the researchers state that both roaming wolves and settled wolves should be expected in these areas, and that effective protections for livestock are therefore recommended. This research also looked at other habitat analyses. Human influences – including agriculture, road density and human population density – were found to have a negative effect on wolves in all studies. Variables such as forested areas and prey density were particularly associated with the presence of more wolves.

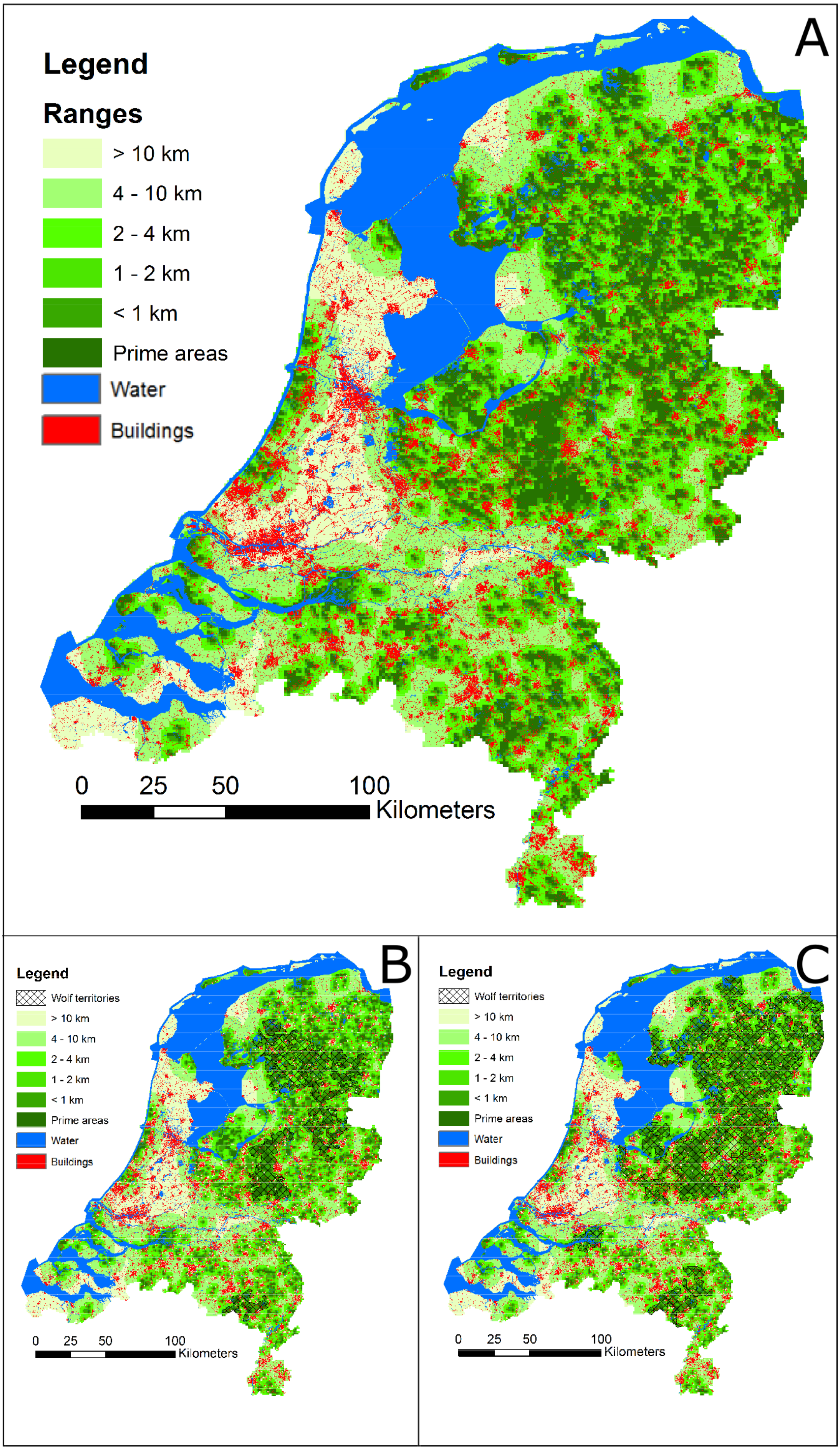

Figure 5.6.1 *Habitat suitability analysis of the Netherlands (A), including the distribution of potential wolf territories in accordance with two model calculations (B & C; see main text for explanation). Source: Lelieveld 2012.*

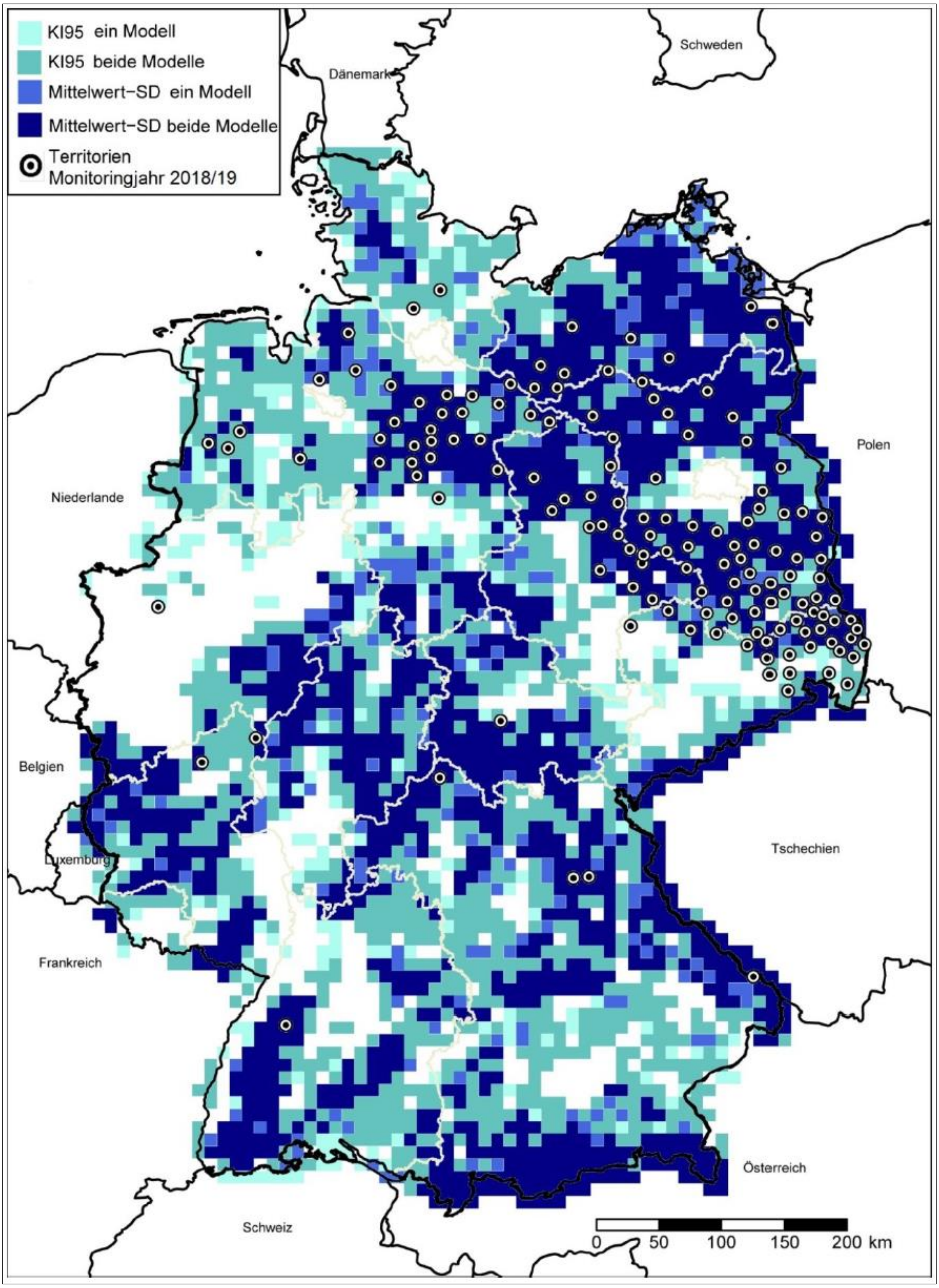

Figure 5.6.2 *Habitat suitability analysis of Germany, showing territories of established wolves in the year 2018-2019 plotted as dots. Overall, dark blue indicates the best habitats for wolves, as determined by the model. In north-eastern Germany, the best habitat for wolves corresponds closely with where wolves currently occur (shown by the circles). Source: Kramer-Schadt et al., 2020.*

5.6.2.3 Wallonia

A habitat suitability analysis has also been performed for Wallonia (Figure 5.6.3; Crismer, 2018; Schockert et al., 2020). The research suggests that there is room for around 18 wolf territories.

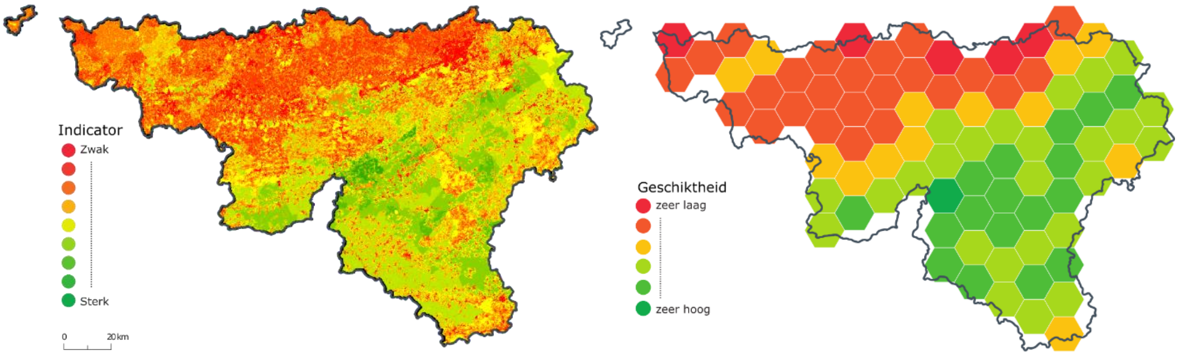

Figure 5.6.3 *Habitat suitability according to Crismer (2018), at the cellular level (left) and at the level of hexagons of 200km^2. The darker green hexagons suggest that there is room for about 18 territories.*

5.6.3 Recommendations regarding the ecological carrying capacity in the Netherlands

In order to estimate the ecological carrying capacity for wolves in the Netherlands accurately, data is required regarding the various factors that determine that carrying capacity, such as wolves' preference for certain habitat types and the size of their home ranges in the context of the Netherlands. Ideally, the method of Kramer-Schadt et al. (2020) would be applied, whereby assumptions are tested using a statistically valid carrying capacity model based on the actual occurrence of wolves. In order to validate the model inputs, sufficient tag data would be required. This could be used to determine habitat use and the size of territories. In theory, this could be used to draw reasonably reliable conclusions regarding potentially suitable habitat types and the associated carrying capacity. For the current German population, Kramer-Schadt et al. (2020) conclude that this is not (yet) possible, because tag data from German wolves does not cover all types of habitat and extrapolating from their current model would involve significant uncertainties. (Also see section 5.7 for additional information on this subject.)

In order to study carrying capacity in the Netherlands properly, then, it would be necessary to conduct research into wolves' use of terrain in the Netherlands, preferably based on tag data.

5.7 Forecasting the numbers of wolves in the Netherlands and their distribution

It is currently not possible to forecast the numbers of wolves in the Netherlands, either over time or in terms of their geographic location. The data required to do so with a reasonable degree of accuracy is not currently available. The rate of population growth among wolves is in the approximate range of 25-35% per annum at present. If we assume that the Netherlands could support 16-89 packs, that number could be reached within 8 to 18 years. Wolves could, in principle, settle temporarily or permanently in almost every type of landscape in the Netherlands. However, they prefer areas that have large swathes of natural habitat, with enough areas for them to rest (see section 5.9). Human tolerance plays an important role here, and this factor is difficult to predict.

5.7.1 Suitable habitat types and expected population trends

Wolves have a strong preference for wild areas such as nature reserves with approximately 40-50% forest cover, where they can find sufficient prey and resting places. The more roads there are in an area, the less attractive it is to wolves. All other types of habitat, including farmland that is used intensively by humans, will also be used by wolves, albeit mainly to move from one wild area to another wild area, mainly at night. See sections 5.6, 5.9 and 4.5.

In the Netherlands, wolves have not been around for long enough and are not well established enough to estimate rates of population growth. One option that is currently available in order to predict broad population trends is to look at the population growth rates observed in Germany. Simple extrapolation to the Dutch context is not a reliable method, because mortality factors vary (e.g. traffic accidents, legal or illegal hunting, disease, food supply), litter size and carrying capacity can also differ (food supply) and it is also unclear how much emigration and immigration is to be expected. In addition, the early colonisation phase is unpredictable, and wolves could easily disappear from the Netherlands once again, after which recolonisation from neighbouring countries may occur once again. Population growth can be strongly influenced by demographic stochasticity (random processes relating to birth and death rates). Demographic trends in larger populations are determined by averages, while in small populations they are determined by the fate of individuals. For example, if there are two pairs but both females are killed by vehicle strikes, this can spell the end for that particular population.

In Germany, the net population increase is approximately 28%/year (packs, established pairs, established solitary wolves (Reinhardt et al., 2020), after an initial growth rate of approximately 36% in the period 2000-2015 (Reinhardt et al., 2019); https://www.wolfsmonitoring.com/monitoring/verbreitung/; retrieved 14 June 2021; Figure 5.7.1). Population growth varies considerably between federal states and appears to be levelling off somewhat in Germany as a whole, possibly because most suitable areas have now been occupied. In the US, population growth is approximately 25%/year (Wielgus & Peebles, 2014).

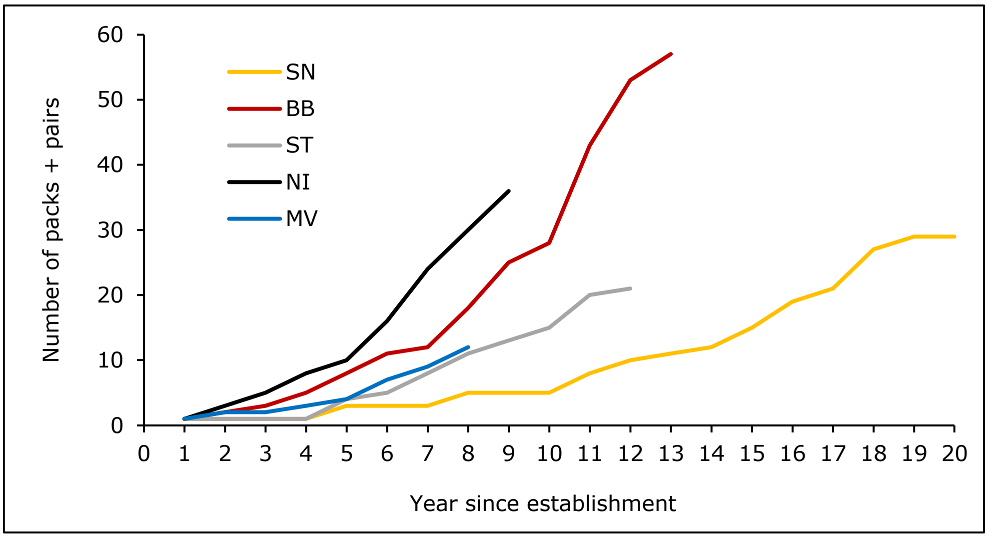

Figure 5.7.1 *Population trends in certain German federal states. SN: Saxony; BB: Brandenburg; ST: Saxony-Anhalt; NI: Lower Saxony; MV: Mecklenburg-Vorpommern (Source: Reinhardt et al., 2021).*

Based on the approximate estimate provided in the studies by Lelieveld (2012) and Potiek et al. (2012) (see section 5.6), the ecological carrying capacity could be reached at approximately 16 and 89 territories, respectively, and in theory these numbers could be reached in the Netherlands at the growth rates mentioned above within 8 to 18 years.

A more reliable forecast of population trends in wolves in the Netherlands is possible using a dynamic population model. However, the data required to do this is currently missing. A good option for visualising the viability and population trend in a wolf population is to carry out a population viability analysis (PVA). A PVA is a form of risk analysis that estimates the probability that a population will survive over a period of a randomly chosen number of years, given certain characteristics of the species, a given habitat carrying capacity and a given population size (Boyce, 1992). The PVA requires input data relating to the chance of spontaneous settlement, emigration and the suitability and carrying capacity of the habitat. Given that the wolf population in the Netherlands will be part of a cross-border (meta)population, adequate data is also required regarding wolf populations in neighbouring countries. In order to make a forecast, data is also required regarding growth, mortality and migration in various age groups, including the variation in those parameters over the years (Reed et al., 2003). This data is currently unavailable for the wolf populations of the Netherlands and neighbouring countries. A spatially explicit model that predicts numbers and distribution would go one step further still, but at present this is impossible (also see sections 5.6 and 5.9).

5.7.2 Wolf behaviour and adaptability in areas populated by humans

Wolves are intelligent, adaptable animals that are able to survive in many different habitats (Reinhardt et al., 2019; Drenthen, 2020). Following one German study into carrying capacity, the researchers concluded that wolves are such generalists that they can find a niche in many different types of landscape (Kramer-Schadt et al., 2020). Section 6.1 explains that in the Netherlands, which is densely populated by humans, wolves that are tolerant of human activity are more likely to settle. By the same token, it may also be desirable for humans to adapt to the return of wolves to our landscape. There are various perspectives on this question (also see section 4.7). Drenthen (2020) indicates that in the landscape of the Netherlands, there will always be an overlap between wolves' territories and areas inhabited or used by humans. According to Drenthen, we should ask ourselves 'to what extent are we really prepared to make way for species other than wolves.' Drenthen takes the view that: *'If farmers take a consistent approach to protecting their sheep, so that wolves have to make a lot more effort and take more risks in order to prey on them, wolves will lose interest in doing that and will modify their behaviour – provided, of course, that there is enough wild prey to hunt. Experience elsewhere shows that after a few generations, young wolves pick up the culture of the adult wolves, and they will ignore livestock too. It should be noted, however, that young wolves, just like human adolescents, like to experiment and may be tempted to take sheep if an easy opportunity presents itself. It is important that young wolves learn, whether from their parents or from us, that it is easier and safer to hunt wild prey and to leave the sheep alone behind their fence. One way to do this is to ensure that any attempt to approach or attack sheep results in an unpleasant experience, such as an electric shock. Fences and other means of protection should be seen as a means of communicating with wolves that can help avoid conflicts between humans and wildlife as they live in parallel worlds, but share the same landscape.'* Drenthen argues, then, that wolves can be conditioned reasonably well to leave livestock alone. This is supported by the fact that there is not necessarily any direct relationship between wolf numbers and incidents involving livestock (*Managementplan für den wolf in Sachsen*, 2009). We know from Lower Saxony that while the number of wolves has risen, the number of incidents involving farm animals actually fell in 2019-2020, almost certainly as a result of measures taken to protect livestock (https://www.wolfsmonitoring.com/nutztierrisse?). The role of humans is less predictable and is therefore rarely included in any carrying capacity models (Mech, 2017). It is difficult to predict how public opinion with respect to wolves may evolve. We cannot assume that the ecological carrying capacity will be reached, and we should expect the societal carrying capacity (i.e. public opinion) to play a role here too (section 5.6). If there are more frequent conflicts between wolves and humans due to the predation of livestock and confrontations with humans, local people's tolerance may decrease rapidly. Illegal persecution may then prevent wolves from recolonising suitable habitats (Mech, 2017).

5.8 The average size of a wolf territory in the Netherlands

The average size of a territory in neighbouring countries is around 200km^2 (ranging between 80 and 400km^2), depending on how many daytime resting places there are, ungulate population density, competition and the social status of the wolves. A pack needs slightly more space than a solitary animal and a territory in a saturated region will be smaller than one in an empty region due to competition between packs. In a cultivated landscape that features smaller areas of natural habitat surrounded by larger areas of agricultural land and residential areas, the size of the territory may be considerably larger. This is because the territory then includes large areas of terrain that is less suitable or unsuitable, with those areas mainly being used by the wolves to move from one suitable habitat to another within the territory.

Detailed analysis

The area in which a wolf is active depends on many factors (Mech & Boitani., 2003; Groot Bruinderink et al., 2012). The size of wolf territories varies as a function of the availability of prey, population density, time of year, geographical location and land use (Jedrzejewski et al., 2007; Myslajek et al., 2018). Wolves are highly territorial, claiming and defending an area that is large enough to feed a pack without overhunting the local populations of prey (Mech et al., 2015). When there is an abundant supply of food (high density of ungulates), territories may be smaller than in areas where food is more scarce. The number of settled animals also affects territory size. A solitary wolf or pair of wolves will need a smaller hunting ground than a pack. The presence of adjacent territories will lead to a clearer demarcation of boundaries and smaller intermediate zones between territories. Although territories cannot always be reduced in size, increased competition can lead to slightly smaller territories and also to different marking behaviour. Where there is no adjacent territory and no competition, territories may be larger, and the boundaries less clearly demarcated. Territorial boundaries are not fixed permanently, and may shift over the year as a result of factors such as population changes, the passing of the seasons, ungulate migration, and so on. The method used to determine the size of territories is also important. Territories can be determined through studies using tags or by analysing DNA from the droppings that wolves use to mark their territories. For wolves in the Netherlands, territory size can currently only be determined by genetically testing droppings that are found.

We have little precise knowledge about marking behaviours in relation to territorial boundaries, especially in isolated individual situations where there are no neighbouring packs. Zub et al. (2003) examined urine marking in tagged wolves. Most marking occurred inside the main area (the most intensively utilised part of the territory) and at the boundaries of the territory. Markers were not evenly spaced, but concentrated in areas that might be vulnerable to intrusion by neighbouring packs and around locations where the wolves gave birth. Barja et al. (2005) investigated the marking behaviour of a newly established wolf pair during the first five months. The greatest chance of finding droppings was around the wolves' den and on the path leading to it (16 and 4 droppings/km transect, respectively); the lowest probability was at the edge of the territory (0.01/km transect). The droppings were randomly deposited around the den site, while at the edges of the territory the same spots were marked repeatedly. The starting point for the territory size to be applied was the 100% MCP (minimum convex polygon; also see section 5.4). MCP is the maximum territory size: this is a method whereby the smallest polygon encloses all points, with no internal angles. This almost certainly includes areas that are not used. Another commonly used method is the 95% MCP, in which extreme locations are excluded; however, this can lead to an underestimate of the total area.

In Germany, 200km^2 is accepted as the average size of a wolf territory (Fechter & Storch, 2014; Kramer-Schadt et al., 2020). Whether this also applies in landscapes that are used intensively by humans remains to be seen. A territory of 400km^2 has been calculated for the pack that has settled in Flanders (Van den Berge & Gouwy, 2021). It is illustrative to describe changes in the size of this territory in more detail.

Initially, data from the tagged and settled wolf Naya (while the tag was still working) shows that she was active mainly over a smaller area of about 10km^2. This gradually expanded to around 200km^2. When Naya found a partner ('August'), the territory was enlarged systematically. Now the pack currently uses a vast area of territory. But it is difficult to make direct comparisons as no tag data is available (Naya's tag stopped working after six months). Naya is no longer alive but her place has been taken by the female wolf Noella. Young have been born in recent years, forming a pack, and the wolves may therefore need more space to find enough food for the whole pack (see section 4.6). The current territory has been observed using all C1 and C2 observations. These come from intensive monitoring, supplemented with observations from third parties. Using monitoring data, it has been found that the area of the territory is approximately 400km^2, but this does not include outliers (the extreme observation locations). Essentially, that 400km^2 is the MCP95%. The larger-than-average size of this territory could be explained by the presence of large residential areas, industrial areas and other areas of unsuitable habitat, as well as by intensive human activity in the area. This means that much of the territory is used mainly to move from one area to another. Interestingly, more livestock is being taken in those areas. The fact that there are no neighbouring packs will also play a role. The principle of a larger territory, within which wolves move between smaller areas of the most suitable habitat, is familiar in parts of Germany, too. The average territory size of 200km^2 in Germany is based on Lusatia – a sparsely populated region in the east with large contiguous areas of habitat that is suitable for wolves.

Ilka Reinhardt mentions that these cover 200km^2 (MCP95) or around 300km^2 (MCP100). In Lusatia, territories range between 80km^2 and 300km^2 (MCP95). Territories may decrease in size slightly as more wolf packs settle in a given area. The 200km^2 MCP95 did not change substantially between 2009 and 2021. Ilka Reinhardt also indicates that she expects territories in rural areas to be larger because less natural habitat is available; however, exceptions are possible due to the adaptability of wolves. Where prey density is higher, territories may be smaller than 200km^2. In summary, wolf territories in the Netherlands are also expected to range between 80 and 400km^2, with an average size of 200km^2.

Within the Netherlands it is possible to make a reasonable estimate of the number of packs that could become established in the Veluwe area. The Veluwe area consists of approximately 1000km^2 of more or less continuous forest. With an average territory size of 200km^2, this would provide room for around five packs. If ungulate density is very high in certain areas, and/or there are more daytime resting areas, that number could be somewhat higher, as long as some of the packs could manage with a smaller territory. Outside the Veluwe area, the number of packs that could become established is less easy to predict because of the smaller and more fragmented scale of wild areas (see also section 5.9).

5.9 Long-term colonisation of habitats in the Netherlands

Wolf territories that are home to breeding pairs need to contain a high percentage of forested area and provide sufficient food. Road density (traffic hazard) and human activity (disturbance and illegal hunting) also play a major role. The larger forested areas in the Netherlands, particularly in the Veluwe area, are expected to be important habitats for wolves. However, wolves are habitat generalists, and the majority of the Netherlands could actually prove suitable for wolves in the future, with the exception of built-up areas and landscapes that are used intensively by humans (although wolves may pass through these areas) and the Wadden Islands (which are practically inaccessible). Any regions that have wild areas of approximately 200km^2 (the average size of a territory), with enough resting areas and a healthy population of ungulates, would be potentially suitable as wolf habitats. However, humans are the most important factor in whether wolves will actually settle in suitable habitats on a long-term basis.

Detailed analysis

Sections 4.5 and 5.6 describe which types of habitat are suitable for wolves, and we have already seen that wolves are such generalists in terms of the habitats they can live in that they are able to exist in many types of landscape. It is clear, however, that quieter, more wooded areas lead to the highest survival rates for wolves (lower risk of vehicle strikes or illegal persecution; also see sections 4.5 and 5.1). In Germany, military training areas have played a particularly important role in the recolonisation of the country by wolves because they not only provide plenty of forested areas and ungulates, but there are also few roads and little human activity (Reinhardt et al., 2019).

Figure 5.9.1 shows the larger nature reserves, as well as the many roads and large swathes of human habitation and land use. In 2019, the province of Gelderland designated a territory for the pack of GW998f x GW893m (parents) in the North Veluwe area, and adjacent to that a territory for the solitary wolf GW960f in the Central Veluwe area (viewed as one habitat; number 1 in the figure). In 2021, a territory was also designated in the Southwest Veluwe area for the (almost) settled wolf GW1490m (number 2 in the figure; also see Figure 4.2.2. and text for further explanation). In Noord-Brabant, a provisional territory has been designated for settled wolf GW1625m in the Groote Heide area, but this has not yet been defined for administrative purposes (number 3 in the figure). Wolf GW1261m also formally settled in Drenthe in October 2020, but this animal later moved into German territory. Nevertheless, the province of Drenthe has designated an official area: not a territory, but a risk area (number 4 in the figure). Grants for preventive measures are currently (July 2021) available in areas 1-4 (IPO, 2019).

When the potential habitat for wolves identified by Lelieveld 2012 (Figure 5.6.3) is compared with the current situation in terms of settled wolves and wolf activity (translated into the territories and risk areas in Figure 5.9.1), it is clear that there is a degree of similarity. Since no updated analysis of habitat suitability is available at present, Figure 5.6.3 by Lelieveld (2012) seems to be the best starting point for understanding which areas wolves are likely to use to a significant extent.

Ungulate density in the Netherlands appears to be relatively high for roe deer (almost nationwide) and red deer, fallow deer and wild boar (locally) (see also section 7.5), so that food availability would not appear to be an immediate impediment to wolf colonisation. The large expanse of forest in the Netherlands, particularly the larger military sites in the Veluwe area, is expected to provide a significant amount of habitat for wolves. However, wolves are habitat generalists, and the majority of the Netherlands could actually prove suitable for wolves in the future, with the exception of built-up areas and landscapes that are used intensively by humans (although wolves may pass through these areas) and the Wadden Islands (which are practically inaccessible). Noord-Holland and Zuid-Holland are expected to be too densely populated, and natural areas with cover to be too small and fragmented for it to be likely that wolves would remain there for long. One exception could be the area of dunes along the coast where there is a high density of fallow deer in certain places. Larger predators, occasionally including wolves, are also increasingly seen on the outskirts of large cities (Louv, 2019). Section 5.7 explains how public opinion is an important factor. Illegal persecution could prevent wolf-friendly areas from being colonised (Mech, 2017; Sunde et al., 2021). Humans are therefore the most important factor that determines where wolves may settle. Drenthen (2020) describes this as follows: *'Coexisting with large predators such as wolves inevitably leads to tensions and the need to keep our distance from each other, even though we inhabit the same landscape. Often we will be able to coexist peacefully, but sometimes our relationship will be more challenging.'*

Figure 5.9.1 *Basic map of the Netherlands including the official territories for wolves in the Veluwe (1 and 2), the preliminary habitat in Noord-Brabant (3*), and the wolf risk area (4) in Drenthe. *The Groote Heide area has not yet been officially designated as a territory at the time of writing. It is expected to be formally designated and established by the province of Noord-Brabant in the autumn of 2021.*

5.10 Favourable conservation status for European wolf populations

The European Habitats Directive and the Bern Convention aim to bring about favourable conservation status for wolves, in the sense of ensuring basic protection for the species rather than achieving a target population. Each member state can interpret what constitutes favourable conservation status for itself, and is also responsible for achieving that status. For species with populations that straddle national boundaries, this effectively requires a coordinated approach between member states to share responsibilities and align their objectives.

Several complementary criteria can be used to define favourable conservation status. One of the clearest and most objective criteria (but not the only one) is the population size that is required to maintain genetic diversity. Isolated populations consisting of more than 1,000 packs are not endangered, according to international criteria. But currently, neither the Central European population (about 300 packs) nor the Alpine populations come close to meeting this criterion. If the various European populations continue to grow and there is regular genetic exchange, it will be easier to meet the criterion for preserving genetic diversity. However, this has no impact on other criteria.

The creation of new barriers to migration, such as long fences intended to limit contact between wild boars and domestic pigs within national borders, could have a negative impact on the conservation status of wolves.

Detailed analysis

Favourable conservation status can be interpreted as a situation in which a population of wild animals has a low marginal probability of extinction over a 100-year period based on its population size, the condition of its habitat and genetic diversity (Evans & Arvela, 2011). However, the way in which this is achieved in practice is left entirely to EU member states to decide. Reinhardt et al. (2016) see favourable conservation status as depending not only on the number of wolves, but also on their distribution and their access to suitable habitat, so that they can also find their own niche within the ecosystem.

Some commonly used abbreviations and terms:

FCS = favourable conservation status

FRR = favourable reference range (favourable status of the area in which the species is distributed)

FRP = favourable reference population (favourable status of the number of individuals in a population)

MVP = minimum viable population

PVA = population viability analysis

HD = Habitats Directive (European legislation on species conservation)

Ne = effective population size (the part of the population that contributes to reproduction)

One of the criteria that needs to be met with respect to favourable conservation status is maintaining genetic diversity. A minimum effective (‘genetic’) population size (Ne) of 500 individuals is recommended for an isolated population (for an overview of the literature, see Hoban et al. (2020)). The effective size of a population takes account of the fact that not every individual contributes equally to the next generation, and so genetic diversity will diminish more quickly than would be predicted based solely on the number of mature individuals. In wolves, this genetic population size is approximately four times smaller (Forslund et al., 2009), meaning that the minimum size of an isolated sustainable wolf population should actually be 2,000 adult wolves. Because wolves only reach adulthood at two years of age and packs usually consist of one adult pair, yearlings from the previous year and pups from the current year, this translates into approximately 1,000 packs. By comparison, the average pack size in Europe is five wolves, including non-adults.

The Central European wolf population is currently, 2021, made up of around 125-130 packs in Germany, 3 in Benelux, 1 in Denmark, 1 in Austria, around 10 in the Czech Republic and another 150 in western Poland. This is a total of around 300 packs, which is still a long way off the genetic threshold of 1,000 packs. However, favourable conservation status (FRP/FCS) encompasses more than just the preservation of genetic diversity. It also includes the geographical distribution of the species, for example (Favourable Reference Range (FRR); Evans & Arvela, 2011).

These genetic criteria (NE>500, number of packs>1,000) would apply to a completely isolated population. But when multiple subpopulations are functionally linked to one another (i.e. more than one effective migrant is exchanged per generation), these subpopulations can be counted as one because they behave like one genetic metapopulation for the purposes of genetic sustainability goals (Spieth, 1974; Hössjer et al., 2015).

Currently, the Central European population remains functionally isolated from other subpopulations of wolves in Europe. At present, there is no regular exchange with the Alpine population (France, Northern Italy, Switzerland): there has been one instance of reproduction in the last ten years in Germany. No further mixing has occurred (DBBW 2016), so that case should still be considered isolated. Exchange with the Carpathian population (south-eastern Poland, Slovakia) and the Baltic population (eastern Poland) is also very sporadic (Szewczyck et al., 2021). The Central European population should therefore be regarded as largely isolated, and so the goal should be at least 1,000 packs in the Central European region.

If the various European subpopulations continue to grow, so will the likelihood that they will become more closely linked to one another genetically, and form a metapopulation that consists of several large subpopulations. It is interesting to note that Ilka Reinhardt mentioned concrete plans to reinforce the fence along Poland’s border with Germany (from a single fence to a double fence) in order to prevent the spread of African Swine Fever (ASF) in migrating wild boars. Although the fence is unlikely to be an insurmountable obstacle to wolves, it probably will restrict their movement to some extent. If the fence is indeed reinforced and animals from the West-Polish area are less able to mix with those in the German area, this would divide the Central European population somewhat and the population would therefore also become more isolated from neighbouring countries in Eastern Europe.

Simulations based on wolves’ actual use of their habitat show that in Germany alone there is enough capacity in ecological terms (coverage, supply of prey) to support 700 to 1,400 packs (Kramer-Schadt et al., 2020). The population there has been increasing by about 25% every year since 2000. If the growth curve is a logistic (S-shaped) curve with an r value of 1.3, the maximum number of packs (1,100-1,400) can be expected to be reached between 2040 and 2050. By then, favourable conservation status should certainly have been achieved in terms of genetic criteria. With respect to the ecological criteria, Reinhardt et al. (2016) report that favourable status will be achieved when wolves occur within the appropriate reference area (based on what we now consider to be favourable habitat for wolves).

As for the Alpine population, it can be argued that this is functionally linked to the rest of the Italian population. Mech et al. (2016) report an effective number of migrants between the Alpine and Apennine populations of 2.6 migrants per generation, which is sufficient to classify these two populations as one linked metapopulation (one effective migrant per generation; Mills & Allendorf, 1996). Together, the two populations have about 2,400 wolves (about 480 packs; Source: Office Française de la Biodiversité; Boitani & Salvatori, 2019). This value remains below the genetic threshold of 1,000 packs. In France, the Office Française de la Biodiversité considers 2,500 to 5,000 adult wolves as the minimum viable population size (Duchamp et al., 2017). This corresponds reasonably well to the numbers mentioned above of 1,000 packs based on purely the genetic criteria. However, this applies to an isolated population, and we do not have a clear picture of how this relates to populations in neighbouring countries.

In order to guarantee long-term viability, it is important that states set clear goals together and allocate responsibilities jointly, so that together they can achieve favourable conservation status for populations that straddle political boundaries. The principle of proportionality (‘the broadest shoulders bear the heaviest burden’) would seem the most obvious approach to doing this. It is essential to realise that when subpopulations are functionally linked, the genetic criteria for favourable conservation status can be met more easily than when populations remain isolated. This is because it is possible to add the effective size of the subpopulations together to achieve NE>500 (also see Boerema et al., 2021). European member states would therefore benefit from the amalgamation of the current subpopulations (Baltic, Central European, Alpine-Italian, Carpathian, Dinaric-Balkan populations) in spatial terms, linking them functionally, insofar as the countries where these populations are located are subject to the same strict protection of species as in the European Union. By doing this, most European subpopulations could then meet the genetic criteria for favourable conservation status even if there was only a fairly modest increase in current ranges and population sizes.

Although Norway is a signatory to the Bern Convention, which was translated into the Habitats Directive for European member states, the Norwegian Supreme Court recently issued a ruling which subordinates the strict protection of wolves to societal interests (https://www.domstol.no/globalassets/upload/hret/avgjorelser/2021/mars-2021/hr-2021-662-a.pdf). This is forcing EU member states Sweden and Finland to adopt stricter policies of their own, because they cannot count on Norway to achieve favourable conservation status jointly (see Boerema et al., 2021). However, every member state can (and must) draw up its own national objectives and policy based on other, non-genetic criteria, such as the ecosystem function of a species, and the provision of adequate habitat of sufficient quality and size in order to achieve favourable conservation status locally (see Boerema, Freriks & Van den Brink, 2021).

The importance of the Netherlands in achieving favourable conservation status at the European level must be seen in proportion to the amount of habitat that could be available for this species. In addition, the Netherlands and Belgium form an obvious link between the Central European population and the Alpine population via the Meuse and Rhine valleys. This is also clear from the genetic monitoring carried out within CEwolf, with one wolf of Alpine origin settling in the province of Noord-Brabant. Similarly, it is also expected that the Netherlands and Belgium could act as a corridor for the colonisation of France by Central European wolves, as has already been observed several times (see section 4.6).

5.11 A viable wolf population in the Netherlands

As has also become apparent in Sections 5.6 and 5.10, it is not yet possible to draw a definitive conclusion regarding the carrying capacity of the Netherlands for wolves and whether wolves in the Netherlands will always be part of a cross-border population. It takes 1,000 packs to constitute a viable population of wolves. It is unlikely that a wolf population of that size could exist in the Netherlands. For this reason, it is important that enough movement is possible between the different subpopulations of wolves in Europe, in order to maintain genetic exchange and diversity.

Detailed analysis

It is unlikely that the Netherlands could ever support a wolf population of 1,000 packs, given the estimated carrying capacity of the landscape of the Netherlands today for wolves (see sections 5.6 and 5.10). However, wolves in the Netherlands are all part of the Central European population, which means that an ‘independent’ (isolated) population in the Netherlands is not required.

More research into the genetic parameters for a metapopulation of wolves, i.e. a population that consists of several subpopulations with mutual exchange through migration, is described in Laikre et al. (2016). They investigated this for the Fennoscandinavian population of wolves. This population consists of a few subpopulations with only limited exchange between them. The Swedish-Norwegian subpopulation in particular is isolated and there is a high degree of inbreeding. The authors report that the starting point for a population or metapopulation that is viable over the long term is reached when the system-wide inbreeding coefficient remains low enough, and this corresponds to an effective population size (NE) of >500 individuals (Hoban et al., 2020). They conclude that each subpopulation must consist of at least 500 individuals and that at least 5-10 effective migrants per generation must join and reinforce a local subpopulation in order for it to maintain its genetic vitality. It is therefore important for the Dutch population that enough exchange can take place with neighbouring countries.

6 Behaviour and the relationship between wolves and humans

6.1 How wolves adapt to a human-dominated cultivated landscape

Wolves are highly versatile animals and they quickly adapt to the presence of humans in a cultivated landscape. Their adaptability means that in principle they can live anywhere where there is a good supply of prey and there are safe places to rest during the day. As long as wolves see humans as a potential threat, or top predator, they will avoid confronting them. The risk lies in habituation, which results in wolves becoming less shy of contact with humans, which is often the result of previous contact with humans. The risk of conflict (see section 6.2) can occur particularly when wolves begin to associate humans with food (positive conditioning). In addition, they can learn that inadequately protected livestock, particularly sheep, is an excellent source of food, even though sheep are nearly always found in the vicinity of humans.

Detailed analysis

The original question was 'Which behaviours in wolves, including behaviours towards humans, can be regarded as natural and which behaviours are abnormal?' This is a philosophical question rather than a purely scientific one, since it depends on the definition of 'natural'. In a conceptual framework in which humans are regarded as outside 'nature', any effect that humans have on nature must by definition give rise to an 'unnatural' situation. In this case, there is no 'nature' at all in the Netherlands, only 'cultivated nature'; and any adaptation of organisms to the cultivated landscape that humans have created would constitute an unnatural situation. A 'natural' situation could only arise through the complete absence of people: a purely hypothetical scenario. However, if we view humans as an intrinsic part of nature, any interaction between people and other species would constitute a 'natural' situation. The question would therefore be meaningless. Wolves adopt certain behaviours readily without the active involvement of people (and we could consider these 'natural' behaviours because they arise completely spontaneously); however, those same behaviours may be highly undesirable for humans. For this reason, after consulting the client, the original question has been reformulated as follows: *'Which changes in wolves' behaviour can be expected as a result of their adaptation to a cultivated landscape that is dominated by humans?'*

Inset 6.1.1 Key Behavioural Terms (LCIE 2019; Reinhardt, 2020):

Habituation is a learning process whereby an individual animal becomes accustomed to certain regular stimuli when there are no positive or negative effects for the animal. Wolves that have become habituated to humans have learned that humans pose no immediate threat and they therefore tolerate the presence of humans to some extent. The behaviour in question is not problematic provided it is not accompanied by a specific focus on humans, human infrastructure, activities or vehicles.

Strong habituation occurs when wolves tolerate humans in very close proximity (<30 m). This can easily lead to more frequent interaction with humans and positive conditioning.

Conditioning is a learning process whereby a certain type of behaviour is rewarded or punished due to a positive or negative stimulus. Example: Pavlovian conditioning. If stimulus A (sound) repeatedly precedes stimulus B (feeding), this will induce a specific response (saliva production), and stimulus A will eventually produce that response even if it is not followed by stimulus B.

Positive conditioning means reinforcing a behaviour through a positive experience associated with that behaviour. The positive experience or reward could be food, an interesting object, or some other pleasurable experience, such as play. We speak of **food conditioning** when a wolf comes to associate the presence of humans or human infrastructure with food, and therefore actively seeks out humans or human infrastructure.

Aversive conditioning (or negative conditioning) occurs when a particular behaviour is associated with a negative experience. This response can be used to prevent undesirable behaviour (in the most effective scenario) or to ‘unlearn’ positive conditioning retroactively (a much less effective scenario). This is discussed in more detail in Section 7.4.

A **close encounter** is when a wolf and a human are less than 30 metres from each other, so that the wolf can recognise the human as such (i.e. the human is not in a car or a hide).

Conspicuous behaviour refers to behaviour around humans that is outside the normal range of behaviours of most wolves. This includes unusual, undesirable or bold behaviour.

Flight distance: the distance up to which a human can approach a wolf before the animal will run away.

A **bold wolf** is a wolf that voluntarily and repeatedly tolerates humans that it can distinguish as such within 30 metres, or which repeatedly approaches people up to 30 metres. This can be dangerous for people if the situation escalates.

A **predatory attack** by a wolf is understood to mean an attack with the aim of killing and eating prey.

Neophobia refers to the fear of new or unknown things or stimuli (see Photo 7.3.1).

6.1.1 Wolves and humans

The wolf is an apex predator and is often said to have no natural enemies. However, the notion of a hierarchical food pyramid as the basis for ecological interaction is largely outdated (Stahler et al., 2020b; Estes et al., 2010). Instead, we can think of an ecosystem as being a web of countless ecological interactions. Wolves suffer from numerous pathogens and parasites, and there are also animals that will predate wolves as well as animals that may kill wolves because they pose a threat. The Eurasian lynx (*Lynx lynx*) is an important predator of wolf pups and can have a significant impact on local wolf populations (Sidorovich et al., 2018), and the brown bear (*Ursus arctos*) is another predator that wolves need to be wary of. In addition, prehistoric humans were natural predators of wolves for tens of thousands of years. Wolves had to be wary of other large predators, including humans, wherever they went.

In situations where wolves truly never come into contact with other large predators, such as in the Arctic tundra of northern Canada where the arctic wolf is found (*Canis lupus arctos*), their timidity around humans is usually rather low, but neither are they aggressive towards humans (Mech, 1989). Wolves in Europe, by contrast, have been persecuted for centuries and it is likely that natural selection has made them more wary and withdrawn, avoiding any confrontations with humans (Linnell et al., 2002). This behaviour is now seen as both ‘natural’ and desirable. However, as within any population, individual wolves vary in their character. There will always be individuals who are bolder than average and those who are more wary than average. In Yellowstone National Park, about 50% of wolves are wary and avoid humans; about 40% are tolerant of humans but keep an appropriate distance; and a small number are bold around humans, and are 'highly habituated'. It is the latter which pose the greatest risk when it comes to conflict between humans and wolves (Smith et al., 2020b).

In human-dominated cultivated landscapes, it is almost inevitable that natural selection will occur for wolves that are less wary: the more wary individuals are more likely to avoid this type of habitat, move elsewhere or fail to survive (Linnell et al., 2021). There is also variation among those wolves that are more tolerant of humans: some accept human activity but avoid humans when possible, while bolder wolves are not put off by human activity and may therefore be seen by humans at times. Bold behaviour is not problematic in itself, provided it is not accompanied by undesirable behaviours that could be regarded as problematic (see section 6.2). The landscape of Belgium and the Netherlands is, perhaps like nowhere else on earth, characterised by extensive human presence and fragmentation by roads (Jaeger et al., 2011). Wolves living in such a landscape may encounter people every day without necessarily taking flight immediately. In fact, wolves may have little choice but to largely ignore humans until they are so close that their presence is perceived as a risk. As long as wolves do not actively seek out and approach humans up close, this behaviour should be regarded as normal and low-risk. Incidentally, there are also wolves (mainly roaming and juvenile animals) that pass through residential areas, often ignoring humans and moving at a trot. This behaviour is not abnormal, and poses no intrinsic risk to humans. Nevertheless, it is essential that wolves continue to see humans as potential predators which tolerate wolves nearby to some extent.

One important component of animal behaviour is not genetically determined, but is learned and subsequently reinforced by positive or negative experiences ('behavioural conditioning'). The first year of life is when new behaviours can be acquired easily (also see sections 6.2 and 7.2) (Langenhof & Komdeur, 2018). In addition, young wolves that are learning to fend for themselves rarely make effective hunters, and this makes them more prone to experimental, atypical behaviours in an attempt to get food. This effect is probably stronger if the young animal's parents have been killed prematurely (due to a traffic accident, injury, illegal hunting, legal culling, …). It is important to prevent young wolves from associating humans with easy access to food or ceasing to view humans as a potential danger, and thus becoming positively conditioned to humans (see sections 6.2 and 7.2). After all, most recent cases of negative interactions between wolves and humans in Europe are attributable to this scenario (section 6.2; Linnell et al., 2002, 2021; Reinhardt et al., 2020; Nowak et al., 2021). Strong habituation and positive conditioning can also occur when humans deliberately seek out contact with wolves (e.g. to take photographs of them) at 'rendez-vous sites'. See section 6.2 for more information on this subject.

6.1.2 Wolves and livestock

From a wolf's perspective, livestock and wild ungulates are one and the same thing. All livestock are descended from wild ancestors who would themselves have been natural prey for wolves. There is no reason to assume that wolves would make any objective distinction between livestock and wild prey. Wolves can almost certainly distinguish between different species based on their appearance and smell. If wolves do seem to avoid livestock as prey, it is not necessarily because of the species itself, but because they often associate livestock closely with proximity to humans and will avoid them for this reason. By contrast, wolves will not avoid free-range livestock or livestock that is kept without any protection in large areas of open land or right in the heart of a wolf's territory; indeed, it will probably be viewed just like any other potential prey (Alvares et al., 2015).

In cases where wolves come to 'specialise in livestock', this should be viewed in the context of how that livestock is kept: if it is kept in proximity to humans, tolerance of human presence (habituation) will also be involved. In small-scale landscapes with highly mixed land use (such as in much of the Netherlands and Belgium), such habituation is inevitable and essential for the survival of wolves in this environment. If this occurs in a large nature reserve where there are very few humans on a permanent basis (e.g. mountainous areas with seasonal grazing, such as in the Alps), then no habituation at all may be involved. It is therefore up to humans to communicate to wolves that livestock is not appropriate prey by using direct and indirect signals (e.g. livestock protection measures) and using aversive conditioning by means of those signals (Bovenkerk & Keulartz, 2021; Drenthen, 2021).

6.2 Problematic situations involving wolves

In the human-dominated environments that we live in, there are occasional reports of wolves that seem to be displaying conspicuous behaviours. In many cases, these behaviours are not dangerous and involve people's perceptions of how wolves 'should' behave, and/or how habituated wolves are to humans and human activity. If a wolf displays boldness, such as tolerating humans less than 30 metres away, this is cause for concern. In such a case, close monitoring of the situation is appropriate, combined with information for the people concerned. In most cases this means that the wolf has become highly habituated to humans and, subsequently, developed a positive association between humans and food. A wolf that is displaying this kind of behaviour may then actively approach humans or areas where humans are present in the expectation of obtaining food. This may occur directly (being fed by people) or indirectly (feeding on food waste near buildings). If the wolf is not rewarded, it may become frustrated or aggressive and may bite. Other triggers that can result in problem behaviours are rabies and human provocation. Wolves can view dogs as social partners, mating partners or rivals. This can also lead to conflicts. For wolves, there is no immediate difference between a wild ungulate and an ungulate kept as livestock; essentially, these are both potential prey. However, the fact that livestock are usually associated with humans is one important difference.

Detailed analysis
In the Wolf Plan, the IPO subdivides the subject of 'problematic situations involving wolves' into wolf-human, wolf-dog and wolf-livestock situations (Table 1a, 1b and 1c; IPO 2019). These situations range from wolves visiting built-up areas or approaching dogs (considered as normal behaviour) to wolves reacting aggressively to people or dogs, or repeatedly attacks on livestock that are well-protected. Some of these situations may be hazardous for humans or dogs, but they are not necessarily unnatural. For a wolf to attack a dog inside its own territory is a natural response, but it is still a problem for the dog and the dog's owner. Wolves do not see a difference between a wild ungulate and an ungulate kept as livestock: predating ungulates is natural behaviour for a wolf, but the owners of the livestock involved perceive this as a problem for obvious reasons. The answer to this question is therefore based on *problematic situations*, rather than on *problematic wolves*. The answer is in part addressed in section 6.4 (wolf attacks on humans or dogs). Attacks on livestock are addressed in section 8.1 (wolves' diet) and section 6.3 (surplus killing).

6.2.1 Problematic situations involving humans

The German authorities (BfN; Bundesamt fur Naturschutz) recently produced an extensive report on bold behaviour in wolves and how it can be handled: 'How to deal with bold wolves' (Reinhardt et al., 2020). In addition to German scientists, an expert from the Swedish Wildlife Damage Institute (Viltskade Center VCS) is also involved. This institute may have the most experience when it comes to undesirable behaviour towards humans on the part of large predators. In addition to providing general information about the behaviour of wolves and behavioural change in wolves, the report also describes the various situations in which conflicts can occur, how reports can be handled and the many cases that have occurred in Germany. Some important definitions are given in inset 6.1.1. The overview below summarises the main findings of that report.

Behavioural researchers place the character of individual wolves on a scale from shy to bold (the *shyness-boldness continuum*). Character implies consistent behaviour, and in most cases a shy wolf will remain shy throughout its life. This phenomenon will be familiar to anybody who has owned a dog. Within a pack, there can therefore be differences, with some individuals being shier and others bolder. Given the intensive exposure of wolves to humans in areas where humans live, it is remarkable that bold wolves are not encountered more frequently.

Young wolves tend to run away less quickly and can therefore become accustomed to proximity to humans (and also, therefore, come to associate humans with food, for example). Wolves first develop a kind of habituation to humans. Later, a positive association with humans may arise if wolves are fed directly (being actively offered food) or indirectly (finding food close to vehicles, car parks and/or buildings) by humans. This risk is higher in young wolves. Young wolves are often left at the rendezvous site by their parents while they go hunting. If humans enter this area, the parents are not there to warn the young wolves in time. The wolf pups are inquisitive and will be curious about the humans instead of hiding away. If pups are fed by humans or taken home during this phase, they can quickly become habituated to humans and come to associate humans with food. It is when a positive association can develop between humans and food, when the risk of bites or conflicts is greatest. These wolves will, to a greater or lesser extent, actively visit humans or the human environment in the expectation of food. If they do not obtain food from humans, they may become insistent and possibly even aggressive. Similar behaviour is well known in wild boars, and also in foxes and semi-wild grazing animals living in the Netherlands. However, wolves can cause much more damage if an incident occurs. This behaviour is independent of any measures taken to manage wolves. There is no scientific evidence to support the notion that if wolf populations are managed, they are shier and therefore pose a lower risk to humans. Again, the analogy with foxes and wild boars applies. Despite intensive management of these species, there are cases of brutal and food-conditioned foxes and boars every year; in short, this behaviour can occur in all populations. Food-conditioned behaviour in wolves is difficult to change through aversive conditioning because this requires repeated exposure to negative experiences (fireworks, shots with rubber bullets, etc.; see section 7.4) in situations that the wolf can clearly recognise. This is difficult to achieve in practice, especially if the wolf is not tagged. Tolerating people within 100 metres may occur occasionally, but if it is observed repeatedly in the same individual it is an indication of strong habituation or positive conditioning. Wolves usually run away as soon as they know a human is nearby even some distance away, but they do not always perceive buildings or machinery as dangerous. This is why humans can often get much closer if they are in a car or hide.

6.2.2 Problematic situations involving dogs

Wolves may approach dogs, or humans with dogs, in quite a different manner than humans without a dog. This is because wolves may see dogs as social partners, potential mates or rivals. In all these cases, the wolf may completely ignore the human accompanying the dog, as has been witnessed several times in Germany. This can also lead to a wolf staying in the vicinity of a village for weeks waiting for a potential mate (Reinhardt et al., 2020). If a wolf sees a dog as a rival, it may attack the dog even if there are humans around. In such cases, the attack is always directed at the dog, never at the humans present. Experience in Germany shows that if a wolf is interested in a particular dog (such as a bitch in heat), moving that dog elsewhere temporarily can be enough to stop the wolf from returning. It is simply a case of removing the stimulus that is attracting the wolf.

In addition to dogs kept as pets or companions, there are also working dogs such as watchdogs used to guard livestock. These dogs have been bred for centuries to work independently and protect herds of livestock, and this has become a part of their character (Bommel et al., 2020b). These dogs are generally a little heavier than wolves and are not scared of confronting them.

6.2.3 Problematic situations involving livestock

Conflict situations between wolves and livestock can occur for a range of different reasons. Habituation to people plays almost no role in this. For wolves, an ungulate is an ungulate, and there is essentially no difference between a fallow deer that is kept by humans and a fallow deer living wild in woodland. The same applies to farm livestock. Young wolves do learn which prey to hunt from their parents, and young wolves are conditioned to these habits. There is more information on conditioning in section 7.2. If a young wolf learns from its parents that sheep kept in its territory are not suitable prey due to unpleasant experiences with electric fencing and/or a livestock guard dog, for example, and wild ungulates are also available, the parents will generally focus on hunting wild ungulates and that behaviour will be passed on to their offspring (see section 8.1). A young wolf that has left the parental pack may also encounter farm livestock such as sheep for the first time. Wolves can then learn that sheep are suitable alternative prey, and may therefore prey on sheep more frequently. Once a wolf has learned that farm livestock are suitable prey, this is not easy to unlearn. If a human chases a wolf away from livestock, that wolf is unlikely to develop an aversion to livestock as prey; above all, it is likely to conclude that people are dangerous. The wolf remains likely to attack an unprotected herd elsewhere – in other words, the problem has simply been postponed.

Photo 6.2.1 *Conflict between a wolf and sheep. Inadequately protected livestock is vulnerable to attack from predators such as wolves. DNA testing using a saliva sample taken from a bite wound can determine whether the perpetrator was a wolf. Photos: Marielle van Uitert (left) and Hugh Jansman (centre and right).*

6.2.4 Monitoring bold wolves and a framework for action

Reports of bold wolves can be divided into two categories: 1) situations in which the human expectations of a wolf's behaviour did not match the behaviour observed; and 2) situations in which a wolf actually displayed unnaturally bold behaviour. Strong habituation to the presence of humans is a prerequisite for bold behaviour. Past human behaviour is therefore almost always the underlying cause of such behaviour.

After a report has been received and it turns out that there is indeed a bold wolf, it is important to ensure that human behaviour does not result in further habituation and food conditioning in the wolf in question. As with all wild animals, the basic principle is: do not approach them and do not feed them. This obviously includes not adopting them as 'pets', which does still happen occasionally (Nowak et al., 2021). It is also important to record all findings and measures taken properly, in order to facilitate evaluation and communication. In addition, it is advisable to ascertain whether the wolf in question is being attracted by something in particular, such as an attractive dog or food waste. To handle the situation properly, it is important to start some kind of monitoring, keep local residents and/or the public informed about the steps being taken, and ask them to report what they see. Depending on the situation, catching the wolf and fitting it with a tag may be considered, in order to study its behaviour better and also to facilitate aversive conditioning if desired. The options for aversive conditioning are described in section 7.4.

As well as Reinhardt et al. (2020), Linnell et al. (2002) also address this subject, with an emphasis on wolf attacks on humans. Linnell identifies four scenarios that can lead to bold and/or aggressive behaviour in wolves:

1. Rabies, which leads to a highly abnormal form of aggressive behaviour. This situation almost never arises in Western Europe. See inset 6.4.1.
2. Strong habituation: the wolves have learned that humans are completely harmless. This occurs particularly in wolves that come into direct contact with humans when they are young, for example through feeding, or which have lived partly in captivity.
3. Provocation, where a wolf is cornered and its only option is to attack.
4. Wolves in highly artificial landscapes with very little natural prey and which are highly dependent on livestock and human food waste.

A fifth scenario can be added: a wolf that is weak due to illness or injury, for example, and that may approach people in search of food.

Linnell et al. (2021) also recommend more research on habituation and bold behaviour in wolves in order to gain a better understanding of the mechanisms by which this comes about and how it can be prevented. This is increasingly relevant as more and more wolves are present in human-dominated landscapes and brutal wolves are a potential danger.

6.3 Surplus killing of prey

The killing of more livestock than a wolf actually eats is the result of an unnatural situation. In the Netherlands, sheep, in particular, are often unable to act on their natural flight instinct. Predators take advantage of such situations by killing multiple animals at once. In nature, these would be consumed, but in a human environment the wolf feels threatened and this can lead to the animal making a swift departure.

Detailed analysis

6.3.1 Surplus killing or 'henhouse syndrome'

The killing of prey in excessive numbers is also known as surplus killing or 'henhouse syndrome'. Virtually all carnivores, including bears, felines and canids, will sometimes kill significantly more prey than they need for their energy needs. Kruuk (1972) defines surplus killing as 'the killing of prey by a predator without the predator, or any other individuals in its social group, consuming it, in situations where prey is freely available and would normally be eaten.' It is not so much about numbers and availability, then, but an apparent predation reflex that is activated regardless of whether the prey will be eaten. This distinction is not black-and-white, however. There are many situations in which predators kill prey and only partially consume it. Grizzly bears that catch migratory salmon often only eat the eggs, killing far more prey than is strictly necessary for their dietary requirements. In a situation of abundance, there is no reason for the bear to be frugal, after all. The killing of multiple animals when hunting is not uncommon in other predators as well. Often, the carcasses will be stored somewhere temporarily to be consumed later. However, in a henhouse or a field of sheep this is not possible because there is a fence that forms a barrier, and because humans may be in the vicinity. Wolves often return to places where they have left dead prey, especially during periods of food scarcity and sometimes months later (Mech & Peterson, 2003). Surplus killing is made possible when prey animals are unable to escape. This occurs not only in farm animals that are enclosed by a fence, but also in wild ungulates (Kruuk, 1972; Miller et al., 1985; DelGiudice, 1998). There are a number of rare scenarios in nature that can result in surplus killing. The first is unnatural exposure, such as ground-nesting birds in a place where predators can access them. This can result in situations where a single predator, such as a fox or a cat, kills many animals in a short time and only eats a fraction of them. Another scenario is extreme darkness, when ungulates freeze and will not run away if a predator is stalking them (Kruuk, 1972). Ungulates probably respond to extreme darkness by freezing due to natural selection and adaptation: this adaptation may help individuals avoid injury, for instance. But the disadvantage of this behaviour becomes painfully apparent when predators show up during a dark night. Deep snow can also create opportunities for predators to catch multiple ungulates in one go (DelGiudice, 1998).

Small wolf packs in Scandinavia can kill more than three times as many moose as they need to meet their energy needs, even when prey density is low (Zimmermann et al., 2015). Large packs (of 6-9 wolves) display less surplus killing.
Zimmermann et al. suggest that surplus killing by smaller packs is associated with optimising their foraging strategy, consuming only the most nutritious parts of easily accessible prey and minimising the chance of detection by humans. Another factor is that scavengers can eat more from carcasses that have only partially been eaten than from carcasses that have been almost completely consumed. There is therefore an optimum pack size that ensures that prey is consumed efficiently (see section 8.1). It is clear that under most circumstances surplus killing is not a frequent phenomenon. Nonetheless surplus killing is a normal reflex: it is not in the nature of either animals or humans to be frugal. However, surplus killing is wasteful and may become disadvantageous for predators if it results in a reduction in the amount of prey available. Because such situations rarely occur under natural conditions, the consequences on the larger scale are negligible. However, it can have an impact at the local level, such as driving colonies of ground-nesting birds to safer places. Kruuk (1972) explains that surplus killing is the consequence of behavioural compromises in both predator and prey in order to be able to deal with various opposing demands in their environment.

6.3.2 Differences in behaviour in terms of species and situation

It is uncommon for wolves to kill wild prey in large numbers. Where this does occur, it only happens under unique circumstances such as when there is extremely deep snow. However the surplus killing of domesticated animals which cannot act on their normal anti-predator reflexes is not uncommon (Mech & Peterson, 2003). In some cases, this is the result of selective breeding for traits that are useful to humans, such as tameness, but which make an effective response to a predator more difficult. It can also be the result of placing animals in an unnatural habitat that prevents them from acting on their natural anti-predator reflexes (or animals which do not have any predators in the wild). One example here is the mountain goat, which normally runs up rocky cliff faces in order to escape from predators; in the flat terrain of the Netherlands, however, this is not an option.

The risk of surplus killing is greatest in sheep and goats in the Netherlands, because they are unable to engage their normal anti-predator reflexes and are often enclosed in relatively high densities in a relatively small enclosure. Cows and horses, especially when kept in herds, are usually better able to repel an attack by a wolf (see sections 4.3 and 8.1).

It is not easy to estimate whether there is a difference in the chance that a certain breed of sheep is more susceptible to surplus killing. Landa et al. (1999) found that lighter breeds of sheep experienced less predation from wolverines (*Gulo gulo*) than heavier breeds, but whether this extends to other predatory carnivores is not known. There may be a difference in the likelihood of predation and surplus killing depending on the anti-predator reflexes of certain species or breeds. In Italy, attacks on livestock mainly occur on sheep, and only rarely on goats (Russo et al., 2014). Surplus killing has never been observed in goats, but it is observed in sheep. On average, 7-15 mainly adult sheep are killed in cases of surplus killing. Gijsbert Six, member of the Platform for Sheep and Goat Smallholders and involved in the wolf area committees in Gelderland and Drenthe, explains that there is a sliding scale among the different breeds of sheep. Broadly speaking, there are domestic breeds such as Texelaars which have been highly bred, as well as crosses between these breeds; and on the other hand there are less bred animals, such as Dutch heath sheep. He suspects that the non-thoroughbred sheep respond to predators more effectively, running away from the predator. In addition to the response of the animals, however, circumstances also play a role, such as the type and size of the enclosure, the size and composition of the flock, grazing within a fenced area or supervised by a shepherd, the time of day and the season. Shepherd Wilfried Buitink indicates that the stability of the flock is also important. If the composition of the flock has remained basically the same for some time, it will be more peaceful. According to him, factors such as the type of dog, the presence of a shepherd and night-time shelter are also important. BIJ12 indicates that at the time of writing (July 2021), it is not possible to obtain more clarity on this subject based on the registration system. For more clarity, it is recommended that in the event of damage, the assessor focuses more on recording information such as the breed of sheep, flock and area, and that more targeted research is done using, for example, camera traps around night-time shelters in outlying areas.

6.4 Attacks by wolves on humans and dogs

The risk of an attack on humans or dogs is an aspect that dominates people’s perceptions of wolves. Nevertheless, in Western settings the number of incidents is limited, and the risk of a human being bitten by a wolf is negligible. The greatest risk is posed by wolves that have little or none of their natural timidity around humans and that associate humans with receiving food. This often occurs in wolves which have been fed by humans frequently when they were young, and which therefore associate humans with food. If such a wolf approaches humans expecting food and then does not receive any, it may become aggressive. Older wolves or sick wolves that are no longer able to hunt for prey independently may also approach humans, or wolves infected with rabies. Dogs can be seen by wolves as potential mates, but also as rivals. This can lead to wolves approaching dogs to lure them out into the wild, but also to wolves attacking and killing dogs.

Detailed analysis

The potential risk of attacks on humans and dogs by wolves is a prevalent theme in the media and in people's perceptions. In Reinhardt et al. (2020), this subject has been addressed in a report on how to deal with 'bold wolves' in Germany. That report also details certain incidents in Germany in which wolves have approached humans and/or dogs at very close proximity or even attacked dogs (see section 6.2 for a summary of that report).

6.4.1 Attacks on humans

Linnell et al. (2021) detail wolf attacks on humans over the past eighteen years. Their report is a follow-up to an earlier report (Linnell et al., 2002), and together the two reports provide a thorough overview of the facts as well as recommendations for further research. The overview below is a summary of these two reports.

Historically, there is plenty of well-documented evidence for numerous attacks on humans by wolves. There have been three categories of attacks. The majority have involved attacks by wolves with rabies (1). In addition, there have been attacks where the behaviour of the wolf is described as inquisitive or defensive (2). Most instances of biting in that category involved situations in which the wolf was acting in self-defence. In addition, wolves have occasionally bitten humans to find out whether humans are potential prey for them. The third category concerns attacks in which a human is actually taken as prey, based on the wolf's natural hunting instincts (3). This behaviour has primarily been observed under a specific set of sociological and ecological circumstances, in areas where wild prey is scarce and there are poor and vulnerable human communities (such as in parts of Asia and the Middle East, where children often work herding livestock). These attacks have chiefly involved children. Under these circumstances, the wolves were also foraging in waste dumps in search of carrion due to the absence of natural prey, and were therefore in frequent proximity to human settlements (also see sections 6.1 and 6.2). Linnell et al. (2021) indicate that despite this, only a very small proportion of wolves actually tried to find out whether children could be potential prey. It is possible that these wolves were injured or weaker and therefore no longer able to take natural prey and on the look-out for an easier meal.

Inset 6.4.1 Rabies

Rabies is a deadly infectious disease caused by a virus. Rabies can be transmitted to humans by means of a bite, scratch or lick from an infected animal. The infection affects the nervous system. Cases of rabies almost never occur in the Netherlands, and the very small number that do have involved patients who contracted the virus abroad. Rabies still occurs in most countries in Eastern Europe, Asia, Africa and Latin America (Source & more information: www.rivm.nl/rabies). However, because wolves sometimes roam more than 1,000 kilometres from their parental pack in search of their own territory (see section 6.5), it is possible that they could bring the disease with them from areas of Eastern Europe where the virus is still endemic.

In Europe, the risk of wolf bites involving humans has decreased considerably in recent decades as rabies is virtually non-existent and has been eradicated completely in Central Europe. Sociological and ecological conditions have also changed. The density of ungulates, wolves' natural prey, is relatively high in Central Europe, so wolves very rarely need to search for alternative prey. In addition, the standard of living for people has greatly improved and risky situations, such as children tending to flocks of sheep, no longer occur.

Although the density of humans in Europe is high and there are now more than 15,000 wolves, the number of biting incidents is remarkably low. Linnell et al. (2021) therefore conclude that although the risk is greater than zero, it is incalculably small. Most incidents involving wolves occur in Asia and the Middle East, where rabies is still prevalent, the supply of prey is low and there are still areas where human poverty prevails.

A literature review presented data on 489 human victims of wolf attacks in the period 2002-2020, with the vast majority of them occurring in Asia. For North America and Europe, that data is reasonably reliable. For Asia and the Middle East, the information is more difficult to obtain, let alone verify. Often no investigation has been done to determine whether the attack actually involved a wolf or, for example, a stray dog. In 67 cases, 9 of which were fatal, the attack involved a wolf (see section 6.1 for the definition of 'attack'). Some 380 cases, 14 of which were fatal, involved a wolf with rabies. In 42 cases, 3 of which were fatal, the attack involved a wolf that had been provoked or was exhibiting defensive behaviour. Of the 489 victims, six were in North America and seven in Europe, and these mainly involved bite wounds. Two of the cases in North America were fatal, and one of these involved an injured wolf. In the other case, the reason for the attack was completely unknown. All other cases in North America and Europe involved situations in which wolves were regularly seen in close proximity to humans, were not shy around humans, and in many cases were accustomed to finding food around humans or to killing domestic animals. Habituation to people therefore seems to play a major role in the risk of biting incidents, and Linnell et al. (2021) therefore strongly recommend focusing more on preventing habituation, investigating how this arises in wolves and how it can be reversed. See sections 6.1, 6.2 and 7.4 for more information on this.

Reinhardt et al. (2020) report that research has been done in Sweden into the behaviour of wolves when they are actively approached by humans. The daytime resting places of tagged wolves were identified and the wolf or wolves were approached on foot, as carefully as possible. In all cases, the wolves ran away without any aggressive behaviour. The average flight distance was 100 metres. In Russia and Belarus, it is customary to remove pups from the wolves' dens to reduce the wolf population. Wolves do not defend their young against humans, as they would against bears for example. Even carrion from prey is not defended by wolves against humans. In short, wolves are not naturally aggressive towards humans.

The Netherlands
Since the return of wolves to the Netherlands, no attacks on people have been reported. Public perceptions, on the other hand, have been investigated. The Motivaction study carried out by the Ministry of Agriculture, Nature and Food Quality in November 2020 states that 76% of respondents in areas with wolves indicated that they are shy animals that are not aggressive towards people (Grient & Kamphuis, 2020).

6.4.2 Attacks on dogs

Wolves may see dogs as rivals to be chased out of their territory in the same aggressive manner as unknowns wolves would be – sometimes resulting in the killing of the intruder. However, wolves can also see dogs as potential mates and thus actively approach them or even try to lure them away deeper into their natural habitat (Reinhardt et al., 2020). There have been no known serious incidents involving wolves and dogs in the Netherlands (Bommel et al., 2020). In Germany, there have been a number of problematic situations involving wolves and dogs (Reinhardt et al., 2020; Bommel et al., 2020). Ilka Reinhardt reports that over the past 21 years, the number of confirmed cases of wolf attacks on dogs has been limited. In one case this was a hunting dog (although it was not hunting at the time), which escaped from its owner, followed the scent of a wild animal and encountered one or more wolves. In another case, a dog encountered a wolf and began barking. These dogs did not survive. In both cases, this incident took place during the mating season, when wolves are more aggressive towards intruders. Two other cases involved situations where dogs were attacked and killed by wolves at night outside in the yard. The latter case involved a former pack wolf that had been expelled from his pack by a rival. The animal was injured, had mange and was in a poor condition. The animal has been sighted frequently by humans for some time. It eventually attacked a dog that was chained in a yard overnight. That animal was later shot with a permit. Other non-fatal cases are detailed in Reinhardt et al. (2020) and section 6.2.

In Scandinavia (Sweden, Norway and Finland) the risk of wolves to dogs is much higher because of more frequent interactions. Liberg et al. (2010) report that 151 dogs were killed by wolves in the period 1995-2005. Some 80% of these were hunting dogs. Approximately 38 hunting dogs are killed in Finland every year (Tikkansen & Kojala, 2020). Many more are injured. This not only represents an economic loss for the owners, but often an emotional one as well, since the hunter-dog relationship involves many hours of training (Liberg et al., 2010; Skogen et al., 2017; Tikkansen & Kojala, 2020). The risk of a wolf attacking a hunting dog while hunting is greater in Scandinavia than in the Netherlands. In moose hunting, the hunting dogs often run very far ahead of the hunters. When they find a moose, they stop it by barking at it so that the hunters can shoot the animal. Wolf attacks on hunting dogs generally occur in situations where the hunter is more than 200 metres from the dog (Tikkansen & Kojala, 2020). If a hunting dog encounters a wolf or a pack of wolves, this often leads to an aggressive confrontation, because the wolves often regard the dog as an intruder. This form of hunting is not practised in the Netherlands, so the risk of a wolf attacking a hunting dog is also smaller, especially if dogs are well trained or kept on a leash.

In Scandinavia, attempts have been made to reduce the risks for hunting dogs. Because scientific research in Norway and Sweden is united under the Scandinavian Wolf Research Project, SKANDULV, it is possible to work together. Every winter, 10-20 wolves are fitted with tags, so the position of the pack can be monitored remotely. This also makes it possible to communicate to hunters when there is an increased risk of encountering wolves in a certain area. It has permitted a telephone information line to be set up for hunters. Such a system has also been developed in Finland. There, too, information from tagged wolves is shared, in this case on a website showing data at the scale of 5x5km^2. The number of attacks on dogs has fallen in areas with tagged wolves because hunters are able to take account of the presence of wolves. It is an expensive system and can also result in the illegal killing of wolves, but the approach has been very important in ensuring support among hunters in particular (Tikkansen & Kojala, 2020). Hunters also value being able to call the telephone line (Liberg et al., 2010).

In Eastern Europe, particularly in Belarus, dogs are frequently killed by wolves. A well-known phenomenon is the killing of guard dogs that are chained up outside (Jedrzejewski et al., 2010). Usually, however, it is stray dogs or dogs in regions virtually uninhabited by humans that are attacked by wolves. This may be due to rivalry between the wolf and the dog, but some wolves just seem to view dogs as easy prey (Sidorovich, 2017).

In Flanders, one case in 2020 was well documented as part of determining the damage caused by wolves in order to obtain compensation. A dog had escaped from the fenced garden of a house in a wooded area and was killed and found partially eaten outside the perimeter fence. In addition, a dog was also once found as a prey item in wolf droppings (section 8.1; Van der Veken et al., 2021). There was no connection with the documented case, however, since the droppings in question were collected before the incident happened.

6.4.3 Prevention

An analysis of recorded wolf attacks on humans throughout human history indicates that (apart from rabid individuals) these are mainly perpetrated by wolves in a weaker state (young, sick or mangy animals) and that this is more common when there is a lack of natural prey (Linnell et al., 2002). It is worth noting that wild ungulate densities are currently at an all-time high in many parts of Europe (Apollonio et al., 2010), with wild ungulates becoming increasingly prevalent even in cultivated landscapes (Morellet et al., 2011). This means that in many cultivated landscapes, the supply of prey is no impediment to colonisation by wolves (Linnell et al., 2021). Given the increasing age of forests in the Netherlands, the increase in years with a bumper crop of acorns and beechnuts (staple food for ungulates), coupled with milder winters, the conditions for ungulates are only getting more favourable (Den Ouden et al., 2020).

Linnell et al. (2002) propose three steps to help prevent undesirable behaviours in wolves:

1. Eliminate rabies. The Netherlands was declared rabies-free by the World Organisation for Animal Health in 1988, and the same applied to Belgium in 2001 and Germany in 2008.
2. Restore populations of wild prey and protect livestock with new methods so that wolves are not dependent on food sources that are located in proximity to humans.
3. Keep wolves wild: prevent wolves from associating the presence of humans with an easy meal or other positive conditioning.

6.5 Possible consequences of the presence of wolves in the Netherlands for road safety and recreation

The direct effect of wolves on road safety in the Netherlands is currently very limited. In the period between 2015 and July 2021, there were five vehicle strikes involving wolves on roads in the Netherlands. No information is available on indirect effects, such as changes in the number of vehicle strikes involving wolf prey. Although the number of vehicle strikes involving wolves will increase as the population of wolves grows, the direct effect on road safety is expected to remain limited. This is firstly because the expected number of vehicle strikes involving wolves remains relatively low compared to the number of ungulates that are hit each year, for example, and secondly because it is easy to reduce the number of vehicle strikes by using fencing and wildlife crossing points, for instance. It is not possible to draw any conclusions regarding any indirect effects of the presence of wolves on road safety, as yet. On the one hand, the presence of wolves can reduce ungulate populations, thereby reducing the number of vehicle strikes with those animals; but on the other hand, it is possible that ungulate habitat use may be affected, leading them to cross roads and railways more frequently and thus increasing the risk of vehicle strikes. Too little research has been done – either in the Netherlands or elsewhere – to reach any substantiated conclusions about this.

As far as recreation is concerned, wolves may attract visitors (ecotourism) or put visitors off (out of fear). In addition, the risk of wolves becoming habituated to humans may increase as a result of the increased likelihood of interactions.

Detailed analysis
For the detailed analysis of this question, the subject of traffic safety was considered first, followed by the subject of recreation, which also includes hunting.

6.5.1 Traffic safety

To what extent are we already seeing that the presence of wolves in the Netherlands is affecting road safety?

Since 2015, five wolves have died on roads in the Netherlands (Table 5.1.1): four male animals and one female. In addition, two wolves observed in the Netherlands died on roads in Germany and Belgium after having left Dutch territory (Table 6.5.1).

Table 6.5.1 *Wolves observed in the Netherlands that died on roads in the period 2015 – July 2021; see section 5.1. *The identity of this wolf became known at the time of completion of this report.*

Year	Month	Location	Road	Wolf ID	Sex
2015	March	Hannover (Germany)	E7	GW368m	Male
2017	March	Hoogeveen	A28	GW657m	Male
2017	November	Kloosterhaar	N36	GW843m	Male
2018	March	Opoeteren (Belgium)	Neeroeterenstraat	GW913m	Male
2020	March	Epe	N309	GW1626m	Male
2021	March	Ede	N224	GW1729f	Female
2021	May	Appelscha	N381	*GW2362m	Male

No research has yet been published in the Netherlands on the effect of wolves on the animals that they prey on (ungulates), in terms of their behaviour, habitat use and the number of traffic casualties. In the North Veluwe area, research is underway into the effect of wolves on ungulates and the growth of vegetation (also see section 8.1). However, we do not know whether the presence of wolves has an indirect effect on road safety through changes in the number of vehicle strikes involving ungulates.

Predicted effects of the presence of wolves in the Netherlands on road safety
Vehicle strikes with wolves are not uncommon and in some cases they may even make up the majority of annual deaths in wolves (Wydeven et al., 2001; Fritts et al., 2003). Wolves have a

relatively high chance of being struck by a vehicle. They require a large territory and often travel long distances within that territory on a daily basis. In central Italy, for example, it has been found that wolves travel an average of 27 kilometres per night (17-38 km/night) (Ciucci et al., 1997). The distances that wolves cover in search of new territory during their roaming phase are many times greater still. Research on the distances travelled by roaming wolves in the Central European population has revealed the following:

- From the northern Apennines in Italy to the western Alps in France: at least 958 kilometres (Ciucci et al., 2009).
- From Saxony in Germany to Thy National Park in Denmark: at least 800 kilometres (Andersen et al., 2015).
- From the Dinaric Mountains in Croatia to the Eastern Alps in Italy: 1,176km (Ražen et al., 2016).
- From Lusatia in Germany to Belarus: 1,550km (Reinhardt & Kluth, 2016).
- From the Abruzzo, Lazio and Molise National Park to Majella National Park in Italy: 422km (Mancinelli & Ciucci, 2018).

During both day-to-day movements within a wolf's territory and when roaming, wolves may frequently cross roads and railways, depending on the distance travelled and the type of area being traversed. In Wisconsin, USA, wolves regularly crossed a four-lane highway (Kohn et al., 1999; 2009). There was no wildlife fence along the road. The majority of crossings (81%) involved wolves that were roaming. Of the 20 wolves fitted with transponder tags, 13 eventually arrived at the highway; 12 of them crossed the road, some several times. Wolf Naya, who entered the Netherlands in Drenthe on 18 December 2017 and left the country two weeks later moving into Belgium, covered an average distance of 14.1 kilometres per day (also see section 4.6; Jansman et al., in prep.). During her journey through the Netherlands, she crossed an estimated 361 roads and railways, including 30 national roads, 68 provincial roads and 19 railways.

Roads can even attract wolves. Roadside verges often provide a good habitat or migration corridor for potential prey, for instance. The carcasses of animals hit by vehicles can encourage wolves to seek out roads during their foraging trips (Grilo et al., 2015). On the railway that runs through Glacier National Park in Canada, most vehicle strikes with wolves (and coyotes) occurred near the carcasses of ungulates that had been killed by train strikes (Wells, 1996). Consequently, Kohn et al. (2009) recommend the rapid removal of any ungulate carcasses and the use of less attractive types of grass on verges and embankments to reduce the risk of accidents involving herbivore ungulates and therefore also accidents involving wolves.

In some cases, roads and adjacent verges also provide an attractive corridor for rapid movement between different areas. For example, Dickie et al. (2017) found that wolves in Western Canada seek out linear infrastructure, including roads and railways, when foraging. They can move along these two to three times faster than they would move through natural forested areas. They are also able to cover greater distances per day by doing this. However, the use of roads as corridors for wolves is mainly confined to unpaved roads and paths. Paved roads with more traffic are avoided, especially during busier periods (Thurber et al., 1994; Gehring, 1995, in Kohn et al., 2009).

The situation in Germany offers us some insight into what we might expect to see in the Netherlands as the wolf population grows. The first reports of wolves struck by vehicles occurred in the early 1990s (Figure 7.5.1). In all cases, these reports came from eastern Germany, not far from the border with Poland or the Czech Republic (Source: https://data.dbb-wolf.de). No vehicle strikes with wolves were reported in the period 1995-2005. Since 2006, however, the number of reports in Germany has increased, gradually at first but rising sharply after 2015 (Figure 7.5.1). The average annual increase in the number of vehicle strikes registered was about six animals over the period 2005-2020 (Figure 7.5.2). In the period 2010-2020, this was around 10 percent on average. Over the past five years (2015-2020), the average annual increase has been about 17 wolves. Vehicle strikes are therefore the primary cause of death (75%) based on wolves that are found dead in Germany (Figure 4.5.2). The German wolf population in 2019-2020 was estimated at 128 packs, 35 pairs and 10 solitary animals. This means that – based on an assumed average pack size of five wolves (Fechter & Storch, 2014) – there were approximately 710 wolves in Germany in that year. Some 100 wolves were reported killed by vehicle strikes, which is equal to approximately 14% of the wolf population.

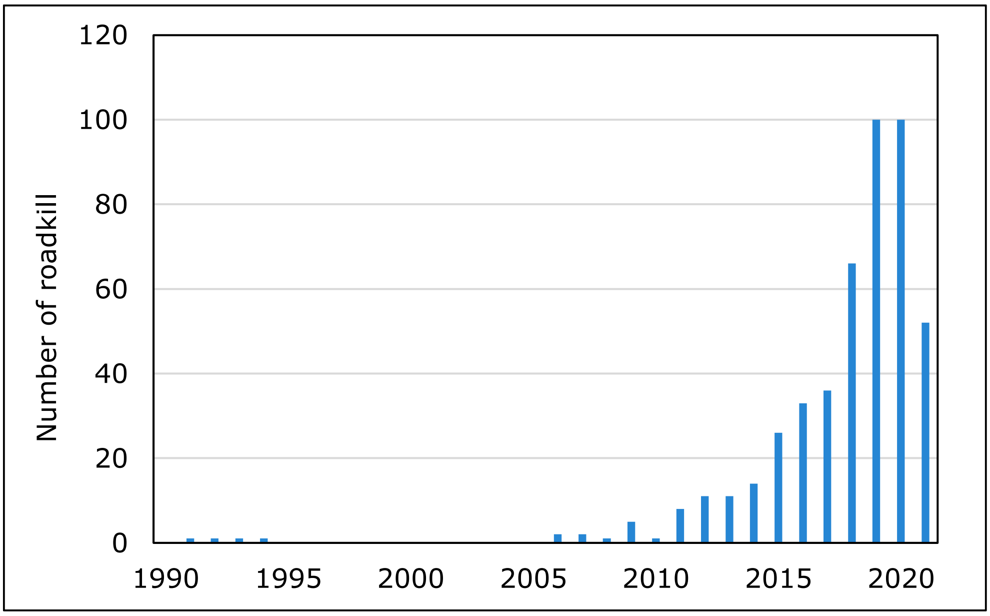

Figure 7.5.1 *Number of wolves reported killed by vehicle strikes in Germany in the period 1990-2021 (until June 15, 2021) (Source: https://data.dbb-wolf.de).*

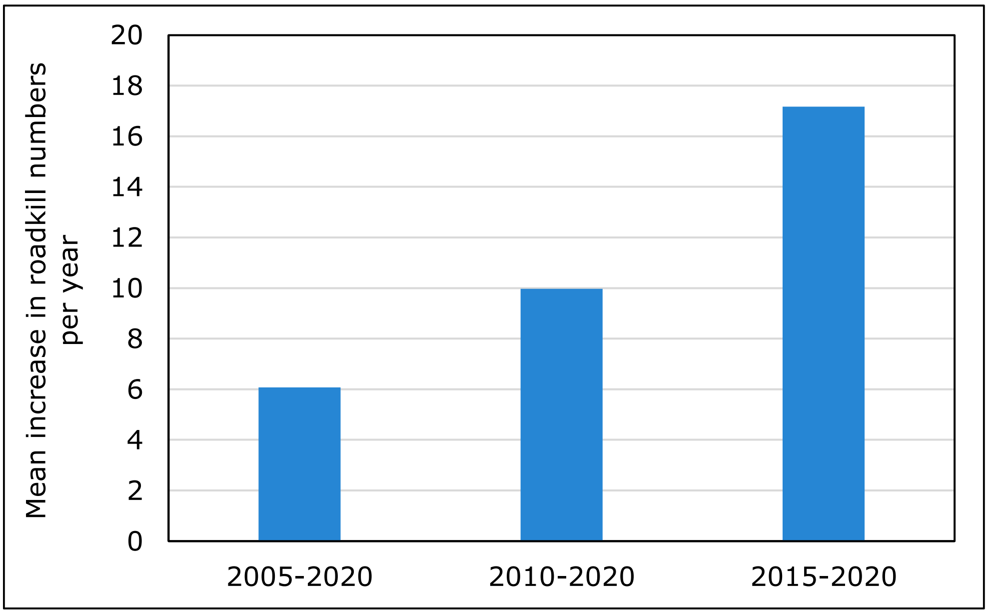

Figure 7.5.2 *Average increase in the number of road casualties per year in Germany over three time periods (Source: https://data.dbb-wolf.de).*

Although an increase in the number of vehicle strikes can be expected in the Netherlands as its wolf population grows, the absolute number of road casualties will nevertheless remain relatively limited. Assuming the most positive scenario with respect to the carrying capacity of the Netherlands for wolves (about 500 animals; Potiek et al., 2012) and a percentage of the wolf population killed by vehicles strikes comparable to the situation in Germany, the number of vehicle strikes in the Netherlands would be expected to rise to 60-75 annually. If this number is compared with, for example, the number of deer recorded killed by vehicle strikes every year – an average of over 6,300 animals in 2016-2017 (Van der Grift et al., 2019) – the effect of vehicle strikes with wolves will remain relatively limited.

Another factor is that mitigation measures have been put in place in many locations in the Netherlands, in order to prevent vehicle strikes involving wild animals on roads and railways (see: www.mjpo.nl). Wildlife fences have been placed along many roads and railways that pass through the habitat of red deer, wild boar and fallow deer, often in combination with wildlife crossing points. The fencing is designed to prevent the animals from wandering onto the road and to guide them to the wildlife crossing points. Wolves, too, will be able to use this existing 'green infrastructure'. Research has shown that wildlife fences along roads can limit the number of vehicle strikes. Some 17 wolves were struck on the Trans-Canada Highway in Banff National Park in the period 1981-2002. Of these, 82% were struck in places where no fences had yet been installed (Clevenger et al., 2002).

Research has also shown that wolves use the wildlife crossing points (both over and under roads or railways) (Clevenger, 1998; Clevenger & Waltho, 2000; Mysłajek et al., 2013; Mysłajek et al., 2020; Plaschke et al., 2021). Clevenger & Waltho (2000) found that the degree of human activity around an underpass as well as the openness and length of a fauna tunnel are the best predictors of the use of such wildlife crossing points by wolves. The use of wildlife crossing points by wolves has also been confirmed in the Netherlands. For example, wolves have been using the Tolhuis Nature Overpass near the Petrea nature reserve in the eastern part of the Veluwe for several years now (Bosscher, 2021). The wolf Naya is also believed to have used various wildlife crossing points to cross roads, although there is no direct evidence (photo images) of this (MJPO, 2018).

From the perspective of road safety, it is also fortunate that wolves prefer a habitat with a (relatively) low road density (Mech, 1989; Fechter & Storch, 2014; Reinhardt et al., 2019). Wolves living in human-dominated daytime landscapes also favour forested areas in order to avoid contact with humans and forested areas make up the core areas within their territories (Kusak et al., 2005; Mancinelli et al., 2018), and wolves avoid roads when choosing a place to give birth (Sazatornil et al., 2016). Whittington et al (2004) found that wolves in Jasper National Park (Canada) crossed roads, railways and footpaths less often than would be expected if their movements were purely random. In the same area, wolf packs were also shown to avoid areas with a relatively high density of roads and footpaths (Whittington et al., 2005). In Finland, wolves avoid areas that are less than 250 metres from a road (Kaartinen et al., 2005). This means that an estimated 48% of the area surveyed was used less frequently by wolves, in comparison with a situation in which there were no roads. Roadworks such as road widening can also affect wolves' use of space. In Eastern Canada, wolves stayed an extra 300 metres away, on average, from roads while roadworks were going on (Lesmerises et al., 2013). However, other research shows that wolves will also colonise areas with a higher road density, provided this is adjacent to suitable habitat with fewer roads (Mech, 1989).

Wolves can also have an indirect impact on road safety. They can reduce the density of large herbivore ungulates (Ripple & Beschta, 2012), thus reducing the chance of vehicle strikes involving them (Mech, 2017). On the other hand, ungulates may change the way in which they use habitat when wolves are around, as evidenced by changes in vegetation due to changes in grazing pressure (Smith & Ferguson, 2012; White et al., 2012; Ditmer et al., 2018). In principle, this could lead to either more frequent or less frequent road crossings by ungulates, but no evidence of this has yet been found in the Netherlands. A study by Raynor et al. (2021) is illustrative in this regard. In Wisconsin, the researchers found that the number of vehicle strikes involving white-tailed deer fell by 24% after the arrival of wolves in the area. The researchers suggested that this could, to some extent, be due to a reduction in the deer population, but was actually mainly due to changes in their behaviour and use of terrain.

Tackling vehicle strikes is also important from a legal perspective. For instance, Boerema et al. (2021) refer to Article 12(4) of the Habitats Directive, which states that member states must ensure that the accidental capture and killing (of species that enjoy strict protection, such as wolves) does not have a significant impact on species that enjoy strict protection; in this respect, then, the Habitats Directive requires member states to achieve a certain result. Vehicle strikes should therefore be so low that they have no significant negative impact on the wolf population in the Netherlands. Measures should be taken in order to achieve this.

In order to better understand the impact of traffic on wolves in the future, the following recommendations are made:

- Record vehicle strikes involving wolves and ungulates on roads and railways systematically at the national level.
- Study the effects of the presence of wolves in the Netherlands on ungulate behaviour and habitat use, as is currently being done in the North Veluwe area by the University of Groningen.
- Study the effects of the presence of wolves in the Netherlands on the frequency with which ungulates cross roads and railways and the number of vehicle strikes involving ungulates.
- Study the extent to which existing wildlife fences along roads actually stop wolves, and what changes could be made to increase their effectiveness.
- Study the extent to which wolves accept and make use of wildlife crossing points, and whether this affects the behaviour of the animals they prey on.

6.5.2 Recreation

As far as recreation is concerned, wolves could attract large numbers of visitors (through ecotourism), or put visitors off (due to fear). Research conducted by Motivaction (Griend & Kamphuis, 2020), commissioned by the Ministry of Agriculture, Nature and Food Quality, indicates that 59% of Dutch people would spend leisure time in nature reserves where wolves are known to live, and that 23% would not. In addition, the risk of wolves becoming habituated to humans may increase as a result of the increased likelihood of interaction, and the risk of conflicts between wolves and humans may also increase accordingly (see section 6.2).

Ilka Reinhardt indicates that in Germany media articles that play on people’s fear of wolves are frequently published. In her experience, however, areas that have been recolonised by wolves were actually more likely to see an increase in recreational visitors than a reduction, in the years immediately following the recolonisation of Germany by wolves. It seems that the presence of wolves attracts more people than it scares away. She also indicates that some commercial projects use wolves as an attraction or proof of quality. She refers to the Live Wolf Alps Project, for instance, which focuses on humans living peacefully with wolves, and conflict-free coexistence between cattle and wolves. Locally produced food carries a wolf logo. We have a similar scheme in the Netherlands for dairy products and the protection of meadow birds, but wolf-related business opportunities are already being seized in the Veluwe area – from wolf confectionary to wolf excursions.

In North America, there is some experience with ecotourism revenues and the relationship between visitors and wolves, especially in Yellowstone National Park, where wolves are relatively easy to spot and tend to attract plenty of visitors. Varley et al. (2020) report that wolves have led to an increase in ecotourism in Yellowstone National Park all year round, with significant added value to the local economy. The annual economic impact of the reintroduction of wolves was estimated at $35.5 million in 2005. There were about 2.8 million visitors in that year. By 2017, the number had already risen to more than 4.1 million visitors, with an annual added economic value of approximately $65.5 million. In addition to providing a chance to observe wolves first-hand, park authorities were also able to educate visitors about wolves at the main viewpoints, which helps to make public opinion more favourable to wolves. ‘Wolf tourism’ has also had some negative effects. There were cases in which wolves had to walk for long distances in order to cross a road, because some tourists followed them along the road. At least 35 wolves have also been struck by vehicles in the park. And occasionally some wolves have become habituated, almost certainly as a result of being fed by humans.

Smith et al. (2020b) indicate that Yellowstone National Park has a special wolf management regime which focuses on: (1) protecting dens and rendez-vous sites against disturbance from humans (possibly by closing areas or trails to the public temporarily, with a buffer of approx. 1 kilometre around dens with young until the end of June); (2) preventing habituation in wolves, including a strict ban on the feeding of wild animals; (3) educating visitors about how to observe wild animals, including wolves, safely; and (4) regulating human observation so that wolves are not disturbed and no habituation can occur. Broadly speaking, this means trying to keep humans and wolves separate. The public must stay at least 100 yards (about 91 metres) from wolves at all times, even if the animal approaches of its own accord.

The Netherlands
For the time being, there is no indication of any noteworthy developments with respect to wolves and recreation in the Netherlands, and given the country’s limited wolf population, none are anticipated for the time being. In light of developments in Germany, however, we cannot rule out future situations in which visitors are able to observe wolves at close quarters. In rare cases, wolves may also approach dogs when the owner is also nearby – whether out of curiosity or aggression (also see section 6.2). There is also the risk of wolves mating with dogs, resulting in hybridisation (see section 5.3). The University of Groningen is conducting research into the effect that wolves, ungulates and humans have on one another (also see section 8.1).

6.5.3 Hunting and managing the countryside

Hunters often engage with wildlife in the twilight hours, and hunters and wardens reach places where regular recreational users of the countryside seldom visit. As such, they are more likely to interact with wolves than most people. This chance is higher still if hunters or wardens use a raised hide or sit inside a vehicle, because wolves are less likely to associate these with humans and are often less hesitant to approach them (see sections 6.1 and 6.2). As explained in section 6.4, this is not dangerous, but there may be a response to any dogs present. Hunting dogs can face risks if they run through the forest far ahead of the hunters and encounter a wolf (section 6.4). Wardens and hunters can be an important source of information for monitoring because they are more likely to encounter wolves, and more especially because they have better knowledge of the stock and behaviour of ungulates in that area through ungulate management and/or monitoring practices (also see FBE 2019b).

7 Policy, damage, monitoring and management

7.1 Policy on derogation from protected status in other countries

There are two main reasons for granting derogations from protected status in the case of individual wolves: 1. high-risk, undesirable behaviour vis-à-vis humans in bolder animals; or 2. significant economic damage. In the first instance, human safety is the priority, and in the second instance the derogation is intended for use in cases where serious economic damage cannot be prevented in any other way. In the first case, there is broad policy agreement between states. In the second case, there are significant differences between EU member states; these are, however, currently under legal review in the respective countries. These are discussed specifically in Boerema et al. (2021). The difference between these two exceptions is fundamental, because the associated habituation and conditioning are very different.

Detailed analysis

The European Union can grant permission to deviate from a generally established standard in a particular way, which is known as derogation. The grey wolf is a protected species and deliberately disturbing, capturing or killing these animals is prohibited if this has a negative effect on the population (see Boerema et al. (2021) for the practical implications of this). However, if there are compelling circumstances, a legal derogation from these provisions may be permitted. The elimination of an animal (either by shooting it dead or by capturing and euthanising it) is the most extreme form of derogation. The modalities for these derogations are laid down in Article 16.1 of the Habitats Directive, and therefore apply to all EU member states. These are discussed in more detail in Boerema et al. (2021).

To summarise, derogations are only granted when they do not endanger favourable conservation status and when other options have been exhausted or are impractical. However, implementation is left to the member states and there is therefore significant variation.

In principle, European legislation allows for derogations in all countries based on the same set of basic principles. One possible reason for a derogation is to prevent ‘significant economic damage’ – a term that is currently open to interpretation by the member states, which again leads to very different policies regarding derogation. France seems to take a relatively flexible approach and has granted 8,287 derogations since 1 January 2018 (http://www.auvergne-rhone-alpes.developpement-durable.gouv.fr/bilan-du-protocole-d-intervention-sur- la-a14246.html, status 8/7/’21), while Germany uses derogations very sparingly, with a total of just 14 derogations over the same period. The following sections provide a summary of the policy with respect to the wolf populations that affect the Netherlands (Central European and Alpine populations), based in part on Boisseaux et al. (2019), but also see Van Bommel (2020a). In countries where derogations are granted on the basis of economic damage, a frequent requirement is that other steps to prevent damage have already been taken. Elimination may then be used as a last resort. In practice, this seems to be a somewhat flexible concept, again with significant differences of interpretation between member states. It is worth noting, for example, that the criteria for ‘adequate protection’ of livestock vary greatly between countries. For example, while an 80cm electrified fence with >3000 volts is sufficient to be considered wolf-resistant in France ((https://www.meurthe-et-moselle.gouv.fr/content/download/18685/130576/file /Formulaire%20demande%20Tir%20defense%20renforcee.pdf), in Flanders a 120cm fence with >4500 volts is required (Everaert et al., 2018), and in Lower Saxony (Germany) a 90cm fence with >4500 volts is required. In the case of the Netherlands, the recommendations for prevention are listed on the BIJ12 website (www.Bij12.nl/wolven). In practice, routine advance checks on the proper implementation of livestock protection measures are rare. Meanwhile, retrospective inspection can never guarantee that electrified fences were actually live at the time of an incident, that there was no significant loss of voltage, or that there were no gaps at the bottom of the fence where a wolf could pass through.

7.1.1.1 France

In France, large-scale seasonal grazing by flocks of sheep numbering hundreds or even thousands of animals is commonplace, and this has an important economic and socio-cultural role. From this perspective, conflicts between wolves and humans often become heated, because most sheep farming takes place in the mountain regions, where wolves are present in the highest numbers. In addition, grazing also plays an important role in regional conservation objectives. France uses Article 16.1 of the Habitats Directive to allow for derogations from the protected status of wolves under the following circumstances (Duchamp et al., 2017; Hulot & Travert 2018):

1. If the derogation does not affect the favourable conservation status of wolves.
2. The derogation must be defined within a previously established framework, in this case to avoid significant damage to livestock farming.
3. There are no other satisfactory means of preventing the damage.

Derogations are granted by departmental prefectures. The conditions under which a wolf may be eliminated are determined by two inter-ministerial judgments, which on the one hand specify the conditions and limitations under which a prefecture may grant a derogation, and on the other hand set a ceiling on the number of animals that may be eliminated within a given period. This ceiling is defined on the basis of the expected annual population growth and the expected mortality rate. Since the natural annual mortality rate in adult animals is estimated at 22% and the population would be expected to decline at a mortality rate of 34%, a maximum of 10% of the population may be culled per year (Duchamp et al., 2017). Under those circumstances, it is estimated that the population would go into decline at 40%. However, since 2019, an annual cull of 20% of the population has been permitted.

The elimination of wolves in France by shooting is divided into two categories: firstly, defensive elimination in response to confirmed damage to livestock (known as *tirs de défense*); secondly, preventive elimination in areas where significant damage occurs and when the maximum ceiling has not yet been reached (known as *tirs de prélèvement*). The former is used mainly in the event of predation during the period of maximum grazing intensity. The latter is almost exclusively aimed at predation in the autumn and makes up a minority of derogations.

In addition, there is also hunting using non-lethal ammunition, which does not require a specific derogation. Wolves should not be lured under any circumstances. A derogation issued by the local prefecture is always required for the use of lethal ammunition. Within France there are various zones in which wolves are present and where, in principle, livestock must be adequately protected (using a combination of livestock guard dogs, electric fences, night fences, shepherds and so on) before a wolf is allowed to be shot. There are also zones where wolves have not yet settled, and where they therefore do not have protected status. In addition, in certain areas it may be judged that livestock protection measures are simply not practical, due to steep slopes or rocky terrain for instance, and where no fences can be erected.

The total estimated wolf population in France is 99 packs plus 15 established territories (total estimate: 577 wolves, status 2020; https://www.loupfrance.fr/suivi-du-loup/situation-du-loup-en-france/), with a total of 2,412 derogations for elimination granted in 2020, of which 9 were for preventive elimination. This means that in 2020 a total of 105 wolves were culled, with a ceiling set at 110 wolves (DREAL Rhône-Alpes 2021). In 2019, 99 wolves were culled (ceiling 100), and in 2018 the number was 51 out of 51. In addition to culling, deaths due to illegal hunting are estimated to be of a similar order of magnitude (Mathieu, 2021).

7.1.1.2 Switzerland

In Switzerland (which is not bound by the HR, but only by the Bern Convention; Boisseaux et al., 2019) culling is allowed under strict conditions in order to protect flocks of sheep. Switzerland had approximately 8 packs and 26 settled wolves in 2019, making an estimated total of 78 wolves (OFEV, 2020). Since the return of wolves in 1995, a total of 23 wolves had been deliberately killed by the end of 2019, including some confirmed cases of illegal shooting.

7.1.1.3 Italy

In northern Italy, the Alpine wolf population includes around 33 packs and a total of around 200 wolves. No shooting is allowed but illegal hunting is common and, together with traffic accidents, contributes to an annual mortality rate of almost 20% of the population (Boisseaux et al., 2019).

7.1.1.4 Germany

In Germany, culling is permitted under exceptional circumstances in order to avoid ‘significant economic damage’. However, the interpretation of that wording is a source of legal disagreement between the federal government and the various German states. The states interpret the current – in their view excessively strict – federal guidelines (Dejure, 2021) in different ways, particularly when it comes to defining adequate measures to keep wolves out of farmland and checks on these (Ilka Reinhardt, personal communication). Unlike in France, culling is limited to specific individual animals that have been identified as having caused damage (through genetic monitoring). If the specific individual is unknown, the derogation is limited to a specific territory and culling may continue for as long as damage continues to occur, or at least until the end of the derogation period.

In Germany, exemptions have been granted in a number of cases where a wolf was exhibiting undesirable behaviour towards people, in order to prevent suffering or in cases where a wolf was unable to survive in the wild independently. The reasons for this included illness or conditions such as blindness (in one case) and extreme habituation in combination with undesirable behaviour (in two cases) (Reinhardt et al., 2020). In addition, culling permits have been issued for wolves that repeatedly attacked adequately protected livestock, particularly recently in Lower Saxony.

So far, 14 derogations have been granted, of which 12 were in Lower Saxony (4 wolves culled), 1 in Brandenburg (0 wolves culled) and 1 in Schleswig-Holstein (0 wolves culled).

Reinhardt et al. (2020) state that each case is unique, that thorough research is necessary to assess cases properly and take preventive measures, that shooting is a last resort, that it is often not clear which wolf is causing the problems, that it is not easy to shoot the right wolf and that culling permits should only be issued for a specific area and period. Good communication is also important because of the high degree of sensitivity surrounding the management of wolves, and it is therefore advisable for culling to be carried out by professionals whose identity is not made public.

7.1.1.5 Poland

There are three different wolf populations in Poland: the Central European population to the west of the River Vistula, the Baltic population in the north-east and the Carpathian population in the south-east (Figure 4.2.1). Unlike most of the other countries covered here, Poland’s wolf population has a more limited protection status under the Habitats Directive, namely as an Annex V species (in contrast to the stricter protected status of Annex IV species in many other countries, including the Netherlands; see Boerema et al., 2021). Despite this lower level of protection, which in principle allows for the active management of wolf populations, derogations across the territory are granted mainly for non-economic reasons in order to eliminate problem wolves and/or to eliminate confirmed hybrids. Between 2016 and 2018, derogations were granted for the culling of 36 individuals, 12 of which were killed (Boisseaux et al., 2019).

7.1.1.6 Austria

In Austria, the culling of wolves is not permitted, but deterring wolves using non-lethal ammunition (rubber bullets) has been permitted since 2018.

7.1.1.7 Belgium

In Flanders, the ‘Intervention Protocol for Problem Situations involving Wolves’ states that population management measures are possible in the event of repeated attacks on adequately protected livestock (see Everaerts et al. (2018) for details on livestock protection) when other measures have not had the desired effect. In Wallonia, the Wolf Plan 2020-2025 (Schockert et al., 2020) only provides for culling on the grounds of ensuring human safety.

7.1.1.8 Denmark

Denmark applies almost identical criteria as Flanders and Germany, and currently only allows the culling of specific animals due to problematic behaviour (excessive economic damage or behaviour towards humans). No derogations have been granted hitherto (Miljøstyrelsen, 2021).

7.1.1.9 Czech Republic

In the Czech Republic, the Law on the Protection of Nature and Landscape (‘Zákon o ochraně přírody a krajiny’, Decree 395/1992 Coll.) provides for no possibility of culling wolves for economic reasons or other forms of population management. This situation was reaffirmed in 2019 by a ruling from a Czech judge.

7.2 Experiences with the culling of wolves

No research has yet established any causal link between the culling of wolves, as envisaged within the legal boundaries of the Habitats Directive (i.e. provided there is no deterioration in conservation status) and reducing the predation of livestock. The studies that have been carried out and that indicate a positive effect are correlative, and cannot differentiate between the effect of culling itself and the effect of the associated increased human presence in areas of significant damage. In just over half of these studies, the culling of wolves was associated with (localised) reduction in damage, while the others found no difference or a slight increase in damage. Where culling is highly intensive and removes more animals than can be replaced through reproduction, the amount of damage will admittedly decrease, but only due to the smaller population of wolves. Depending on which individual is killed and at what time of year this occurs, the effect on the pack and on the behaviour of the pack members can range between limited to very significant. Because culling is often non-selective at the level of individual animals, there is a chance that it may actually lead to an increase in damage – the opposite effect to that intended.

Providing for the option of culling through legal derogations is often also intended to increase support for wolves in conflict situations and thus indirectly also to reduce illegal hunting. However, research indicates that where culling is permitted, the illegal hunting of wolves actually increases rather than decreases.

Detailed analysis

One of the primary causes of human-wolf conflict is the predation of livestock by wolves. The risk of conflict increases when the areas where wolves live overlap with areas where livestock is kept. The aim of actively managing wolf populations is often to reduce losses to livestock; however, the literature on this subject unanimously points out that very few firm conclusions can be drawn regarding the effectiveness and causality of population management measures and protection measures. (Van Eeden et al., 2018).

Of course, there is a positive correlation between the size of wolf populations and the predation of livestock (Kompaniyets & Evans, 2017): the fewer wolves there are, the less predation there can be. However, the aim of derogations granted under the Habitats Directive is not to reduce the wolf population by undermining the favourable conservation status of wolves. Rather, their aim is to limit predation on livestock. There is little scientific evidence of causal relationships on which to base policy and the management of large carnivore populations, however, partly due to inadequate scientific standards in experimental evaluations of this type of research, which in turn is partly due to the difficulty of setting up large-scale controlled experiments (Van Eeden et al., 2018). No studies have been done in which a policy measure (culling) can be compared with a control situation (no culling, but the same degree of disturbance) under controlled conditions in which external side effects can be excluded. We certainly cannot reliably estimate the effectiveness of a measure (e.g., what percentage reduction in the predation of livestock is achieved?), so that we can judge whether the effort required is warranted by the effect that is achieved. What is essential here is statistical repetition (Treves et al., 2019), which will enable us to compare variation in the results within a group (several separate areas where culling is carried out or several areas without culling) with the variation between groups.

Of the twelve studies that have attempted to gauge the effect of the culling of wolves, seven have discovered a reduction in predation, three an increase and two no effect at all (Grente et al., 2020). However, in the cases where a positive effect was found, this could have been purely correlational and not necessarily linked to culling at all. This could be because, for example, allowing the culling of wolves also leads to increased human presence in the area affected, discouraging the presence of wolves there, displacing the wolves elsewhere and extending their range of activity (Harper et al., 2008). Although there is a localised deterrent effect, this is not due to the culling but to the disruption caused by increased human activity. The problem is displaced and possibly even spread further, with no fundamental effect on the essential human-wolf conflict (e.g. Reinhardt et al., 2018). In France, a short-lived positive correlation has been found between culling and losses to livestock (Grente et al., 2020), but causality does not appear to have been sufficiently established: culling is carried out mainly at the end of the grazing season, when wolf pups are almost fully grown, their food requirements are very high and predation on livestock reaches a peak. Shortly afterwards, the grazing period ends, resulting in fewer losses to livestock because there are fewer sheep for the wolves to predate. As such, the positive effect attributed to culling may be purely correlational (Grente et al., 2020) and is probably also a consequence of the limited scale of the evaluation in terms of time and space.

The divergent effects that have been observed when it comes to the relationship between culling and livestock predation may also be because this relationship is nonlinear, as proposed by Wielgus & Peebles (2014) and Fernández-Gil et al. (2016). If the scale of culling is modest, the disruption it causes to the wolves' social structure may actually lead to higher rates of predation on livestock. This is the case if young, inexperienced animals survive, but can no longer count on a supply of food from their parents. If on the other hand the scale of culling exceeds the capacity of the wolf population to grow, or if an entire pack is culled, the number of wolves will decrease (temporarily) and so livestock predation will also be reduced (temporarily) (see also Imbert et al., 2016).

However, within the framework of the Habitats Directive for Strictly Protected Annex IV species, the culling of wolves as a means of reducing livestock predation is not intended to reduce the size of the wolf population, but rather to reduce damage by selecting for shyer animals (Meuret et al., 2018) and to increase public support in the rural communities which have to coexist with wolves (Fernández-Gil et al., 2018). In fact, however, culling can only lead to negative natural selection as far as wolves' behaviours towards humans are concerned. It cannot be assumed that culling will lead to negative conditioning towards humans, since it matters very little what a dead wolf has learned about humans. Neither can that lesson be passed on to other pack members. Attempts at culling do lead to an increased human presence, however, and can thus lead indirectly to negative conditioning towards humans. However, in a landscape where the human presence is everywhere, there is also a positive natural selection in the other direction, in favour of a certain degree of tolerance towards humans: in such an environment, wolves must be able to tolerate the presence of humans and the disturbance they cause. In addition, there is the risk of destabilising the social structure of a pack through a cull, possibly resulting in more damage (see above). It is therefore doubtful whether legal culling can ever lead to the desired effect, especially in landscapes that are dominated by humans.

Furthermore, legal culling can only ever have a limited impact on population size, unless the resulting mortality rate exceeds the natural growth rate – which is itself flexible. However, such intensive culling would not be legally permissible under the Habitats Directive (Fernández-Gil et al., 2018). What is more, allowing legal culling (also known as 'tolerance hunting' or allowing hunting of a predator in order to increase public support vis-à-vis that predator), is often accompanied by an increase in illegal hunting, rather than a decrease in it. This phenomenon has been observed repeatedly in Europe and North America (e.g. Browne-Nunez et al., 2015; Hogberg et al., 2016; Santiago-Avila et al., 2020; Louchouarn et al., 2021). In France, which has the most liberal derogation policy in Europe with respect to wolves (which in principle enjoy strict protection under Annex IV), an estimated 15-20% of wolves are hunted illegally, in addition to the annual loss of 20% of the population through derogations (Mathieu et al., 2021). The incidence of illegal hunting is no lower in northern Italy, where no derogations are granted (Boisseaux et al., 2019). Santiago-Avila et al. (2018) recommend halting all forms of culling and killing and, in cases where governments do choose to allow them, commissioning an independent party to monitor and evaluate effectiveness thoroughly.

7.2.1 Wolves regulate their own population size

In the absence of human intervention, apex predators such as wolves regulate their own numbers. This situation comes about naturally through territoriality and density-dependent regulation (see section 4.5; Wallach et al., 2015). Within an area of 200 km^2, there will be only one wolf pack with a limited number of individuals, on average. If that pack is eliminated, another will quickly emerge and settle into the same territory based on normal dispersion pressure from other areas (e.g. Bjorge & Gunson, 1985; Brainerd et al., 2008). If these additional human-induced deaths no longer occur, the wolf population will not explode. Rather, after reaching a ceiling locally (the limit of the size of the pack), and later also regionally (once all suitable habitats have been occupied by a pack), the population will remain stable. Once the ceiling on numbers has been reached, the primary cause of wolf mortality will be direct competition between wolves, including aggression over territory (Cassidy et al., 2017; Cubaynes et al., 2014). However, when the mortality rate is higher due to culling, for example, the pack will make up the extra numbers to compensate to some extent (Murray et al., 2010). This will include having several reproducing females per pack, having larger litters, reproducing at a younger age and shifting the sex ratio at birth to more females (Sidorovich et al., 2007; Schmidt et al., 2017). In populations that fall below regional ecological support, this effect is also achieved through reduced mortality due to intra-species aggression. In Belarus, where wolf numbers are placed under significant pressure due to hunting every winter, two or even three litters per pack are no exception (Sidorovich & Rotenko, 2019). Another effect of this compensatory growth is a change in the wolves' social structure: more younger animals, less transfer of habits and knowledge to those younger animals from older generations, greater dispersion among young wolves and, therefore, more inexperienced animals and more potential for conflicts between humans and wolves (see section 6.1; Haber, 1996; Wielgus & Peebles, 2014; Imbert et al., 2016). When the social structure and the natural process of intergenerational knowledge transfer is disrupted because, for example, parents disappear and younger wolves are left to fend entirely for themselves, there is an increased risk that those less experienced younger wolves will be forced to target easy prey (Haber, 1996; Imbert et al., 2016). In the Netherlands, that primarily means sheep. There is also a good chance that more prey will be caught, in relative terms, because in stable territories there is a balance between prey caught and consumption in the form of pack size or territory size, but this mechanism works less effectively when populations are disrupted (see section 6.3 and Chapter 8). The presence of scavengers means that the pack will have to hunt again sooner (Haber, 1996).

7.2.2 Managing wolf numbers and damage by wolves

The fact that settled wolves are highly territorial and their numbers stabilise at low densities has important implications for dealing with any damage caused by wolves, such as the predation of sheep. After all, this means that locations that are susceptible to damage, such as grazing land for sheep, can only ever be located in the territory of one wolf pack, and that those sheep will only ever be threatened by a limited number of wolves. As is typical of damage caused by predation, damage caused by wolves is a question of the presence or absence wolves in a particular area, rather than of a local population of predators that has grown too large. This is a stark contrast with species that live in large groups or colonies, such as boar, geese or cormorants: in those cases, the damage that can be caused will vary greatly depending on the local population level. When these animals are present in low numbers, the damage will not usually be serious and is therefore considered acceptable, but as numbers increase the seriousness of the damage increases. In such cases, when the numbers of a species that cause damage in a one place become excessive, in an ecological sense they become a plague. This may be caused by exceptionally favourable weather conditions (in the case of aphids, for example) or by a temporary increase in the food supply (brown rats, for example). The occurrence of such plagues is often unpredictable, but is typical in species that are able to reproduce quickly. There is no such thing as a 'predator plague' however (Van Den Berge & Gouwy, 2021).

When it comes to managing wolves in order to limit potential damage, this has important consequences. It is clear, and has already been demonstrated several times, that when livestock are not adequately protected, the presence of even a single wolf will frequently result in damage (see section 4.6). Incidentally, the concept of the 'presence' of wolves should be viewed according to their natural way of life and population structure. There is therefore no contradiction at all with the fact that a wolf pack (two parents with a few juveniles) can cause more damage than a solitary animal or a pair, or that parents have to catch prey more frequently when they are raising young. After all, it would be unethical to allow a species to be ‘present’, but at the same time to systematically prevent it from reproducing in a natural way by, for example, eliminating litters or decimating the number of juveniles.

The conclusion is, then, that if we wanted to prevent wolves from causing damage in the Netherlands by managing their numbers, the species would have to be pushed back far beyond our borders or be eradicated entirely once again over a large swathe of Europe (Krofel et al., 2011). But given the growth of the wolf population of Western Europe, new wolves will always reappear, and their presence will make itself felt through repeated losses to livestock. That could only ever be stopped by eradicating wolves to such an extent that the situation returned to the one that prevailed some years ago, in an international context, and not merely by removing a few specific individuals. The only workable alternative to this is to take appropriate preventive measures in order to minimise and prevent losses. It is clear that once such measures have been implemented effectively, it no longer matters how many wolves live near a field of sheep (even though this number will never be high).

7.3 Experiences of preventing losses to livestock and providing compensation in other countries

Livestock protection measures work well in principle, but their effectiveness and practicality are highly dependent on the situation on the ground and on local circumstances (e.g. terrain profile, size of the flock or herd to be protected, livestock species, type of grazing). The most common and effective measures are the use of electric fences, livestock guard dogs and the presence of a shepherd; these measures are often combined. In Belgium, Germany and France, the government provides compensation for losses suffered and grants to put preventive measures in place.

In addition, there are several other less efficient protective measures that are based primarily on neophobia (fear of the new) in wolves. These can have some temporary effect, but in the absence of a deterrent these can also lead to habituation, or even positive conditioning.
In order to optimise livestock protection, it is essential to understand the natural behaviour of wolves: how wolves respond to new stimuli in their environment and the concept of neophobia, how they become accustomed to new stimuli (habituation) and may respond both positively and negatively, and how they can be conditioned to those stimuli through both the positive or negative experiences which they associate them with.

Long stretches of fencing designed to keep wolves out are not desirable, as they impede the natural movement of wildlife.

Detailed analysis

7.3.1 The likelihood of livestock predation

Wolves in western and central Europe have territories of 200km^2 on average, which means they almost always overlap with areas of human activity and livestock farming. Livestock protection measures are essential in order to minimise conflicts between humans and wolves. The species that are most at risk of predation are sheep, goats and fallow deer. The latter are frequently kept in captivity, and captive deer are subject to the same risks as other small ruminants when it comes to predation. In addition, there is also a small (but not absent) risk of predation for cattle, with calves in particular being more vulnerable. In Germany, of all the livestock that is predated by wolves, cattle make up between 2 and 4 percent (DBBW, 2021). With respect to horses, a high risk of predation has only been confirmed in regions where horses live largely unattended on semi-wild terrain and in high densities, particularly in northern Spain and northern Portugal (Alvarés, 2011; Pimenta et al., 2018). Elsewhere in Europe, the risk of predation for horses is marginal due to the very different way in which horses are kept (Hendrikx, 2021).

In one seven-year study, Stone et al. (2017) compared the risk of predation for large, free-range flocks of sheep in areas of Idaho (USA) which were protected using a range of tailored measures (livestock guard dogs at certain times of the year, electric fences, flashing lights and audio deterrents at times of elevated predation risk, active shepherding, …) with unprotected sheep combined with the culling and trapping of wolves. They found that area-wide protection measures led to 3.5 times less predation, with the risk of predation falling to just 0.02% per sheep. However, this finding also demonstrates that even for unprotected sheep, the risk of predation is low (0.07%) and that there is a ceiling on this risk due to territoriality in wolves: within one wolf pack territory there will be an average of around five adult wolves (active and hunting independently). Doubling or halving the number of sheep would not result in double or half the losses. Within an individual territory, the number of wolves will be limited because wolves regulate their own population levels naturally, and the overall intensity of predation – and thus the number of losses that can be expected per pack – also has a ceiling. It probably makes little difference whether there are 1,000 sheep or 10,000 sheep in a single territory: if no protections are put in place, a similar number of sheep are likely to be lost per wolf per year.

By the same token, if there are 5,000 sheep in a territory and half of them are well protected, the number of losses may not fall by half – after all, there would still be plenty of unprotected sheep. Losses can only be reduced when a large proportion of sheep are well protected. In other words, as soon as wolves learn that small livestock make ‘easy pickings’, losses among unprotected livestock are bound to occur (Fernandez-Gil et al., 2018).

The situation is somewhat different when it comes to cattle and horses. Compared to the wild ungulates that feature prominently in the natural diet of wolves (roe deer, fallow deer, immature boar, red deer; see section 8.1), cattle and horses make very large prey. This makes the risk of injury much more likely, even in a well-organised pack (see also section 4.3). This is why calves and foals are usually targeted, as opposed to adult animals (Alvarés, 2011; Pimenta et al., 2017). In northern Spain and northern Portugal, horses and cattle make up a significant proportion of the diet of wolves (Alvarés et al., 2015; Pimenta et al., 2018). However, this is due to the fact that these animals graze unattended and live semi-wild in large open areas, so they exert a negative influence on numbers of wild ungulates (Pimenta et al., 2017, 2018; Lopez-Bao et al., 2018). This again underscores the need for an adequate supply of wild ungulates (see section 7.5). The protection of calves (or herds of calves) during the first three months after birth greatly reduces the risk of predation in cattle (Pimenta et al., 2017), particularly if they live in natural herds.

7.3.2 Effectiveness of damage prevention

Compensation, sometimes combined with grants for protection measures, is provided in almost all EU Member States where wolves are protected under Annex IV (France, Italy, Germany, Slovenia, Belgium, the Netherlands, Austria, Denmark, Sweden, Portugal, …). In countries or regions where wolves are protected under Annex V (and may therefore be hunted under certain conditions), this is less often the case. Nevertheless, Poland does provide some compensation.

Fernandez-Gil et al. (2018) provide an overview of policies in various EU countries with respect to compensation, preventive measures and lethal control, and also provide policy recommendations. They conclude the following:

1. Culling is not an efficient method of managing livestock losses because the required reduction in population size is incompatible with the objectives of the Habitats Directive.
2. Preventive measures (livestock protection) and a willingness to move away from counterproductive livestock farming practices are essential to long-term coexistence with large carnivores. Compensation for losses suffered and support for investing in protection should go hand in hand. They advise against compensation without prevention.
3. Governments, agricultural organisations and NGOs have a key role to play in informing and disseminating good information about preventive measures and support for livestock farmers.
4. Maintaining a healthy population of wild ungulates is essential to providing an alternative to livestock predation and thus limiting livestock losses.

7.3.3 The effectiveness of prevention policy

There is range of different livestock protection measures that can be taken, all of which can be effective under certain circumstances. Rossi et al. (2012) focus on various large-scale livestock farming practices that are common in France, where factors such as the species and type of livestock, the size of the operation and the terrain type determine which measures it is best to deploy.
Van Eeden et al. (2018) provide an overview of the effectiveness of preventive measures in limiting livestock predation (not limited to predation by wolves), which has been synthesised from four other review studies containing 114 cases altogether. Although few quantitative effects are included (‘how much is predation reduced by?’), it does show that most livestock protection measures do reduce predation.

Photo 7.3.1 *Wolves and neophobia (also see inset 6.1.1). Wolves are usually very suspicious of new or strange objects, in this case a camera trap. This wolf runs away as soon as it sees the camera trap. Photo compilation: WENR.*

Methods of keeping wolves away – such as fladry fencing (fencing with flags or strips of fabric attached to it – wolves are afraid of these and so this type of fencing can be used around livestock to keep wolves out of fields), flashing lights, audio deterrents (noises emitted to scare wolves away) (…) activated when no people are around – only have a short-lived effect because they are based on neophobia, and suspicion or fear around new situations. (See Photo 7.3.1 and inset 6.1.1 for definitions regarding behaviour.) In the case of methods that are not based on actual physical deterrents (such as an electric shock), wolves usually learn that there is no risk to them (Shivik & Martin, 2000), which eventually renders the measures useless (Khorozyan & Waltert, 2019). In some cases, this can even lead to positive conditioning (Ward et al., 2008). However, these forms of mild alarm can have a longer-lasting effect if they are accompanied by aversive conditioning towards people and are not left in place permanently (Shivik, 2006; Stone et al., 2017). These methods can be used more or less selectively, rather than as standard, using motion sensors: if movement is detected in the vicinity of a particular location, an audio deterrent, flashes of light or even an olfactory stimulus is triggered. It is recommended that a given deterrent is not used for more than six consecutive weeks, in order to avoid habituation (Stone et al., 2017). An even more selective approach is based on GPS data from a tagged wolf, using a ‘radio-activated guard’ (RAG; Breck et al., 2002). This also enables humans to actively repel a specific individual wolf (see below).

According to Khorozyan & Waltert (2019) and Bruns et al. (2020), electric fencing appears to be the most effective measure for protecting livestock, with a longer-lasting effect and a strong reduction in predation. With proper installation and maintenance, the effectiveness of electric fences is almost 100% – by far the most effective measure for small-scale operations or amateur smallholders (Bruns et al., 2020). The criteria for what constitutes an effective, wolf-resistant electric fence differ between countries, however, and sometimes even within the same country (Reinhardt et al., 2012). However, electric fences are also relatively sensitive to faults and the larger the area that needs to be fenced off, the greater the chance of a fault occurring. No aversive conditioning appears to be associated with electrified enclosures: if the fencing loses power due to a fault (and so there is no physical deterrent), the wolves will resume predation relatively quickly. This means that aversive conditioning only occurs when there is actual electrical voltage, and it is possible that wolves can detect this without direct contact with the wire.

The use of livestock guard dogs to protect livestock is generally assessed as a reasonably effective measure (Van Eeden et al., 2018; Bruns et al., 2020; Van Bommel, 2020b), but its effectiveness depends greatly on how many animals need to be guarded, the number of dogs relative to the size of the wolf pack, how well the dogs are trained and interaction with the shepherd. In France, livestock guard dogs (and other measures) are usually used in combination with night enclosures, sometimes electrified, and/or the presence of a shepherd (Rossi et al., 2012). In Germany, where conditions correspond fairly closely with those in the Netherlands, Bruns et al. (2020) recommend the use of electric fencing and, for larger herds of sheep, combining this with livestock guard dogs. Although Rossi et al. (2012) report that livestock guard dogs appear to be less suited to guarding herds of cattle due to their more dispersed grazing pattern than sheep, Gehring et al. (2010) identify livestock guard dogs as highly effective for cattle.

7.3.4 Collars

Collars for sheep that emit a loud ultrasonic signal in the event of an attack are commercially available but have never been proven effective (for details, see Mergeay et al. (2019)). The sound emitted by these collars is inaudible to humans, but perfectly audible to both sheep and wolf. Extensive tests have been done on many species to ascertain whether loud noises can keep unwanted animals at bay (see Edgar et al. (2007) for an overview). A short-term effect as a result of neophobia cannot be ruled out, and differences between individual animals can also be significant, but the general rule is rapid habituation (Crawford et al., 2018). One question which has not yet been answered scientifically is whether the physical deterrent produced by the collar (a loud noise) is enough to offset the reward of the act of hunting, combined with previous positive conditioning concerning small livestock as suitable prey. In some cases, wild animals have actually become *positively* conditioned to noises that were intended to deter them: the noise came to be associated with food, rather than frightening the animal away (Ward et al., 2008).

In South Africa, wide PVC collars (‘King Collars’), metal mesh collars (‘Dead Stop Collars’) or similar collars are used to provide physical protection to the necks of sheep in order to reduce the risk of predation by jackals, leopards and cheetahs (Shivik 2006; The Predation Management Forum 2016). According to Smuts (2008), this reduces predation by 80 to 100%. Jackals will sometimes adapt by killing the sheep in ways other than bites to the throat, but the collar does make predation much more difficult. The PVC collars are not expensive, making it possible for African livestock farmers to use them (Smuts, 2008). This practice does not appear to have been adopted in North America or Europe in order to protect sheep from wolves, possibly because wolves quickly learn to kill sheep by other methods.

Wolf collars have also been developed and tested (Hawley et al., 2009, 2013; Rossler et al., 2012). This method involves catching a wolf, fitting it with a shock collar and possibly tagging it. If the wolf comes too close to a livestock farm or enters a predefined controlled zone, the collar will give the wolf an electric shock. This has a major effect on the collared wolf, and this also rubbed off on other members of the pack to some extent, but was it only effective for as long as the battery lasted. The longest battery life achieved was 60 days. All the effects had worn off by forty days after the battery failed (Rossler et al., 2012). This technique is barely useful at all, in fact, due to the significant effort that is required to catch a wolf and how little time the collar remains effective. What is more, in a highly fragmented landscape dotted with small-scale livestock operations, the result would be a labyrinth of permitted and prohibited zones, which would not appear to be compatible with the Habitats Directive.

An alternative method involves attaching a GPS transmitter or a radio transmitter to a wolf. When the wolf enters an undesirable environment, various deterrence methods (flashes of light, loud noises, …) are triggered, simulating proximity to people (Breck et al., 2002). Since most wolves are already somewhat negatively conditioned to human activity, they will avoid those places temporarily. This method generally works relatively well, but it also requires a tag to be fitted to the wolf and involves the risk of habituation if not accompanied by actual regular human presence (Stone et al., 2017). However, this method can be used to adversely condition ‘problem wolves’ to humans. Due to the lack of shyness in these wolves, it is easier to approach them with a tranquiliser gun, after which they can be tagged. Their position can then be closely monitored using a GPS transmitter and measures can be applied to deter them in a very targeted manner, so that they develop an aversion towards a certain behaviour.

7.3.5 Long-distance wolf-resistant fencing

There is currently one instance in the Netherlands (July 2021) where a deliberate attempt is being made to exclude wolves using a long-distance fence. The Hoge Veluwe National Park, which is also a Natura 2000 area, is surrounded by a fence that was originally designed to allow wild animals to pass through it in certain places, based on the policy of allowing connections between fragmented areas of wild habitat; however, in 2019 the openings in the fence were closed up to prevent wolves from entering the park (NOS,2019). In addition, the Wolvenhek Fryslân Foundation created a test set-up in July 2021 as an illustration. The organisation’s ultimate plan is to realise a fence of approximately 150 kilometres near the provincial border with Groningen, Drenthe, Flevoland and Overijssel, with the intention of preventing wolves from settling. From the perspective of vital ecosystems and the natural movements of fauna, this is an unfortunate development that should be seen as contrary to the spirit of nature conservation legislation and species protection (Boerema et al., 2021; Trouwborst, 2018). The province of Fryslân has therefore indicated that it cannot issue a permit or exemption for the construction of the whole wolf fence. There is no known case in neighbouring countries in which wolves have been deliberately excluded using a long-distance fence. Until 1989, Germany was divided by the ‘Iron Curtain’, which also restricted animal migration (and the same probably also applies to the recently constructed fences that are designed to stop refugees in Bulgaria, Greece, Hungary, and other countries).

However, several countries have currently physical sealed off part of their territory from neighbouring countries as a measure to reduce the spread of African swine fever from wild boars. This is currently the case along the border between Germany and Poland over a distance of about 300 kilometres (https://blog.wwf.de/schweinepest-zaun-polen/) and between France and Belgium over a distance of about 140 kilometres. These fences are expected to be fairly resistant to wolves as well (personal communication Ilka Reinhardt). However, the plans of the Wolvenhek Fryslân Foundation are the only ones intended specifically to keep wolves out. Such a fence is undesirable from the point of view of nature conservation objectives. It would form a barrier for many species and thus negatively affect the vitality of animal populations. This will be particularly true for species that are mobile. Wolves are highly mobile, but also resourceful when it comes to finding a way through or around obstacles like fences. It is therefore unlikely that such a fence would even achieve its goal: to keep wolves out permanently.

7.4 Experiences in other countries

The aim of driving wolves away is to discourage and deter undesirable behaviours in the future, in the hope that the wolves may associate this negative experience with their own actions. However, repelling wolves from livestock is an ineffective method because the wolves actually come to associate this with humans, and not with the livestock. Although repelling wolves can have a localised effect, the wolves' behaviour remains unchanged. At most, they may develop an aversion to humans. This can be beneficial if the livestock in question is kept in the vicinity of humans, however.

Deterrence has proven valuable for wolves that are highly habituated to humans, and can reverse this habituation. In such cases, it is advisable to use the most forceful possible method, which generally means firing non-lethal ammunition.

This should only be done by people who have undergone appropriate training. The distance within which rubber bullets can be fired with sufficient accuracy (without hitting vital organs) is less than 30 metres. This limits the option to wolves that can be approached at this distance.

Detailed analysis

7.4.1 Deterring wolves and conditioning their behaviour

In any form of conditioning, there is a relationship between 1) perception, 2) response, and 3) reward or punishment for that response; this ultimately leads to the reinforcement or weakening of the behaviour (Shivik et al., 2003). This is also how animals learn which foods are edible or harmful and which other animals or plants are a danger to them. In the animal kingdom, bright warning colours often serve to advertise toxicity or inedibility ('aposematism'), helping to speed up spontaneous conditioning. For example, if a juvenile wolf is curious about a wasp's nest and gets stung on the nose a dozen times with a painful toxin, the next time it may recognise the distinctive markings of a wasp and be more cautious.

The aim of repelling wolves is to break and reverse an existing positive association between a particular behaviour on the one hand and a reward on the other hand, through aversive conditioning. This can be tried when a wolf has come to associate humans with the presence of food, for instance, possibly because the animal has been fed by humans in the past. Because the wolf has been positively conditioned to humans, it will actively seek out humans in the hope of finding food (see Nowak et al., 2021). This kind of conditioning towards humans is common in countless animal species (foxes, bears, baboons, macaques, meerkats, hedgehogs, badgers, sea gulls, geese, songbirds, carp, sharks, ...).

It can sometimes be reversed, but reversal requires much stronger aversive conditioning towards humans: the wolf needs to undergo a highly unpleasant experience every time it encounters humans, so that the unpleasant experience becomes its primary association with humans. The longer the animal has been positively conditioned towards humans, the more difficult that conditioning is to reverse. This is where the expression 'a fed bear is a dead bear' comes from: when a bear has become conditioned to receiving food from humans, it will be very difficult to condition that same bear aversively to humans and their environment, and often there is no option other than to kill the bear (Shivik et al., 2003). In Yellowstone National Park, wolves that get too close to tourists (because they are habituated to humans and are inquisitive about what they may have to offer) are shot using paintball guns (Smith et al., 2020b). This is very painful, and is usually enough to keep the wolves away permanently and ensure that they avoid humans in the future. However, once the wolves have been fed, this is much more difficult to achieve (Reinhardt et al., 2020).

In Europe, the need to condition wolves aversively to humans is highly unusual: bold wolves are rare and in most cases they have been fed as young wolves, or were taken from their parents as pups and then kept in captivity for some time (Linnell et al., 2002, 2021). Two well-documented cases from Poland in 2018 can also be attributed to this (Nowak et al., 2021).

7.4.2 Deterring wolves from attacking livestock over the longer term

The main reason for wanting to drive away wolves is economic damage to livestock, and the desire to drive away a wolf that has attacked livestock without actually killing it. Wolf strategies in several European countries refer to the option of non-lethal ammunition to repel wolves following attacks on livestock (see section 7.1).

However, conditioning wolves not to attack livestock is very difficult because all the species that are kept as livestock today are descended from the natural prey of wolves. Wolves have been positively conditioned to prey on ungulates (wild or domestic) from an early age and, of course, they have also evolved to kill and eat ungulates. Repelling wolves from livestock using paintballs or rubber bullets, for example, does not cause negative conditioning to livestock, but merely to the source of the pain: humans (Shivik et al., 2003). After all, a dog that is beaten by its owner because it has stolen a sausage from the table does not learn that sausages are not edible, but that the owner will hit him if he sees him taking one. As a result, the dog simply learns to steal when the owner is not around. If sausages continue to be left unattended on the table, they will still be stolen.

While driving away a wolf that is trying to take livestock may provide some localised relief, the wolf will only keep its distance because of the increase in human activity. The underlying motivations and behavioural patterns will not disappear, but simply be displaced to somewhere with less disruption from humans (Santiago-Avila et al., 2018). After all, the need to protect livestock properly against predation comes from the near impossibility of conditioning predators not to attack their natural prey. So it is important to understand that repelling a wolf that is interested in livestock will not condition that wolf not to attack livestock. Like other livestock protection measures, it may reduce predation, but this will mainly be a result of the predator’s fear of people, rather than any aversion to attacking livestock.

7.4.3 Aversive conditioning to livestock

Attempts have been made to condition wolves against particular types of food by leaving them food that has been laced with an emetic (a substance that causes severe vomiting after it has been ingested) in combination with a novel odour (Rusiniak et al., 1979; Tobajas et al., 2019, 2020a). The function of the new odour is the same as the bright colour warning in insects (aposematism): it creates a new association in the predator and imprints this strongly: for example, vanilla + meat = vomiting or nausea. The expected result is then that other items that have the same odour will also be avoided, without the wolf even having to taste them. When this method was tested on dogs and wolves in captivity, it has appeared to work quite well: 4 in 5 wolves refused after ingesting the emetic odour-treated meat (Tobajas et al., 2020a) and in some dogs the aversion to scent + food without emetic lasted up to 11 months. Of course, this result is a long way from conditioning wild wolves to avoiding the predation of livestock. However, tests involving foxes and nests containing partridge eggs treated with an emetic showed that the principle of conditioned food aversion can reduce the taking of eggs from nests (Tobajas et al., 2020b).

In Belgium, a four-year pilot project was given funding in 2020: an attempt is being made to give sheep an odour and an unpleasant taste, to test whether wolves can be aversively conditioned to a particular combination [sheep + unpleasant taste + odour] (FWO 2021). The goal is for a painful substance to be released into the wolf’s mouth whenever a wolf bites a sheep. The unpleasant odour will serve to create a new association and help condition the wolf not to attack sheep: sheep + odour = pain. This is not intended to protect small privately kept flocks, but to protect large flocks in situations where other livestock protection measures are difficult to implement. If this principle is effective, flock protection is only expected to be achieved if the majority of sheep are permanently treated in this way. This seems unlikely to lead to general aversive conditioning to sheep (M. Chastel, personal communication).

7.4.4 Deterrence and aversive habituation

Any attempt to repel wolves must involve the creation of a clear association between the animal's own behaviour and the fact that it is being driven away. Only then can aversive conditioning occur with respect to the right target animal. If this does not happen, when the unpleasant experience occurs, aversive conditioning will occur with respect to another secondary factor, such as the presence of humans. Whenever the undesirable behaviour goes punished or even results in a reward (e.g. the successful predation of livestock), the aversive association will weaken. The stronger the negative experience, the more effective the aversive conditioning will be. If a measure does nothing more than startle the wolf and make it run away (such as loud noises, flashes of light), with no other negative effect, this risks allowing the animal to simply become habituated to it. It is therefore advisable to repel the animal using the strongest possible methods, without endangering the life of the animal, and to do this as early as possible in the development of positive conditioning, so that the cycle of positive conditioning is broken early (Reinhardt et al., 2020). The more often the animal is 'rewarded' for its actions, the more difficult it will be to unlearn the behaviour. This whole process has much in common with dog training, and every dog trainer understands how important it is to teach an animal at the right time and in the right way. Generally, several repetitions are needed to make a wolf unlearn a particular behaviour and 'reprogram' the animal to adopt a different pattern of behaviour. Obviously, this is difficult to achieve with a wolf that is living in the wild because it is difficult to predict where and when the animal might engage in that behaviour. This is why the authors indicate that catching and tagging the wolf can facilitate this process, because this makes it much easier to monitor the animal. This is relatively easy to do for wolves that associate humans with food and are therefore easier to approach.

Reinhardt et al. (2020) report that wolves are so intelligent that actions taken to repel them must be considered and planned very carefully in advance and then carried out by experts. Every situation is unique and must be assessed in detail: what is attracting the wolf in the first place, and can that stimulus be eliminated (for example, by storing food waste in an inaccessible container)?

It is also important to know how a wolf is conditioned, so that it can be repelled in a targeted way that will definitely result in a negative association. If a wolf is approaching people because it has learned to associate humans with the possibility of food, that wolf will need to develop a negative association with humans. This category is the simplest to tackle because this kind of wolf will tolerate close proximity with humans, making it possible to target it with a paintball gun and modified ammunition (non-toxic gelatine bullets), for instance. Some experience has been gained in Europe with repelling animals in this way, but mainly with bears. There are no published studies on the effectiveness of using aversive conditioning to deter wolves by modifying their behaviour. Linnell et al. (2002) believe this is unsurprising given the small number of wolves that become bold around humans. A firework being fired within 10-15 metres of the wolf will result in the wolf running off immediately, but no long-term effect has been demonstrated. Sharp pain, caused by non-lethal ammunition, will result in a much stronger aversive association than a noise or a flash of light. However, whether this has a long-term effect has not been studied in Europe. Firing non-lethal ammunition also has practical limitations, since it can only be done by a qualified person. The animal must be shot from the right distance: too close will be hazardous for the animal; too far away risks inaccuracy, and vital organs may be hit as a result.

Deterring animals using non-lethal ammunition can be done using firearms and rubber ammunition (shot or bullets). Rubber or plastic bullets can be used safely at a distance of approximately 20 metres and they are therefore suitable for deterring wolves that associate humans with food, and which therefore approach humans at close quarters (Reinhardt et al., 2020). This method is only accurate up to a distance of 30 metres, however. The target is usually the gluteal muscle, because this only entails a minimal risk of serious injury to the animal. At greater distances, the chance of hitting more important parts of the body (e.g. abdomen, head, ribs) is too high.
Another alternative is using paintball guns (0.68 inch calibre) or hard gelatine bullets. These are reusable provided they do not shatter, and they are also made of biodegradable materials. These, too, are only accurate at a distance of 30 metres and have little impact at a greater distances. In North America, this method is regularly used to deter coyotes, wolves and bears (Smith et al., 2020b; Young et al., 2019; Black Bear Conservation Coalition, 2015). The use of beanbags is also limited to very short distances (<15 metres), which makes these less useful.

Conditioning animals to be averse to people can therefore only be done ethically in situations where a wolf can be approached at a distance of less than 30 metres and is therefore generally only possible with wolves that are highly habituated to humans.

7.4.5 Using deterrence methods in the Netherlands in practice

In practice, deterrence is only required and only practical with wolves that are highly habituated to humans. Deterring wolves effectively in the Netherlands will not be easy. Firstly, it is not easy to track wolves down, let alone to successfully repel them. Secondly, it is important to know which animal is being targeted. In cases where deterrence is targeted at a specific wolf (e.g. a wolf that has been shown to have attacked properly protected livestock repeatedly), it is not easy to identify that wolf (unless the behaviour is highly distinctive, see e.g. wolf Billy, section 4.6). Sometimes it is also unclear whether the wolf is a specific individual that has repeatedly engaged in undesirable behaviour or whether several wolves are involved. Thirdly, it is not easy to approach a wolf closely enough (within 20-30 metres) to deploy the deterrence method. If this involves shooting, this is difficult in environments where humans are present due to safety considerations. Reinhardt et al. (2020) also indicate that it is advisable to issue permits that are valid for a specific time and place, that there is adequate communication due to the sensitivity of this deterrence strategy, and that the identity of the people who are shooting the ammunition (lethal or deterrent) is kept anonymous.

7.5 Expected effect of fauna management practices on wolves in the Netherlands

The native wild ungulates present in the Netherlands are roe deer, wild boar, fallow deer and red deer, and these are all part of the diet of wolves. Of these, only roe deer could in theory be present anywhere in the Netherlands; there are still designated habitats for the other species, with no animals outside those zones. Ungulate populations are reduced significantly through fauna management strategies. The number of ungulates is monitored in the Netherlands in order to track changes, but it is difficult to know the true scale of ungulate populations. In the Veluwe area and Noord-Brabant, the presence of wolves demonstrates that the ungulate population is sufficient for wolves to settle. However, the wolf population remains in its colonisation phase and wolf numbers remain low. It is unclear whether fauna management practices limit the extent to which the ecological carrying capacity of wolves can be achieved. The return of wolves to the Netherlands means it is important to look more closely at the effect of hunting game on the availability of prey for wolves.

Detailed analysis
Whether fauna management practices are effective depends on three main factors. Firstly, the number of ungulates that wolves require as prey per year, and therefore what population of ungulates is required. Secondly, an accurate picture of the ungulate population in terms of numbers, composition and dynamics. Thirdly, the number of animals that are removed from the ungulate population every year through population management measures. These factors are analysed further in the sections below.

7.5.1 Wolves’ food requirements

Chapter 8 describes the diet of wolves in neighbouring countries, but no data is currently available for the Netherlands. Groot-Bruinderink et al. (2012) describe the amount of food a wolf consumes and what that means for a given area. They show that a wolf consumes an average of 4 to 5kg of meat per day and that in Lusatia (Germany) one wolf kills an average of 65 roe deer, nine red deer and sixteen wild boars every year. It is clear that an area without a vital population of ungulates will be unsuitable for colonisation by wolves. It is unclear exactly how this would play out in the Netherlands, so any analysis of possible effects remains speculative. It is possible that wolves may specialise in certain kinds of prey; however, we do not know which species of prey are important, what proportion of those are available as prey, whether that availability applies to all wolves, what proportion of the prey is actually eaten, what the effect of a combination of prey species is on that relationship, and to what extent farm animals should be included as potential prey.

7.5.2 Monitoring and managing ungulate populations in the Netherlands

The native wild ungulates present in the Netherlands are roe deer, wild boar, fallow deer and red deer, and these are all part of the diet of wolves. Of these, only roe deer could in theory be present anywhere in the Netherlands; there are still designated habitats for the other species, with no animals outside those zones (IPO, 2019). In some provinces, areas are allocated for ungulates outside their habitats provided they do not cause significant damage, such as for wild boar in Limburg and Noord-Brabant. For all ungulate species, population management takes the form of culling, which entails the killing of between 45% and 80% of the population every year (see www.faunabeheerunit.nl for fauna management plans). Population management therefore impacts on wolves, because it determines where ungulates occur and how many of them there are.

The purpose of fauna management is to limit damage to crops, forestry or valuable areas of nature, and also to ensure road safety. Population management and culling are not a goal in their own right, but a method of limiting the damage or risks associated with high numbers of ungulates. Interventions such as culls are only permitted when they are shown to be necessary, when there is no alternative and when the conservation status of the species concerned is assured. These three criteria mean that decisions must be substantiated carefully using a transparent assessment framework. This also requires an accurate picture of ungulate numbers, population trends and dynamics (Groot Bruinderink & van der Grift, 2015). In a densely populated country like the Netherlands, where areas of wild habitat are highly fragmented, this is frequently a challenge. For example, we know little about the relationship between numbers of roe deer and the incidence of various forms of damage. Similarly, we know little about which factors affect the occurrence of damage and, subsequently, how those key factors can be used to predict various forms of damage and take appropriate steps by managing fauna populations (Van der Grift., 2018). As a result, for example, the relationship between managing deer and the risks to road users is unclear. Similarly, due to the isolation of the Veluwe area combined with the goal of promoting forest rejuvenation, the population of red deer is lower than the minimum viable population size of 4,000 individuals (Den Ouden et al., 2020).

Ungulate populations are monitored in the Netherlands in order to track changes in their numbers. However, it is difficult to estimate the true size of ungulate populations. European research (Croft et al., 2018) as well as research in the Netherlands (Groot Bruinderink et al., 2009) has shown how little knowledge is available regarding population densities, overall numbers, population structure, migration/dispersion, reproduction and mortality, in this case with respect to wild boar, specifically. The same applies to other ungulates, and it would therefore be useful to improve our knowledge of ungulate populations (overall numbers, trends and dynamics) in order to manage their numbers more effectively (Groot Bruinderink & Van der Grift, 2015).

7.5.3 Possible effect of fauna management practices on wolves

The diet of wolves in the Netherlands is currently unclear. We do have figures on how many ungulates are counted, shot and killed, but there is no clear overview of the actual numbers, composition and dynamics of the ungulate population. Based on the wolves that have settled in the Veluwe area and Noord-Brabant (see Figure 5.9.1), we can conclude that local ungulate populations there are adequate to sustain wolves. In short, it is likely that nature reserves with similar ungulate densities and/or compositions would also be suitable for colonisation by wolves. In Germany too, ungulate density and/or compositions differ between localities, but the assumption is that they are generally large enough to enable colonisation by wolves (section 5.6; Kramer-Schadt et al., 2020; Reinhardt et al., 2021). Some studies in Germany have shown that in areas with wolves, the number of ungulates shot did not differ from surrounding areas where wolves are not found, and that ungulate populations underwent similar trends (Sächsisches Staatsministerium für Umwelt und Landwirtschaft, 2009; Nitze, 2012). Ilka Reinhardt (personal communication) also indicates that no change to the policy on culling has yet taken place in Germany in order to support wolves. However, these studies focused on population management and not on wolves, which is our focus here.

In the Veluwe area and Noord-Brabant, the presence of wolves shows that ungulate populations are sufficient for wolves to settle (see Figure 5.9.1). However, the wolf population remains in its colonisation phase and so wolf numbers remain low. It is unclear whether fauna management practices limit the extent to which the ecological carrying capacity can be achieved. In the case of the Noord-Brabant wolf, it is unclear whether the wild ungulate population may be more limited within the available habitat and this is why the wolf attacks sheep regularly (GW1625m; see section 4.6), or whether this individual does this simply because the sheep are easy prey, for example. Attacks on livestock are rare in the Veluwe area, and wolves there eat wild ungulates almost exclusively. The existing number of ungulates and the composition of ungulate populations in those areas therefore appear adequate. Locally, however, wolves may have an observable effect on ungulates. By mid-July 2021, few red deer calves had been observed, while in previous years there had been many more (previous years 30 to 40 calves, this year about 10; personal communication F. Theunissen, Natuurmonumenten Planken Wambuis). This is believed to be the result of predation by the wolves that have been present in that area for a year now (Wolf Habitat Southwest Veluwe; Figure 5.9.1). It is possible that this is happening on a larger scale in the Veluwe area, and that this will eventually have an effect on the biomass of ungulates in the Veluwe area, especially if the same ungulate population is also reduced. It is therefore important to monitor the ungulate population in terms of overall numbers, composition and trend (see section 7.5.2) in order to adjust the number of individuals culled accurately and when required.

In July 2021, the Gelderland Fauna Management Unit (FBE) presented its plans for ungulate management in the Veluwe area for 2021-2022 (FBE 2021). This indicates that in order to preserve biodiversity – and also reduce the risk of road accidents and agricultural damage – the existing stock of ungulates will be reduced drastically. For red deer, the plan is to reduce the spring population (approximately 3,200 deer) or summer population i.e. including calves (approximately 4,600 deer) to a spring population of 1,600; for boars, the plan is to reduce the population from approximately 10,000 to 1,350; and for fallow deer to reduce the population from approximately 1,117 to 414. This represents a reduction in the population of wild ungulates (excluding roe deer) of around 80% by means of culling. In the fauna management plan for large ungulates (FBE, 2019a), the FBE indicates that the effect of wolves on ungulates could lead to interim adjustments to this fauna management plan. It is not possible to ascertain from this document, or from the Fauna Management Plan for Monitoring Species (FBE, 2019b), whether the effect of culling on achieving the local ecological carrying capacity for wolves was taken into account when calculating the target populations of ungulates. It is likely that any such substantial reduction in the availability of prey will influence the presence of wolves and/or future changes in the wolf population. It remains to be seen whether that will result in the wolves adopting different behaviours or a change in the diet of wolves, and to what extent the cull may prevent wolves from achieving their local ecological carrying capacity. Research into the effects of population management on the availability of prey for wolves is therefore recommended.

Outside the Veluwe area, the range of wild ungulates is more limited and is actually zero in the case of boar and/or red deer. Roe deer is the most common species, but numbers have been greatly reduced through fauna management practices. This gives wolves fewer opportunities to settle permanently and reproduce outside the Veluwe area. It may also mean that wolves there claim larger territories in order to compensate for the low availability of prey, and/or prey more often on unprotected domesticated or semi-domesticated ungulates such as sheep (also see section 4.6 and Chapter 8). Indeed, this may also happen in wolves that are already settled, such as those in the Veluwe area, if the ungulate population in their territory is reduced substantially.

The return of wolves to the Netherlands means that it is important to take wolves into account when it comes to managing ungulate populations. It is recommended that current management plans are re-evaluated in order to take account of expected predation by wolves when determining numbers of ungulates to be culled. This is also the recommendation made in the guidance document on large predators drafted for the Council of Europe by the Large Carnivore Initiative Europe (LCIE) (Linnell et al., 2008). That document states that it is very important for wolves and lynx that the presence of larger predators is taken into account when deciding on shooting quotas for ungulate management.

Photo 7.5.1 *Female wolf whose enlarged nipples indicate that she has been raising young. Photo: Hugh Jansman.*

8 Ecology

8.1 Diet: What do wolves in the Netherlands eat?

It is likely that the diet of Dutch wolves is similar to that of wolves in Germany and Flanders. Roe deer are the main component, supplemented by other wild ungulates, such as wild boar and red or fallow deer, depending on what is available in the wolf's territory. Livestock, particularly sheep, make up a small proportion of the diet of settled wolves. Roaming wolves, on the other hand, can appear anywhere and are usually young, inexperienced wolves looking for a territory of their own. Livestock, particularly sheep, are also frequent prey for these roaming wolves, due to chance and convenience.

Detailed analysis

Wolves' diets are generally analysed by identifying the remains of prey in faecal matter. Traditionally, this is done mechanically, by examining fur, tooth and bone fragments under a microscope and with the naked eye (Photo 4.4.1). Recently it has also become possible to do this through genetic analysis. The Dutch Mammal Society, in collaboration with the University of Antwerp and the Leo foundation, has already begun a study into the diet of wolves in the Netherlands, using both these methods. The results are not expected until the end of 2021 (personal communication M. La Haye, Dutch Mammal Society). The University of Groningen is conducting research into the effect of wolves on the ecosystem of the North Veluwe area. This may be supplemented in the near future with a dietary study (personal communication by Bjorn Mols, RuG). Prey remains are also found in the field, and the stomach content of animals killed by vehicle strikes is another possible source of information on the diet of wolves, although the limited amount of data available does not yet allow for any preliminary findings.

The current lack of data does not mean that we have no idea what wolves in the Netherlands eat, however. After all, when it comes to its place in the food chain, the wolf is a well-studied species. We know that the diet of wolves is determined mainly by a combination of the availability of prey (= which species are present and in what numbers) and prey vulnerability (= are those species easy to catch or not; see also section 4.3) (Peterson & Ciucci, 2010; Mech et al., 2015). Individual preferences, learning processes and the life phase of the wolf (e.g. roaming individuals or settled pack) can also influence diet (Mech & Peterson, 2010). Roe deer, red deer and boar are considered the most important prey species in the temperate climate region of Europe, but other ungulates that occur in certain regions, such as fallow deer and mouflon, can also be an important source of food (Okarma, 1995; Jędrzejewski et al., 2000; Kübarsepp & Valdmann, 2003; Nowak et al., 2005; Ansorge et al., 2006; Barja, 2009; Žunna et al., 2009; Nowak et al., 2011; Lanszki et al., 2012; Wagner et al., 2012; Imbert et al., 2016; Mori et al., 2017; Sin et al., 2019). Hare and rabbit is also on the menu, although the importance of this category of prey is limited in the European temperate climate zone (Peterson & Ciucci, 2010). The female wolf killed in the South Veluwe area, GW1729f, had hare remains in her stomach (BIJ12.nl; progress report June 2021). In wetlands, on the other hand, beavers can make up an important part of the wolf's diet (Sidorovich et al., 2017; Mysłajek et al., 2019). When insufficient wild prey is available, whether for a shorter or a longer period of time, the predation of livestock may become an alternative or even the dominant foraging strategy. This phenomenon occurs mainly in nutrient-poor regions in Southern Europe and Norway, where livestock is often left to graze freely and may even live wild (Zlatanova et al., 2014). When both wild prey and livestock are commonly available, a preference for wild prey is generally observed. The presence of adequate protective measures reinforces and perpetuates this preference (Sidorovich et al., 2003; Nowak et al., 2005; Gula, 2008; Barja, 2009; Imbert et al., 2016).

In the areas where wolves currently occur in the Netherlands, there are two different scenarios (see also section 4.6). In the Veluwe area (Gelderland), the available prey is characterised by the sustained presence of red deer, boar, roe deer and fallow deer. Noord-Brabant, on the other hand, lacks a vital population of red deer, fallow deer and wild boar at present. The German federal state of Saxony and the Flemish province of Limburg in Belgium could provide, respectively, a strategy for both of these two scenarios in the Netherlands, taking account of the landscape.

8.1.1.1 Saxony

Between 2001 and 2021, 8,781 samples of droppings were collected and analysed mechanically in the German state of Saxony (Reinhard et al., 2021). The results are expressed in terms of biomass consumed, calculated according to Goszczynski's method (1974), whereby the dry mass of rinsed faecal matter is multiplied using a particular digestion coefficient, depending on the prey species identified. Using this method, it was found that 94.1% of the wolves' diet consisted of wild even-toed ungulates (Figure 8.1.1). Within this category, roe deer were by far the most frequently consumed species (50.9%), followed by wild boar (20.3%) and red deer (13.1%). Based on a subset of the data, Wagner et al. (2012) calculated that roe deer were consumed relatively frequently compared to their share of the even-toed ungulate population (= positive selection). Wild boar and red deer, on the other hand, were consumed relatively less frequently (= negative selection) possibly due to the greater risk of injury when hunting these prey (also see section 4.3).

On a seasonal basis, roe deer were consumed frequently throughout the year with no preference for juveniles, i.e. the proportion of juveniles in the wolves' diet was approximately equal to the proportion in the total population of roe deer. In the case of red deer, a preference for juveniles was found, resulting in slightly higher consumption of this species of prey during the summer period (also see section 7.5 for an example in the Netherlands). Wild boar were mainly found in wolves' diets during the spring, when the boar population includes numerous juveniles. In addition, during the period of study the proportion of wild boar in wolves' diets increased markedly when there was a bumper crop of beech nuts and acorns followed by a milder winter, resulting in higher rates of reproduction. For roe deer and red deer, this factor remained fairly stable on an annual basis.

Mouflon were predated mainly at the start of the study period, after which the species largely disappeared in the wild (2001-02: 8.6%, 2001-21: 0.4%). Fallow deer also made up a small proportion of the wolves' diet (5.9%), which is consistent with the small proportion of the wild even-toed ungulate community that these animals constitute. Other species of prey included lagomorphs (hares and rabbits) at 3.2%. In the Königsbrücker Heide area, one of the nature reserves surveyed, the biomass of beaver consumed was 7.2% during 2005-2014 (Holzapfel et al., 2017). Across the entire study area, cattle, predominantly sheep, made only a limited contribution to the wolves' diet (1.6%). This low percentage may be due to the fact that the majority of wolves are settled (rather than roaming) and also that livestock farmers have many years of experience in preventing wolf attacks. Small mammals, especially voles, were occasionally found in the wolves' droppings, but as a proportion of biomass they only made up a small percentage. Other medium-sized mammals such as muskrats, foxes, cats, raccoon dogs, birds, fish and fruits (mainly apples) were also observed sporadically.

8.1.1.2 Flanders

An initial dietary analysis has already been carried out in Flanders, using the mechanical method (Van der Veken et al., 2021). The frequency of occurrence (FO) was calculated using 140 faecal samples found within the wolf territory in Limburg. The FO is the percentage of samples in which a particular species of prey is found, as a proportion of the total number of samples examined. This method has the disadvantage that greater importance is given to smaller prey species (e.g. lagomorphs and small mammals), since the amount of indigestible material (hair, bone and tooth fragments) per unit of biomass is relatively higher when smaller prey has been consumed.

Wild even-toed ungulates were observed in 90% of the samples. Again, roe deer appeared to be the most frequent species of prey all year round (FO=69.3%), followed by boar (FO=22.9%). In the springtime, juvenile wild boar seemed to be particularly popular prey among the wolves, as in Saxony. Some 59.4% of those boar were found to be younger than 3-5 months. Fallow deer, whether feral or kept by humans, were identified in 7.1% of the droppings.

Lagomorphs were found in 13.6% of the samples examined. For livestock the figure was 12.9%, with sheep being the main prey (63.2%), followed by goats (32.6%) and pigs in one case (5.3%). It was not possible to confirm whether this represents an underestimate of the total number of cattle killed due to the phenomenon of surplus killing (see section 6.3). It is notable that the share of livestock was markedly higher (FO = 47.1%) during the autumn of 2020, compared to the rest of the study period (FO = 8.1%). This seems to be the result of a pack with large, hungry juveniles, which led the parents to predate sheep temporarily. Something similar appears to have happened in the Veluwe area. In the North Veluwe area, incidents involving sheep have been rare with the exception of two cases, both of which occurred during a period when the pack included large hungry juveniles (See section 4.6; GW998F). Small mammals, such as common wood mice and voles, were also regularly found in Flanders, as well as a small number of medium-sized mammals such as dogs (in one case) and cats (in one case), birds and fruit (*Prunus padus* or bird cherry) were found.

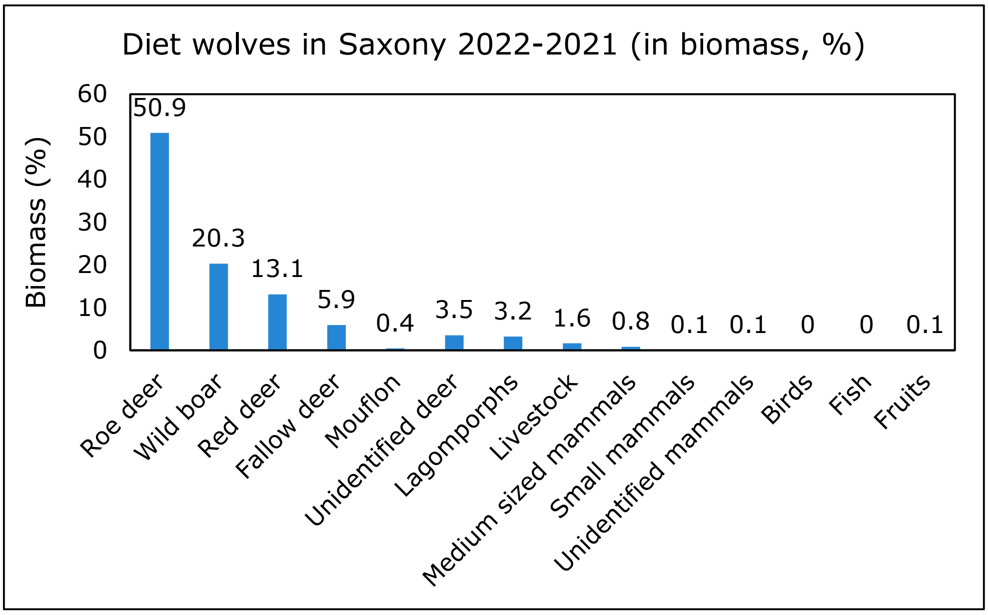

Figure 8.1.1 *Diet of wolves in Saxony, Germany, by biomass (Source: Reinhard et al., 2021).*

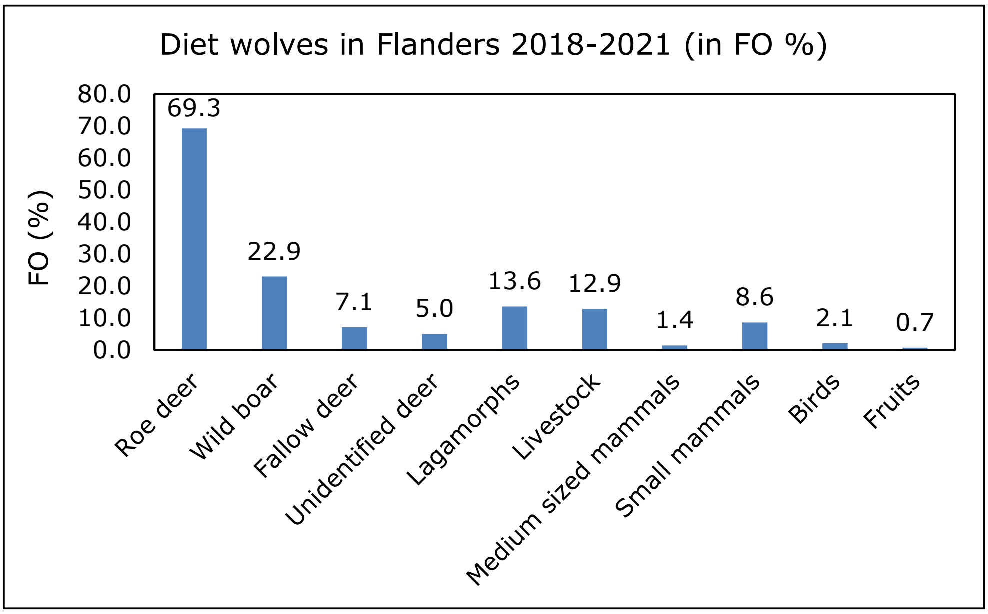

Figure 8.1.2 *Diet of wolves in Flanders, Belgium, by biomass (Source: Van der Veken et al., 2021).*

8.1.2 Livestock versus wild ungulates

The results of both studies clearly indicate that wild even-toed ungulates dominate the diet of wolves, while livestock appears to be limited or virtually absent. This is consistent with research conducted in regions described as rich in natural habitat and wild prey (Zlatanova et al., 2014). It shows that the combination of semi-natural and highly modified forest and agricultural landscapes in both study areas provides sufficient food, without wolves having to resort to livestock. But despite wolves' preference for wild prey, this does not preclude the predation of livestock. After all, wolves are risk-averse, opportunistic predators and they therefore favour harmless prey that is easy to obtain (see section 4.3). Small livestock, such as sheep and goats, are categorised as particularly vulnerable if they are not adequately protected, due to their smaller body size (Everaert et al., 2018). This is confirmed by both dietary studies and is also apparent from data on fatal wolf attacks in the Netherlands: 610 of the 614 cases recorded between 2015 and 2020 involved sheep. One goat was killed during that period. Wolves only predated large livestock very exceptionally: two calves and one Scottish highlander (BIJ12 2021).

Although wolves are capable of taking prey the size of horses or cattle, large livestock is generally not classed as a vulnerable category (with the exception of very young or severely debilitated individuals). In regions where there is an adequate supply of wild prey, this category does not appear in dietary analyses therefore, or only exceptionally. This is down to wolves' natural risk aversion (see section 4.3). In the absence of alternatives, such as in nutrient-poor regions of Southern Europe, livestock may form an important part of wolves' diets. One factor that is worth noting here is those cases often involve free-grazing horses or cattle and ponies that have been released into the wild, and that the wolves always favour young animals or carrion: this situation is not comparable to the situation in the Netherlands (NABU 2015, Lagos & Bárcena, 2018; Ciucci et al., 2020).

For most of the study period in Flanders, small livestock only showed up in low numbers. The exception was the autumn of 2020, which is explained by the timing of the first litter of wolves. The young wolves were growing up during that autumn and could not yet hunt for themselves. They therefore had to be fed with no yearlings to help with hunting. A similar situation seems to have arisen in the North Veluwe area, where two attacks on sheep were reported, both in late summer/autumn when the pack had larger juveniles to feed (section 4.6, GW998f). In the territory of the Hecktel-Eksel pack, a routine check at the end of 2018 showed that only 4% of livestock was adequately protected (INBO). The availability of unprotected livestock therefore provided a simple and attractive alternative at a time when more food was required by the pack. Higher rates of livestock consumption are often observed in the case of roaming wolves too. One explanation for this is that these wolves find themselves in a sub-optimal habitat as they search for a suitable territory; they are also in unfamiliar terrain and they are more likely to be relatively inexperienced hunters (Imbert et al., 2016). In addition, in the absence of protective measures, wolves can come to specialise in small livestock very quickly, and this results in higher predation in this category (see section 6.2).

8.1.3 Wild ungulates

In Europe, the diet of wolves exhibits clear regional differences. In wooded areas of Eastern Europe, such as the Białowieża primeval forest and the Beskid Mountains for instance, red deer are the most important species of prey. Research spanning several years in Białowieża, Poland, has shown that wolf predation was a major cause of death only in red deer, accounting for around 40% of the annual population increase. The predation ratio was found to be inversely related to the density of red deer: when the red deer population decreased, predation pressure increased. As such, wolves do not appear to have a stabilising influence on the red deer population (Jedrzejewski et al., 2010). In southern regions, such as the Apennines (Italy) and Romania, wild boar regularly appear to be wolves' preferred prey (Zlatanova et al., 2014; Sin et al., 2019). However, in places where roe deer are present in high enough numbers, these usually form the bulk of wolves' diet. This is often accompanied by positive selection, as demonstrated in the German state of Saxony (Bunewich, 1988; Ansorge et al., 2006; Barja, 2009; Nowak et al., 2011; Milanesi et al., 2012; Sidorovich et al., 2011 & 2017; Wagner et al., 2012; Sand et al., 2016; Figueiredo et al., 2020). This preference for roe deer can be explained by wolves' risk aversion, since this species of prey is unlikely to cause serious injuries during hunting (= prey vulnerability; section 4.3). The proportion of biomass lost to scavengers also increases with prey size, implying that the actual amount of food available to wolves when they kill medium-sized or larger animals is fairly similar, even though it is riskier for wolves to tackle larger prey (Sand et al., 2016; Sidorovich et al., 2017). In addition, deer typically reach high densities in peripheral habitats, which are characteristic of semi-wild and heavily modified forest and agricultural landscapes (= prey availability). It is therefore unsurprising that deer are wolves' main prey in both Flanders and Saxony.

In contrast to roe deer, wolves' predation of both boar and red deer appears to be more focused on juveniles, during the times of year when these are available. The selective predation of vulnerable individuals within species is mentioned more frequently with respect to larger ungulates in the literature – i.e. risk aversion. In addition to juvenile animals, other vulnerable animals include older individuals, females, animals that are weaker due to the reproductive cycle (e.g. heavily pregnant females, red male deer during or shortly after the rutting season) and malnourished, injured or diseased individuals. External factors, such as weather conditions, can further influence the availability and vulnerability of certain species of prey: e.g. mild winters and wild boar, see above (Mech & Peterson, 2010).

The mouflon is a wild ungulate, but this exotic species does not occur naturally in the Netherlands. Mouflons are a very vulnerable prey species in flat lowland areas due to the mismatch between the environment and their natural response to predators, which is to escape to safety by climbing up very steep rock faces. As a result, this species is disproportionately vulnerable, which usually results in localised extinction. This has been demonstrated in Saxony (Wagner et al., 2012) and the disappearance of mouflons from the North Veluwe area may also be the result of wolf predation. In addition, predation by wolves may also increase to high levels in the case of (recently) escaped even-toed ungulates, such as fallow deer in Flanders, and red deer, because these animals may be semi-tame (Okarma, 1995).

Photo 8.1 *Wolf eating a red deer (Photo: Hugh Jansman).*

8.1.4 Other species of prey

In addition to wild even-toed ungulates, both studies found that the diet of wolves is mainly supplemented by lagomorphs (hares, rabbits and similar animals). Beavers turned out to be a frequently consumed species of prey in a wetland area in the state of Saxony. Although the beaver population in the Netherlands is increasing steadily, this species will not make up a large proportion of wolves' diets. This is because its natural habitat does not overlap near the Veluwe (www.verspreidingsatlas.nl/). Additionally, a large number of different species and categories of prey were found in small quantities, including small rodents, other medium-sized mammals, birds, fish and fruit. This indicates opportunistic consumption, but where it includes other predator species such as foxes and raccoon dogs, this may be driven by competition as wolves attempt to monopolise dead prey and protect their wolf pups, for example. These fellow carnivores are only actually consumed in a minority of such aggressive interactions (Sidorovich, 2011; Martins et al., 2020). The discovery of a dog consumed as prey in the Flemish study was no exception. The killing of dogs is explained by the high degree of affinity between wolves and dogs – to such an extent that dogs are regarded as members of the same species. As such, they are treated as intruders inside a wolf's territory, or as competitors for prey or potential mates. At the same time, dogs are often consumed after they have been killed, indicating that they can also be seen as prey (Kojola & Kuittinen, 2002; Backeryd, 2007). Section 6.4 provides more information on wolf attacks on dogs.

Future research results from dietary analysis in the Netherlands will show whether or not the dietary habits found in both these studies can be extrapolated to wolves in the Netherlands. Although these findings provide some pointers, regional circumstances can play an important role. For example, the Netherlands is characterised by mild winters and the availability of nutrient-rich crops, meaning that wild boar can reproduce very rapidly to reach a high population density. Consequently, the population can consist largely of juvenile and subadult animals at certain times. A similar scenario is found in the Apennines, where wolf predation focuses on vulnerable boars that are one year old or younger, i.e. juveniles and subadults (Heck & Raschke, 1980; Mauget et al., 1984; Capitani et al., 2004; Meriggi et al., 2011; Imbert et al., 2016).

In addition, roe deer in the large contiguous forested areas and nature reserves of the Veluwe area see a high degree of competition from red deer and fallow deer, leading to lower population densities (FBE 2019). Dutch fauna management practices, whereby under certain conditions it is permitted to leave carcasses in the field, should also be taken into account. Normally, wolves prefer to kill their own prey, but if carcasses are consistently left in the field, these may come to form a substantial part of their diet (Ciucci et al., 2020). Finally, the wolf in Noord-Brabant still has solitary status, which means that its diet may include more smaller species of prey such as lagomorphs (Okarma, 1995).

8.2 Expected effects of the wolf on the Dutch ecosystem

Scavengers such as ravens are benefiting from the return of wolves due to the carrion they leave behind. It is not known whether wolves may also have an effect on the numbers and behaviour of ungulates in the Netherlands. It is expected that the effect of wolves on the numbers of ungulates will remain limited, given the effect of human intervention on the population of ungulates in the Netherlands. The indirect effect of wolves on the behaviour of ungulates, and therefore on the ecosystem, is likely to be greater. This applies not only to wild ungulates, but possibly also to the semi-wild grazers that frequently populate Dutch nature reserves.

Detailed analysis

8.2.1 General effects of wolves on ungulates and ecosystems

The interrelationship between predator and prey is complex. Generally, the number of prey will determine the number of predators, and the opposite is seldom true The effect of predators will depend on many factors such as habitat, territory sizes, weather conditions (colder or milder winters), food, the variety of ungulate species present, competitors, shelter, human hunting and land use (Fuller & Sievert, 2001). Another relevant factor is that wild ungulates will start to avoid areas with a high concentration of wolves (Fuller & Sievert, 2001) (see under Landscape of Fear). Wolves, ungulates and the ecosystems in which they live have coexisted and evolved together for many centuries, resulting in mutual morphological and behavioural adaptations. Wolves are apex predators and can affect other species, directly or indirectly, in four ways: 1. they act as ‘health police’, weeding out sick or weaker animals and thus making the remaining population more vital; 2. they regulate the population of prey species; 3. they leave carrion for scavengers; and 4. they regulate non-prey species such as medium-sized predators (Mech & Peterson, 2003; Mech & Boitani, 2003). The impact of wolves on ungulates can also alter the influence of grazing on the ecosystem, specifically as a result of changes in the behaviour of prey animals. This fifth mechanism can be added to the list above.

Scavengers, in particular, benefit from the presence of the wolf initially. This includes ravens, but also wild boars, predators such as foxes and badgers, birds of prey such as buzzards, red kites and perhaps bald eagles, and also many species of insects that feed on carrion in nature (ARK 2021; Walker et al., 2018).

8.2.2 Regulating the population of prey species

Because wolves are highly territorial and claim territories that are large enough to provide food for the pack, it is rare that prey species are overhunted. Sometimes wolves can reduce the population of ungulates, but this rarely happens (Mech & Peterson, 2003; Mech, 1970; Bergerud, 1971). However, they can affect ungulate populations in unnatural situations, such as mouflons in the Netherlands (also see section 8.1).

In 54 studies carried out across Europe and Asia (Melis et al., 2006) the effect of productivity, winter hardiness and the presence or absence of wolves were examined in relation to boar population densities.
Wolf predation had very little effect across the biogeographic scale compared with winter hardiness and productivity. One example of an estimation of the impact of wolves on boar populations is a Spanish study that looked specifically at mortality rates in boar due to wolves and hunting (Nores et al. 2008). It estimated the number of boar killed annually by wolves to be 4.5% of the population, accounting for 12% of boar mortality. Hunting was responsible for 31% of boar mortality, and the number of boars killed by hunting amounted to 12% of the population. The authors conclude that neither wolf predation nor hunting substantially affected the boar population in the study area.

8.2.3 Behavioural change in prey animals

In addition to the fact that wolves kill ungulates, the primary impact they have is due to the changes they cause in the behaviour of ungulates. Deer may alter their behaviour in terms of group sizes, activity patterns and use of terrain. Ungulates will seek to avoid areas that are higher-risk due to predation. This is known as the ‘Landscape of Fear’ (Van Ginkel et al., 2019). It can result in more variation in grazing habits, which can be beneficial to forest rejuvenation. This phenomenon has been well researched in Yellowstone National Park (Peterson et al., 2020). After the introduction of wolves in 1995, the number of ungulates fell, their grazing behaviour changed and the ecosystem became more diverse, with increased vegetation growth and forest development. However, this process is highly complex due to factors such as climate change (major wildfires in recent years), a growing population of grizzly bears which are taking advantage of deer killed by wolves which they appropriate, and a decline in coyote numbers due to competition with wolves. Despite this, the researchers in Yellowstone report that the effect of wolves on the ecosystem is impressive (Smith et al., 2016). Studies of flora in Yellowstone seem to support the idea that wolves play an important role, directly and indirectly, in the development of plant communities (Peterson et al., 2020).

There is an increasing scientific focus on the importance of top-down population regulation by large predators such as wolves for ecosystem health: the presence of predators has effects that penetrate deep into the food chain (Estes et al., 2011; Jepson & Blyte, 2020). Another example of behavioural change comes from Africa. Atkins et al. (2019) examined the effect of experimental mimicry of predators on the behaviour of ungulates (bushbucks) in a national park in Mozambique. Bushbucks prefer cover and will retreat to the forest whenever they feel threatened, unlike some other grazers that run out into the open in the event of danger. Wild dogs and big cats have been wiped out in the area, and as a result the bushbucks now graze more on the open plains, leading to overgrazing. Dietary studies show that they are consuming more nutrient-rich plants. In other words, in this species, there had always been a trade-off between nutrient-rich food versus the risk of predation. The researchers attached GPS loggers to a few animals and then observed the effect of predator noises and odours (faeces and urine) on the behaviour of the bushbucks. The species appeared to respond strongly to these sensory indications of the presence of predators, and avoided the grassland more as a result. The researchers conclude that for bushbucks, following the disappearance of larger predators, the open plains changed from a landscape of fear to a landscape of fearlessness. This had major consequences further down the food chain for both plant and prey populations. The experience of that fear is species-specific; not all ungulates exhibit the same response to the presence of a predator or danger. The researchers also report that the behavioural adaptation of animals like bushbucks to the absence of predators is reversible, and that a response can also be triggered artificially. Nevertheless, they still recommend reintroducing large predators back into the ecosystem (Atkins et al., 2019).

Whether ungulates will change their behaviour in response to the presence of wolves depends on many factors, such as the chance of ungulates encountering wolves, their chance of being caught and killed, other stress factors such as recreation and fauna management practices, and food availability. This, in turn, is directly related to how nature reserves are organised in terms of footpath density, rest areas, management and the age of the forest. It is likely that ungulates will alter their behaviour, in particular by becoming more alert, which may also mean they become more shy towards humans, making it more difficult to manage numbers through hunting. However, the reverse is also possible – that ungulates may actively seek out proximity to humans in order to avoid wolves. In addition, many semi-wild grazers have been introduced into Dutch nature reserves (horses and cows such as Konik horses and Scottish highlanders) for grazing purposes. It cannot be ruled out that wolves will have an effect on the behaviour of these semi-wild ungulates, including grazing, and that their role in the ecosystem will change as a result. Whether wolves will actually have an observable influence on ungulate numbers is questionable, since the impact of humans on the habitat (particularly through forest management) and on the ungulates in that habitat (particularly through population management) is significant. Recent research in Białowieża, Poland, showed that the presence of wolves had little effect on red deer (Van Ginkel, 2020). Behaviour is affected locally, especially when there are obstacles that obscure visibility or block escape routes (Van Ginkel et al., 2019), resulting in a local reduction in forest regeneration. The natural regeneration of oak and beech forests would be a favourable outcome in the Veluwe area (Den Ouden et al., 2020). Based on research carried out in Poland (Van Ginkel, 2020), wolves in the Veluwe area are not expected to have a major influence on forest rejuvenation, in part because of the relatively young age of the forest. In that study, the effect was mainly observed locally. However, research in Yellowstone shows that the effect can also occur on a larger scale (Peterson et al., 2020).

8.2.4 Effects on the spread of disease among ungulates

Predation can have a significant impact on the prevalence of disease in prey species, thus benefiting the ecosystem through disease control. Wolves often select younger individuals and weaker or sick animals. Multiple studies suggest that this selection for weaker individuals is the key to disease control in prey species (Packer et al., 2003; Wild et al., 2011; Tanner et al., 2019). Boars can be carriers of bovine tuberculosis, a major disease in cattle farming which is responsible for significant economic losses. A recent study (Tanner et al., 2019) showed that the prevalence of bovine tuberculosis is reduced when wolves are present. The mortality that occurs in the absence of wolves due to diseases such as TB is offset by mortality due to predation when wolves are present.

8.2.5 Robust connections & natural processes

At present, the Veluwe area is the most important habitat for wolves in the Netherlands. It is also a relatively isolated area, however, and access for ungulates from outside the area is difficult due to the presence of fences. There are also numerous different land owners in the area, which manage their land in different ways. Humans have a significant impact on the ecosystem through forest management and fauna management practices. The Veluwe area is also rather fragmented due to the presence of numerous fences, and the area is under considerable pressure from nitrate pollution, drainage and climate change (Den Ouden et al., 2020). From this perspective, creating more space for wildlife and natural processes would benefit the Veluwe area (Jansman, 2021; Hegener, 2019). If the Veluwe, as a large nature reserve, could be connected to other nearby nature reserves with robust natural corridors for ungulate populations, there would be more space for natural processes rather than human management of nature and ungulate populations. This would improve the viability of wild ungulate populations (and populations of other species), partly because ungulates would regain their vitality through natural selection and adaptation (see Den Ouden et al., 2020 for an explanation of the vital population size for red deer). Ungulates could also migrate to nutrient-rich areas once again via these corridors, depending on the season and climate. In this situation, wolves would have a moderate regulating influence on the population size and behaviour of ungulates. However, this would require much more space for nature and natural processes than is currently possible and/or permitted. One inspiring ambition in this regard is the map showing a vision of the Netherlands with more space for nature in 2120 (Baptist et al., 2019). The question is to what extent, in the current landscape, this would bring about conditions for natural processes and measurable effects of wolves on the ecosystem by regulating ungulate numbers. Liesbeth Bakker, professor of Rewilding at WUR, therefore recommends monitoring of all trophic levels (soil-plants-animals-wolf) in order to monitor developments.

9 Genetic methodologies and data exchange

For the purpose of this report, a survey and workshop were held for an international group of researchers involved in the genetic monitoring of wolf populations in various regions of Europe. The goal was to explore whether it would be possible and worthwhile making improvements to the current methods of identifying species, identifying particular individuals and detecting hybrids in the foreseeable future. The results showed that the methods that have been standard in recent decades, and which are also being applied in the Netherlands, Belgium and Germany, do yield reliable results. These methods include identifying species based on reading the code of a piece of the mitochondrial genome (mtDNA) and analysing a set (also known as a panel) of (nuclear) microsatellite markers to identify individuals.

However, improvements could still be made in terms of lead times and cost-efficiency, particularly if the sample numbers used in periodic monitoring increase. A switch to analysis using high-throughput sequencing (HTS) would seem to be the most promising for this, as this would offer the opportunity to process a larger number of samples in one analysis run and therefore to analyse a combination of different types of DNA markers directly in each sample in order to answer multiple research questions simultaneously: sequence markers for identifying species, microsatellite markers and/or SNP (single nucleotide polymorphism) markers for identifying individuals and a targeted set of SNP markers for the detection of hybrids. This method is becoming ever more cost-effective, and a switch could make sense within a few years. However, this depends on whether this method can at least maintain and ideally improve the success rate for non-invasive samples (such as droppings and saliva traces from dead livestock, which make up the vast majority of samples collected in the Netherlands). If this proves disappointing in practice, an alternative method for identifying individuals is conceivable using the analysis of a targeted panel of SNP markers on the Fluidigm platform. There have been positive experiences of using such a method in countries such as Germany (SGN) and Finland (University of Oulu).

Recently, a similar targeted SNP panel has been developed for the detailed detection of wolf-dog hybrids, distinguishing between a first-generation hybrid (F1) and various levels of later generation hybrids, including backcrosses to wolves or dogs. (Harmoinen et al., 2021). Implementing this panel in the Netherlands would also be valuable in the short term. Occasionally, samples are already sent to SGN for further verification through this SNP panel.

One disadvantage of the HTS method is that efficiency and cost-effectiveness are only achieved if a large number of samples can be processed simultaneously. It will therefore probably be useful to retain the current mtDNA and microsatellite methods for the time being for cases when species or individuals need to be identified urgently. A potentially valuable addition to this is a new detection method which uses the amylase gene. This is involved in the breakdown of starch, and is present at a higher number of copies in the genome in domestic dogs because of their diets that are higher in starch. This method provides relatively quick and inexpensive results, but is less reliable and should therefore be considered mainly as an addition to the more robust mtDNA and microsatellite methods of identification.

Detailed analysis

9.1 Current approach and genetic methodology

Currently, samples that are potentially thought to be from wolves are genetically analysed for two different purposes in the Netherlands. Firstly to identify the species of the culprit in the event of damage to farm animals. This may be a wolf, but also a dog or a fox. Wolves usually kill their prey with a bite to the throat and leave traces of saliva behind when doing this. That saliva is an important source of DNA that can be used in the laboratory to determine whether the attack was carried out by a wolf or some other animal. When a livestock farmer informs BIJ12 that farm animals have been killed or injured and the involvement of a wolf is suspected, an assessor will take a number of DNA samples from traces of saliva in and around the bite wounds using swabs within 24 hours. These are sent to Wageningen Environmental Research (WENR) for genetic analysis to determine which species they are from. These tests are carried out once a month for all the samples received in the previous month.

An important secondary goal of genetic research is to monitor the development of the wolf population in the Netherlands, in accordance with the Wolf monitoring plan (Klees et al., 2018). There are also other methods of doing this, such as camera traps, but DNA trace testing makes up the bulk of the monitoring of wolves. Those traces come from droppings or fur, for example, or from swabs taken from the carcasses of wild prey (including roe deer, deer, wild boar). These samples are collected by volunteers under the coordination of the Wolf Reporting Point, and genetically analysed on a quarterly basis. Initially, the same kind of test is carried out as the one described above in relation to damage claims. All samples in which wolf DNA is confirmed, including samples collected from damage claims, are then subjected to a follow-up analysis aimed at determining the exact individual involved and the sex of the animal. This analysis zooms in on pieces of DNA that together form a profile that is unique to each individual wolf. A DNA profile is drawn up for every sample selected, making it possible to ascertain whether a new individual is involved, or an individual that has been observed previously. It is also possible to trace which European wolf population the individual originates from and, in many cases, the pack of origin can also be determined. The results of these analyses are published in the quarterly reports issued by BIJ12 for monitoring purposes.

In order to identify the species, the method currently used by WENR for samples from the Netherlands entails determining the DNA sequence of part of the highly variable ‘control region’ (CR) of the mitochondrial DNA (Caniglia et al., 2012). The production of an individual genetic profile (also known as: genotyping) is based on a fixed set of 13 microsatellite markers located on the nuclear genome, plus a sex marker located on the Y chromosome. For a detailed description of the methodologies used, please refer to Appendix 3 and the website of the CEwolf consortium.

Europe-wide evaluation of requirements and opportunities in order to improve methodologies in the future

At least 29 different genetic laboratories in 18 different countries are currently actively involved in genetic research on European wolf populations (of which 25 were mentioned already in De Groot et al., 2016; as well as INBO and the University of Liège for wolves in Flanders and Wallonia respectively, the University of Ljubljana for Slovenia, NINA for Norway and the Veterinary University in Vienna for Austria). Most of these institutes regularly carry out species identification analysis and individual genotyping on wolf samples, and are considering ways of improving their practices still further. In order to obtain the most comprehensive picture of the options for improving the methodology used in the Netherlands, the experiences and ideas of these researchers from other countries were explored. Within the current project, this was done in two steps. First of all, in June a digital survey was sent to a total of 32 researchers from laboratories in 17 different countries (including at least one laboratory involved with each of the ten European wolf populations). The questionnaire and a list of the researchers approached is available from WENR upon request. The survey was completed by 12 researchers from a total of ten different countries within the response period (which was short by necessity). Together they represent research that involves six out of Europe’s ten wolf populations (Central Europe, Scandinavia, Karelia, Dinaric/Balkan, Franco-Italian-Swiss Alps and NW Iberia). Subsequently, a digital workshop was held on 11 June 2021, which the same group of researchers was invited to. Eleven participants attended (Appendix 2), including researchers involved in monitoring wolves in seven different countries, and the first or last authors of overarching research studies on all European wolf populations (such as Stronen et al., 2013; Pilot et al., 2010; De Groot et al., 2016) and publications on new genetic methodologies for European wolves (such as Kraus et al., 2015; Harmoinen et al., 2021). During the workshop, the most important results of the survey were presented and the relevant sections were discussed and placed in context.

The survey and workshop covered: 1) needs and developments in the methodologies for identifying species, identifying individuals and identifying wolf-dog hybrids; and 2) the need for a suitable method for exchanging genetic data. The main conclusions are summarised below. For the sake of clarity, the results of the survey are not reproduced here in full, but they can be found in Appendix 2 instead.

9.2 Requirements for the future improvement of genetic methods

Although the methods currently in use are successful, there is still room for improvement in a number of areas. These are outlined below, along with the requirements that future methods should ideally meet. The remainder of this chapter will explore the extent to which new developments will make this possible in the foreseeable future.

1. Applicability to non-invasive samples
The genetic monitoring of wolves is based mainly (95 to 100% of the samples, based on the survey) on non-invasive samples, i.e. genetic material that wolves leave behind on carcasses in their saliva, or from droppings, hairs, urine, blood drops etc. Almost by definition, the DNA contained in such samples is lower in quality and in quantity than DNA from tissue or blood samples. Working with this type of material requires strict protocols and adequate replication. A certain percentage of the samples will fail with each analysis because the quality of the DNA is not sufficient (for example because sampling was done too late or because the droppings or carcass were exposed to heavy rain or high temperatures for a prolonged period). The aim of improving these methods is of course to achieve as high a success rate as possible. The better a method can cope with low-quality samples, the more useful it will be in monitoring.

2. Cost-efficiency versus analysis turn-around time
Given the large number of samples collected and the fact that analysis is funded using public money, it is important to keep costs down wherever possible. An important way to achieve this is to use methods that allow as many samples as possible to be processed simultaneously. The costs per analysis run are often more or less fixed, so the more data that can be obtained in one go, the lower the cost per sample will be. It therefore pays to save samples up in order to achieve the maximum possible number of samples per analysis run. On the other hand, it may also be important to have a result as quickly as possible in some cases. Then, the analysis costs per sample may be of secondary importance, and the priority may be to have a method available that can provide an answer as quickly as possible.

It remains important to find a balance between speed and cost, then, with the ideal method depending on the number of samples received, the research question and the degree of urgency. Scalability – in terms of the number of samples that can be processed – is clearly an advantage. But in many cases it seems useful to have a high-throughput method for the periodic analysis of a large number of samples collected as part of the standard monitoring strategy (at the lowest possible cost per sample, and ideally with results for several research questions simultaneously) and, alongside that, a method that can provide a very specific result for a few samples more rapidly.

3. Possibility of exchanging and pooling data with other countries
The exchange of genetic data on wolves between different countries is particularly relevant with respect to individual genetic profiles. There is broad consensus among the researchers surveyed that it ought to be possible to exchange and compare genetic profiles with institutes in neighbouring countries. This makes perfect sense because wolves can travel long distances, crossing borders regularly, and this is particularly relevant for a small country like the Netherlands. As can also be seen from the overview in section 5.1, most of the wolves observed in the Netherlands so far have originated from Germany, and over time most individuals returned to German territory or moved into Belgian territory. The fact that we were able to visualise these patterns is entirely due to the successful harmonisation of methods for determining individual genetic profiles between the German SGN, WENR in the Netherlands, the INBO in Flanders and the University of Liège in Wallonia. This made it possible to compare the profiles obtained in different countries directly, and to conclude that they must be from the same animal. The main aim is therefore to map the migration patterns of wandering individual wolves better in order to predict changes in the areas recolonised by wolves with more accuracy. Based on experiences in other countries, it seems likely that as the population increases in size, it becomes less relevant and feasible to determine each individual’s exact pack of origin, migratory route and place of settlement. In Germany, it is currently still largely possible to

track individuals and packs, but the number of samples that would need to be processed annually to achieve this is increasing at a rapid pace (Reinhardt et al., 2021). In Poland, meanwhile, the chief aim of monitoring is to monitor the number of territories and packs, while in Southern European countries the aim is primarily to monitor population size and genetic vitality. One special situation where exchange between two neighbouring countries remains particularly relevant is where the territory of an established wolf or pack straddles a national border. The Czech Republic has particular experience of this, with close collaboration with researchers in Germany, Poland and Austria (OWAD, 2021). In the Netherlands, there are no established wolf territories that straddle international borders as yet, but in the Grenspark Kalmthoutse Heide, for example, this could well happen in the future.

There is also broad consensus that it is often necessary to harmonise methods across a larger number of countries if individuals belonging to the same population are present there. This is the only way to monitor the size and vitality of the population as a whole. This was an important motive for establishing the CEwolf consortium (Appendix 3), which brings together eleven different institutes to cover the entire area that is inhabited by wolves. Similar initiatives already exist for the Alpine (Wolf Alpine Group), Scandinavian (SKANDULV) and Baltic wolf population (BALTWOLF).

There is less consensus among researchers about whether it is necessary to harmonise methods fully across all countries in Europe in order to compare or pool results regarding wolves from different populations. Very different sets of microsatellite markers are currently in use to identify individual wolves in different wolf populations (De Groot et al., 2016), and switching to a different marker set or a completely different method would have a major impact on comparability with respect to historical data. In practice, a large proportion of the samples from previous years (“legacy samples”) would have to be reanalysed. Researchers indicate that they would consider doing this if it would lead to greater efficiency over the long term, but many would oppose doing so purely in order to exchange data with other countries. There is also some uncertainty regarding to what extent this is really necessary. With respect to academic research concerning patterns on a European scale, it would be more efficient to reanalyse a subset of samples per population using the same procedure (as was done by Pilot et al., 2010, for example).

From a management and policy point of view, the relevance of harmonisation is largely limited to determining the population of origin. For that purpose, however, complete harmonisation in terms of methodology is not required. One alternative would be to exchange a set of reference samples between institutions, from a number of representative individuals in each population. If each institute or consortium analyses these samples using its own method, the reference data could be used to determine, quickly and easily, which population a newly obtained genetic profile has the best match with using cluster analyses.

Cases where a wolf displaying unusual behaviour migrates to another population would be an exception. One example of this is the ‘problem wolf’, Billy (GW1554m), which led to an exceptional number of claims in the Netherlands in the area of Heusden. Data exchange through CEwolf enabled this wolf to be tracked as it moved from Germany into the Netherlands and then on to Flanders and Wallonia, and south to the border area between Germany and Luxembourg (Figure 4.6.2). It was suspected that Billy then moved on into France; however, this could not be confirmed by comparing the profile drawn up by French researchers with the CEwolf profiles because the French laboratory uses a different set of markers. In the case of Billy, it was possible to confirm this by sending a Flemish sample to France and reanalysing it there using the local methodology. Billy was finally killed with a permit in France.

All in all, the Europe-wide streamlining of methods would only seem to be a realistic prospect if it can be done in a relatively efficient way. Most of the researchers surveyed indicated that they would be willing to expand the set of DNA markers that they use (this set is also referred to as a ‘panel’) in order to achieve greater overlap with data from other countries, but the benefits of Europe-wide harmonisation are not sufficient to warrant a switch to a completely different method for that reason alone. One important aspect here is also that not all currently used markers show sufficient variability for individual recognition and pedigree analysis in all wolf population. A pan-European genetic marker system would need to be optimized for use in all wolf populations.

9.3 Promising methods of identifying species in the future

Determining the haplotype by sequencing the control region of the mitochondrial genome (mtDNA) is by far the most widely used method for species identification across European laboratories involved in wolf monitoring, and this method is satisfactory due to its high success rate on samples of limited quality. It is an established and widely accepted method (e.g. Pilot et al., 2010) and reference data for each haplotype (the exact DNA code) is freely available in online databases. The most successful application when testing saliva swabs (Caniglia et al., 2012) has been the analysis of a relatively short fragment of this ‘control region’, which enables haplotypes belonging to dog, wolf and golden jackal to be identified. One limitation of this fragment is that it does not pick up fox DNA. This requires the use of a second (partly overlapping, but longer) fragment (Fumagalli et al., 1996). In Germany, both fragments are analysed for each sample as standard; in the Netherlands, for reasons of cost, it was decided to focus on distinguishing between dog, wolf and golden jackal. This already answers the most important question with respect to potential compensation: whether there is evidence of the presence of a wolf. Where necessary, follow-up analysis using microsatellites provides a definitive answer regarding the presence of foxes. A second limitation is that the mitochondrial genome used is only passed on through the maternal line. Based on this method alone, then, it is not possible to rule out a wolf-dog hybrid. A separate method is used to do this in cases where there is reason to suspect this could be case (see below). Due to these limitations, in the future it may be useful to move to an analysis method that involves examining multiple fragments simultaneously (multi-locus haplotyping), using a high-throughput sequencing (HTS) platform. This would also enable the integration of markers for species identification and individual identification within a standard set of markers analysed in one run on an HTS platform. In this way, as much relevant information as possible could be obtained on a large number of samples at the same time.

Although such a method would be very efficient for periodic monitoring, it would not be suitable for the urgent analysis of single samples. A new method that could be useful in these cases focuses on a gene for the production of amylase, an enzyme involved in the breakdown of starch. Domestic dog breeds are known to have a higher number of copies of this gene in their genome than wolves, which is probably an evolutionary adaptation to their relatively starchy diet (Axelsson et al., 2013). The number of copies can be determined using a quantitative PCR method (Arendt et al., 2016). Within CEwolf, this method is occasionally used by the University of Vienna and the INBO in Flanders. They use a ‘digital droplet’ PCR (ddPCR) platform, which is capable of processing both a small number (up to 8) and a large number (up to 96) of samples simultaneously and relatively cheaply. WENR also has access to this ddPCR platform and already has experience of using it to detect eDNA in water samples. However, introducing this amylase detection method would still require a brief period of control testing (testing of samples where the species or variety is already known). An important factor is that different dog breeds have a different number of gene copies, with some breeds having a relatively low number and therefore being more difficult to distinguish from wolves. Even if this only occasionally leads to inconclusive results, it would mean that the method is of limited usefulness with respect to compensation claims, for example. The method should therefore mainly be regarded as a quick initial indication, and should be seen as complementary to a more robust method such as the current method based on mtDNA haplotypes.

9.4 Promising methods of identifying individuals in the future

At most of the institutes in Europe, genetic profiling in order to identify individual wolves is currently done by analysing a limited number of microsatellite markers, in which the variation in length per microsatellite fragment is read out as a peak pattern through a capillary sequencer (ABI). However, alternative methods have been emerging for some years now. The following may have particularly potential as part of a monitoring strategy: 1) the analysis of microsatellite markers using high-throughput sequencing (HTS), and 2) the application of another type of marker, known as Single Nucleotide Polymorphisms (SNPs). In both cases, a much higher number of markers can be analysed simultaneously per sample, which considerably reduces the amount of labour required per sample and results in cost savings with larger sample numbers and less sensitivity to the occasional failure of a marker. In addition, the data obtained from both these methods is much easier to compare directly between labs, without the need for an extensive validation process. Finally, for both methods, the exact platform on which the analysis is performed is of minor importance for the result, which would make harmonisation between labs much easier. As long as there is consensus on the panel of markers to be used, each lab could choose for itself which platform it prefers to use to read the data.

The analysis of microsatellites using HTS is already being used by some laboratories (including the University of Lausanne) for research on wolves and being used routinely elsewhere to monitor some other carnivores. However, experience shows that it is not usually possible to continue using the same panel of markers analysed previously using capillary sequencing. Switching to another panel is therefore necessary and (for a continuous dataset) that also means reanalysing historical samples. By definition, the same applies when switching to SNP markers. The advantage of this method is that interpreting the raw data is more straightforward, because only four allele variants are possible per marker (the nucleotides A, T, G and C) rather than a series of length variants. On the other hand, this limited variation makes it more difficult to recognise mixed profiles (for example, due to pollution with fox, or the involvement of several individuals from a pack). An SNP set has recently become available for the Scandinavian wolf population which, perhaps with some extension or modification, could also be used for individual genotyping in other wolf populations.

An important reason why these methods have not yet been widely applied in wolf monitoring has been their limited applicability for non-invasive DNA samples up until now. Good results have been achieved in this respect for SNP markers using the ‘microfluidic 96.96 Dynamic Array’ platform from Fluidigm (or ‘Fluidigm platform’), which is only available in a limited number of laboratories (including SGN). Due to recent innovations in the field of HTS platforms, the sequencing of non-invasive samples also seems to be possible (personal communication with Dr T. Skrbinsek). It is therefore expected that amplicon sequencing using HTS will establish as alternative approach to use of Fluidigm for SNP analysis in the near future. A major advantage of this would be that the analysis of a combined set of microsatellite and SNP markers would then be within reach, so that the benefits of both systems could be enjoyed simultaneously. However, the development and validation of such a combined set of markers will likely take several years.

9.5 Promising methods of identifying wolf-dog hybrids in the future

There was broad consensus among the group of researchers surveyed for this report that it would be much better for everybody to use the same method to identify wolf-dog hybrids. This is not so much due to the desire to exchange data, but the desire to report the incidence of hybridisation in each country in an unambiguous manner. One good option for this, which is either already being used or being seriously considered by several labs, is an SNP panel recently developed by Harmoinen et al. (2021), specifically for identifying wolf-dog hybrids in Europe. This set is now routinely applied by SGN using the Fluidigm platform. Currently WENR still primarily uses the microsatellite profiles that are already available for individual recognition, but occasionally samples from suspect individuals are sent to the SGN for further verification via the SNP panel (for example, if no pack of origin or parent pair consisting of specific wolves could be identified, or if an abnormal mtDNA haplotype had been identified). There is a desire to include this method in the routine analysis in the Netherlands, too, in order to provide fully conclusive answers more rapidly.
A possible future switch to the analysis of microsatellites and/or SNP markers using HTS could provide an opportunity to carry out this set of hybrid detection markers in a single analysis run in addition to a set of markers for species identification and a set for individual identification.

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Appendix 1 Original questions from the authorities (in Dutch)

Primaire vragen

1. (H5 in het rapport) Verspreiding, voorkomen, herkomst en ecologische draagkracht

1.1. Wat is de herkomst van de wolven?

a. Wat is de herkomst van de wolven in Nederland?

b. Wat is de herkomst van de wolven in Europa?

c. Is bekend waar de middels DNA-analyses vastgestelde wolvenindividuen zich momenteel bevinden in Europa in het algemeen en specifiek de individuen van de in Nederland bekende (ooit) aanwezige wolven?

d. Zo niet, hoe groot is het aandeel van 'vermiste' wolven gerelateerd aan de totale hoeveelheid aan vastgestelde wolvenindividuen?

e. Zijn er uitspraken te doen hoe dit te verklaren is?

1.2. Zijn de wolven in Centraal-Europa*, Europ het Alpengebied en/of Nederland (deels) illegaal uitgezet?

a. Welke aanwijzingen zijn er dat er wolven zijn uitgezet?

b. Welke aanwijzingen zijn er dat er daarbij sprake is van illegale introductie?

c. Indien sprake is van illegale uitzetting: wat betekent dit voor de beschermde status van deze individuen en welk beheer is dan aangewezen?

**Wanneer in deze offerteaanvraag gesproken wordt over 'Centraal-Europa' worden daarbij ook de landen in West Europa bedoeld.*

1.3. Is er bij de (genetisch vastgestelde) wolven sprake van hybridisatie met honden?

a. Wanneer wordt er gesproken over 'hybridisatie' (bijvoorbeeld vanaf welk percentage 'hond-DNA' in het 'wolf-DNA' wordt hiervan gesproken)?

b. Is hybridisatie aan de orde wat betreft de wolven in Nederland?

c. Is hybridisatie aan de orde wat betreft de wolven in Centraal-Europa/het Alpengebied?

d. Indien hier sprake van is; wat betekent dit voor de beschermde status van deze individuen en welk beheer is dan aangewezen?

1.4. Zijn er hotspots/corridors in Nederland aan te wijzen die veelvuldig worden benut door dispergerende wolven (vanuit omliggende landen)?

a. Zo ja, waar zijn deze hotspots/corridors in Nederland aanwezig?

b. Wat is het huidige beeld en wat is de verwachting van de hotspots/corridors in Nederland?

c. Hoe is het schadebeeld binnen deze hotspots/corridors? In hoeverre is er tussen de hotspots/corridors een merkbaar verschil te zien?

1.5. Welke functie vervult Nederland voor de wolf als gekeken wordt naar territoriale vestiging, voortplanting en dispersie ('zwervende' wolven) vanuit andere populatie(s)?

a. Hoe kan dit zich gaan ontwikkelen?

1.6. Kan op basis van de huidige inzichten, een uitspraak gedaan worden over de ecologische draagkracht van Nederland voor wolven (in aantallen en aan de hand van bijvoorbeeld geschikte biotopen, voedselaanbod en menselijke beïnvloeding (infrastructuur, steden, verstoring))?

1.7. Wat is de verwachte ontwikkeling van de aantallen wolven in Nederland in ruimte en tijd?

a. Is er daarbij een uitspraak te doen over welke landschapstypes of habitats in Nederland het meeste aangedaan worden door wolven? Zo ja, welke?
b. Is er daarbij een uitspraak te doen over het gedrag en het aanpassingsvermogen van de wolf op door mensen dichtbevolkte gebieden? Zo ja, welke?

1.8. Kunnen er uitspraken (en zo ja, welke) gedaan worden over de gemiddelde omvang van een wolventerritorium in Nederland?

a. Kunnen deze uitspraken gedaan worden voor een wolvenroedel in Nederland?
b. Kunnen deze uitspraken gedaan worden voor een wolvenpaar in Nederland?
c. Kunnen deze uitspraken gedaan worden voor een solitaire wolf in Nederland?
d. Zijn hier veranderingen in te verwachten indien er meer wolven Nederland aandoen?

1.9. Waar in Nederland (geografisch gezien) kunnen wolven waarschijnlijk duurzaam leven (dat wil onder andere zeggen: waar kunnen wolven over meerdere jaren succesvol aanwezig zijn en/of reproduceren)?

1.10. Kan in Nederland een levensvatbare, genetisch vitale wolvenpopulatie ontstaan, gezien de ecologische draagkracht van Nederland?

a. Zijn er ook gebieden aan te wijzen waar wolven waarschijnlijk niet duurzaam kunnen leven?
b. hoe worden deze (geografische) verschillen veroorzaakt?
    a. Zo niet, waarom niet?
    b. Wat is nodig voor een levensvatbare, genetisch vitale wolvenpopulatie?

1.11. Wanneer verkeren de Europese wolvenpopulaties in een gunstige staat van instandhouding?

a. Kunnen er uitspraken gedaan worden over wanneer de Europese laaglandpopulatie in een gunstige staat van instandhouding verkeert? Zo ja, welke en in welke situatie is sprake van een gunstige staat van instandhouding?
b. Kunnen er uitspraken gedaan worden over wanneer de alpiene populatie in een gunstige staat van instandhouding verkeerd? Zo ja, welke en in welke situatie is sprake van een gunstige staat van instandhouding?
c. Is of kan Nederland van belang zijn voor de staat van instandhouding van de Europese wolvenpopulaties (zoals de Europese Laaglandpopulatie en alpiene populatie) en in welke mate?
d. Kan er een uitspraak gedaan worden over de gunstige staat van instandhouding van de in Nederland verblijvende populatie? Zo ja, hoe is dit te bepalen en wanneer is hiervan dan sprake?

2. (H6 in het rapport) Gedrag en wolf-mensrelatie

2.1. Welk gedrag van wolven, onder andere ten opzichte van mensen, is als natuurlijk te beschouwen en welk gedrag is afwijkend?

a. In hoeverre is er sprake van een verandering in gedrag in door mensen dichtbevolkte gebieden?

2.2. Hoe kan een zgn. 'probleem-wolf' ontstaan? Zie het Interprovinciale Wolvenplan (IPO, 2019) voor *voorbeelden* van probleemsituaties.

2.3. Waarom doden wolven vaak meer landbouwhuisdieren (zoals schapen) dan ze opeten (surplus-killing)?

a. Is daarbij ook aan te geven of er verschillen zijn tussen diersoorten en of afhankelijk van het diergedrag, specifiek bijvoorbeeld weideschapen en schapen die elders worden ingezet (bijvoorbeeld in natuurgebieden waar nog kuddegedrag vertoond wordt; heideschapen)? Zo ja, welke?

2.4. Aanvallen van wolven op mensen (en honden): welke ervaringen zijn inmiddels elders in Europa opgedaan met de recent sterk uitbreidende populatie wolven?

a. Zijn hierbij verklarende oorzaken te benoemen? Zo ja, welke?

2.5. Wat zijn de mogelijke gevolgen van de aanwezigheid van de wolf in Nederland voor recreatie en verkeersveiligheid?

a. In hoeverre zijn er momenteel al effecten zichtbaar van de aanwezigheid van de wolf in Nederland voor recreatie en verkeersveiligheid?

b. Wat zijn de verwachte effecten van de aanwezigheid van de wolf in Nederland voor recreatie en verkeersveiligheid?

3. (H7 in het rapport) Beleid, schade, monitoring en beheer

3.1. Wat is het beleid van andere landen# als het gaat om het toestaan van derogaties (bijvoorbeeld voor afschot van wolf)?

a. Welke overwegingen betrekken zij hierbij om die derogaties toe te staan?

#Met 'andere landen' wordt in deze uitvraag in ieder geval de volgende landen bedoeld: Duitsland, België en Frankrijk. Indien relevante informatie beschikbaar is, dan kunnen ook andere landen aangehaald worden zoals Scandinavische landen (o.a. Denenmarken en Zweden) en/of Oost-Europese landen. Te allen tijde moet bij het trekken van conclusies onderbouwd worden of de situaties/omstandigheden vergelijkbaar zijn en/of toepasbaar zijn op Nederland.

3.2. Welke ervaringen zijn er met betrekking tot afschot van wolven en het effect hiervan op het gedrag van de wolvenroedel?

3.3. Wat kunnen we leren van het beleid van andere landen (in ieder geval van de ons omringende landen) ten aanzien van schadepreventie en tegemoetkomingen?

a. Hoe effectief is dit beleid voor wat betreft het voorkomen van schade?

b. Wat zijn de oorzaken van het wel of niet effectief zijn van dit beleid?

c. Daarbij is het ook gewenst zo mogelijk aandacht te besteden aan het over een grote lengte plaatsen van afrasteringen (dit n.a.v. de discussie over het 'Friese wolven-hek').

3.4. Welke ervaringen zijn er in andere landen (die vergelijkbaar zijn met de Nederlandse situatie) opgedaan voor wat betreft het wolvenbeheer zoals het toepassen van verjagingsmethodes?

a. Welke verjagingsmethode(s) worden in andere vergelijkbare landen toegepast (indien aan de orde)?

b. Wat is de effectiviteit van deze verjagingsmethode(s)?

c. Wat zijn de oorzaken van het wel of niet effectief zijn van deze methode(s)?

d. In hoeverre is het in Nederland mogelijk om verjagingsmethodes toe te passen?

3.5. Wat is het verwachte effect op de wolf als gevolg van het gevoerde faunabeheer in Nederland, kijkend naar beschikbaarheid van wilde prooien?

4. (H8 in het rapport) Ecologie

4.1. Dieet: wat eten wolven in Nederland gebaseerd op reeds beschikbare praktijk inzichten (aan de hand van wolvenkeutels, kadavers prooidieren etc.) en literatuuronderzoek?

4.2. Wolf in het ecosysteem: wat zijn volgens de meest recente inzichten en ervaringen (op basis van literatuur) de effecten van de wolf op het ecosysteem? Wat zijn daarbij de verwachte effecten als naar de Nederlandse ecosystemen wordt gekeken?
Bijvoorbeeld voor:

a. De verwachting van profiterende soorten

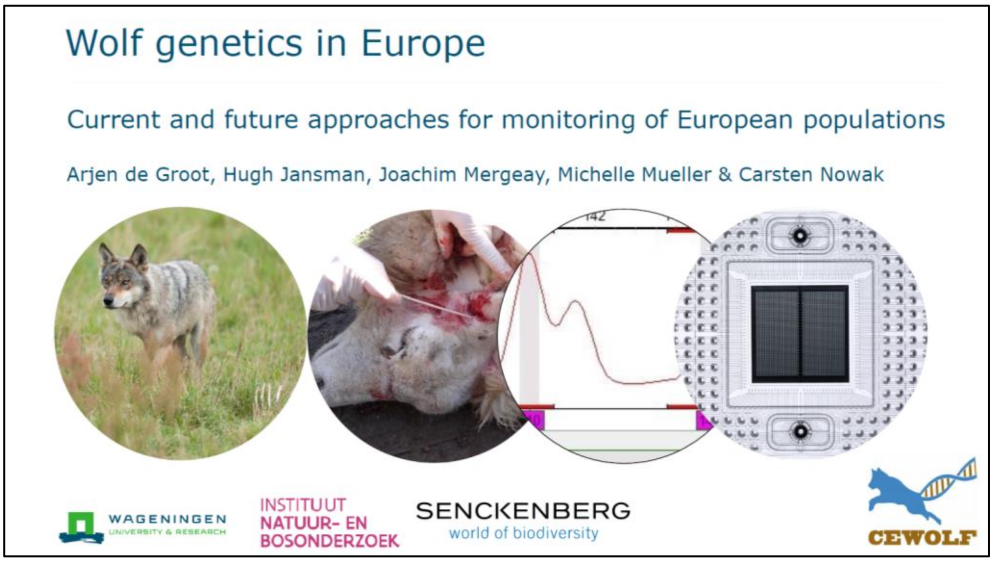
b. Effecten op hoefdieren

c. Verandering landschap (o.a. door aanpassing graasdruk)

Secundaire vragen (H9 in het rapport)

a. Welke nieuwe ontwikkelingen zijn er op het vlak van genetische methodieken & uitwisseling van data met andere landen in Europa? In hoeverre bieden deze nieuwe ontwikkelingen een meerwaarde ten op zichtte van de huidige methodieken?

Appendix 2 Genetical workshop: results of the questionnaire



Wolf genetics in Europe

Current and future approaches for monitoring of European populations

Arjen de Groot, Hugh Jansman, Joachim Mergeay, Michelle Mueller & Carsten Nowak

WAGENINGEN UNIVERSITY & RESEARCH

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Agenda

1. **Introduction**
   - Background and focus
   - Questionnaire
2. **Individual genotyping**
   - Current and future methods
   - Need and approaches for data exchange
3. **Species identification**: current and future methods
4. **Wolf-dog hybridization**
   - Need for management?
   - How to define a hybrid?
   - Current and future methods
5. **General discussion**

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Participants today

Arjen de Groot, Hugh Jansman, Margreet Laar (WENR, the Netherlands)

Joachim Mergeay (INBO, Belgium)

Carsten Nowak (Senckenberg, Germany)

Malgorzata Pilot (Oxford University, UK)

Jenni Harmoinen (University of Oulu, Finland)

Linnéa Smeds (Uppsala University, Sweden)

Raquel Godinho (Porto University, Portugal)

Astrid Stronen, Tomaz Skrbinzek (University of Ljubljana, Slovenia)

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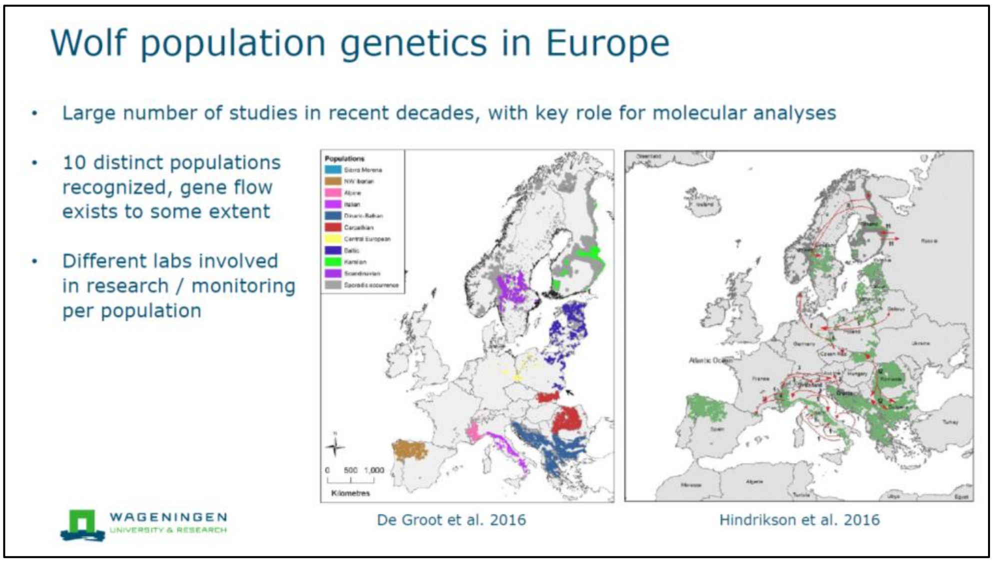

Wolf population genetics in Europe

- Large number of studies in recent decades, with key role for molecular analyses
- 10 distinct populations recognized, gene flow exists to some extent
- Different labs involved in research / monitoring per population

De Groot et al. 2016

Hindrikson et al. 2016

Wolves in the Netherlands: range expansion zone

2013: Factfinding study WENR
→ wolves will likely reach NL soon

Since 2015:
→ So far 30 individuals, various settled
→ First pack with 3 years of litter
→ Mainly from CE but also Alpine

2021: Factfinding study 2.0
→ Ecological effects of settled individuals
→ Best practises management/policy
→ **Future approaches for monitoring**

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Current methods and future directions

Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Decades of population genetic research reveal the need for harmonization of molecular markers: the grey wolf *Canis lupus* as a case study

G. Arjen DE GROOT*1 *Animal Ecology, Alterra, Wageningen UR, P.O. Box 47, 6700 AA Wageningen, The Netherlands. E-mail: g.a.degroot@wur.nl*
Carsten NOWAK *Conservation Genetics Group, Senckenberg Research Institute and Natural History Museum Frankfurt, Clamecystrasse 12, 63571 Gelnhausen, Germany. E-mail: carsten.nowak@senckenberg.de*
Tomaž SKRBINŠEK *Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, Ljubljana 1000, Slovenia. E-mail: tomaz.skrbinsek@gmail.com*
Liselotte W. ANDERSEN *Department of Bioscience, Kalø, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark. E-mail: lwa@bios.au.dk*
Jouni ASPI *Department of Biology, Genetics and Physiology, University of Oulu, P.O. Box 3000, 90014 Oulu, Finland. E-mail: jouni.aspi@oulu.fi*
Luca FUMAGALLI *Department of Ecology and Evolution, Laboratory for Conservation Biology, Biophore Building, University of Lausanne, 1015 Lausanne, Switzerland. E-mail: Luca.Fumagalli@unil.ch*
Raquel GODINHO *Research Center in Biodiversity and Genetic Resources, CIBIO/InBIO, Campus Agrário de Vairão, 4485-661 Vairão, Portugal, Department of Biology, Faculty of Sciences, University of Porto, Rua do Campo Alegre s/n. 4169-007 Porto, Portugal, and Department of Zoology, Faculty of Sciences, University of Johannesburg, Auckland Park 2006, Johannesburg, South Africa. E-mail: rgodinho@cibio.up.pt*
Verena HARMS *Conservation Genetics Group, Senckenberg Research Institute and Natural History Museum Frankfurt, Clamecystrasse 12, 63571 Gelnhausen, Germany. E-mail: verena.harms@senckenberg.de*
Hugh A.H. JANSMAN *Animal Ecology, Alterra, Wageningen UR, P.O. Box 47, 6700 AA Wageningen, The Netherlands. E-mail: hugh.jansman@wur.nl*

- Two review studies published in 2016
  - SNP / HTS likely to become the standard
  - Need for harmonization / exchange
- Current status (5 years later)?

BIOLOGICAL REVIEWS

Cambridge Philosophical Society

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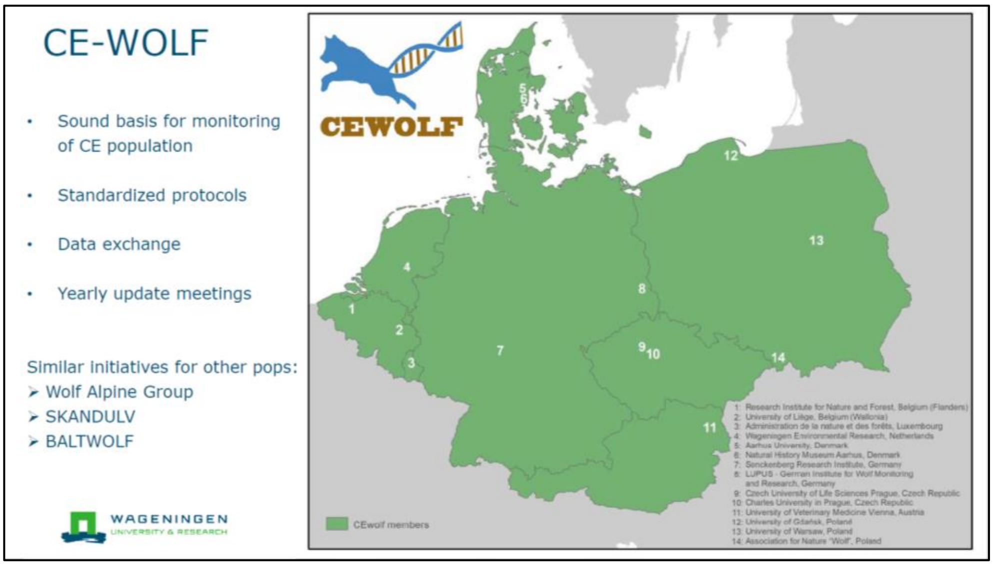
doi: 10.1111/brv.12298

Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management

Maris Hindrikson[1], Jaanus Remm[1], Malgorzata Pilot[2], Raquel Godinho[3,4], Astrid Vik Stronen[5], Laima Baltrūnaitė[6], Sylwia D. Czarnomska[7], Jennifer A. Leonard[8], Ettore Randi[5,9], Carsten Nowak[10], Mikael Åkesson[11], José Vicente López-Bao[12], Francisco Álvares[3], Luis Llaneza[13], Jorge Echegaray[8], Carles Vilà[8], Janis Ozolins[14], Dainis Rungis[14], Jouni Aspi[15], Ladislav Paule[16], Tomaž Skrbinšek[17] and Urmas Saarma[1,*]

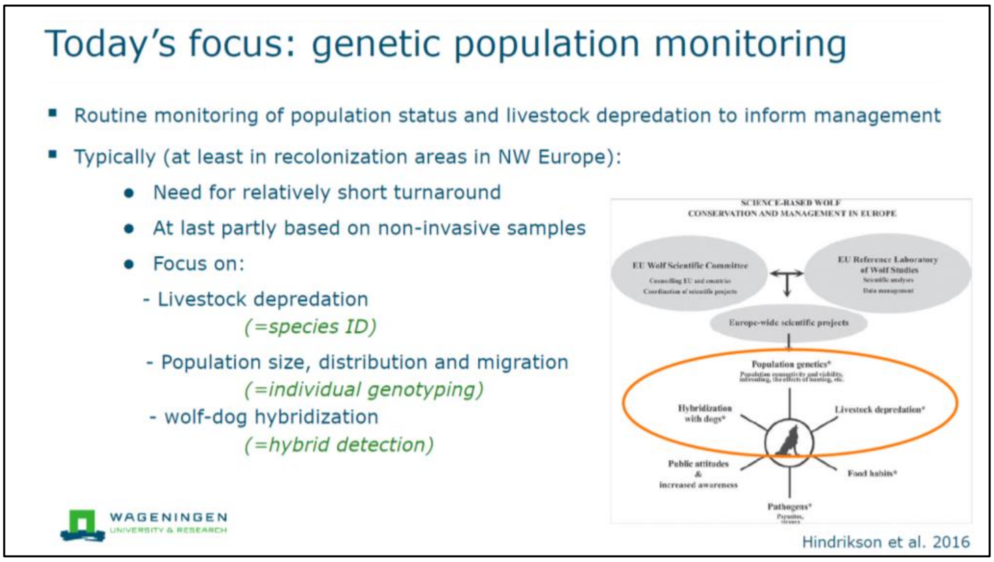


CE-WOLF

- Sound basis for monitoring of CE population
- Standardized protocols
- Data exchange
- Yearly update meetings

Similar initiatives for other pops:
- ➢ Wolf Alpine Group
- ➢ SKANDULV
- ➢ BALTWOLF

1: Research Institute for Nature and Forest, Belgium (Flanders)
2: University of Liège, Belgium (Wallonia)
3: Administration de la nature et des forêts, Luxembourg
4: Wageningen Environmental Research, Netherlands
5: Aarhus University, Denmark
6: Natural History Museum Aarhus, Denmark
7: Senckenberg Research Institute, Germany
8: LUPUS - German Institute for Wolf Monitoring and Research, Germany
9: Czech University of Life Sciences Prague, Czech Republic
10: Charles University in Prague, Czech Republic
11: University of Veterinary Medicine Vienna, Austria
12: University of Gdańsk, Poland
13: University of Warsaw, Poland
14: Association for Nature "Wolf", Poland



Today's focus: genetic population monitoring

- Routine monitoring of population status and livestock depredation to inform management
- Typically (at least in recolonization areas in NW Europe):
  - Need for relatively short turnaround
  - At last partly based on non-invasive samples
  - Focus on:
    - \- Livestock depredation *(=species ID)*
    - \- Population size, distribution and migration *(=individual genotyping)*
    - \- wolf-dog hybridization *(=hybrid detection)*

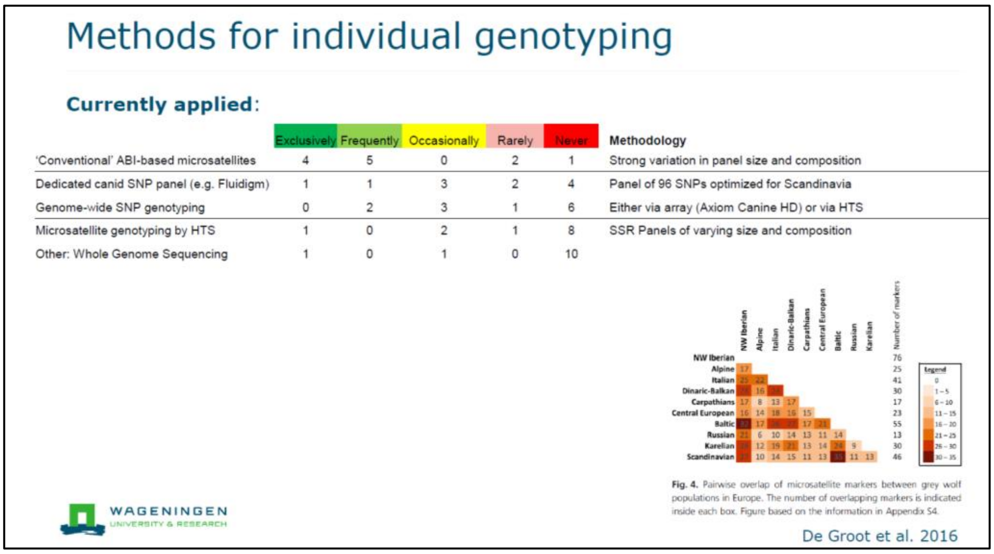
Hindrikson et al. 2016

Questionnaire June 2021

- Sent out to scientific researchers working on wolf genetics
- Covering all main European populations
- 28 invitations in total
- 12 respondents with varying background
  - ➢ Covering at least Scandinavia, Central-Europe, NW Iberia, Dinaric/Balkan
  - ➢ 4 with strong academic/fundamental research focus

    Non-invasive samples: most 0-20%, one with >97%
  - ➢ 8 with focus on monitoring, but all fundamental science as side-goal

    Non-invasive samples: 95-100%
- <u>Goal today</u>: Share results, discuss universality and consequences of some key findings



Methods for individual genotyping

Currently applied:

	Exclusively	Frequently	Occasionally	Rarely	Never	**Methodology**
'Conventional' ABI-based microsatellites	4	5	0	2	1	Strong variation in panel size and composition
Dedicated canid SNP panel (e.g. Fluidigm)	1	1	3	2	4	Panel of 96 SNPs optimized for Scandinavia
Genome-wide SNP genotyping	0	2	3	1	6	Either via array (Axiom Canine HD) or via HTS
Microsatellite genotyping by HTS	1	0	2	1	8	SSR Panels of varying size and composition
Other: Whole Genome Sequencing	1	0	1	0	10	

Fig. 4. Pairwise overlap of microsatellite markers between grey wolf populations in Europe. The number of overlapping markers is indicated inside each box. Figure based on the information in Appendix S4.

De Groot et al. 2016

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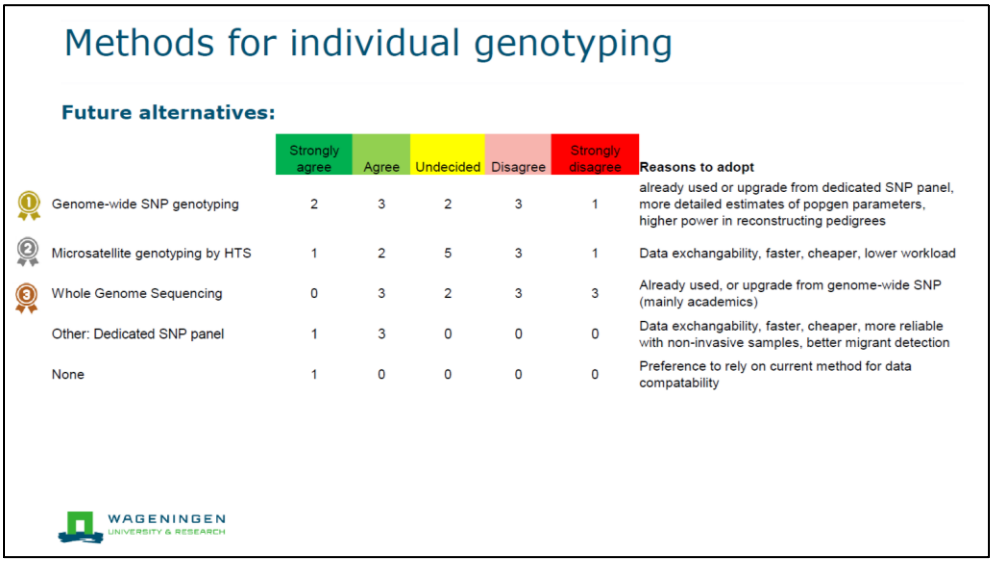

Methods for individual genotyping

Future alternatives:

	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	**Reasons to adopt**
① Genome-wide SNP genotyping	2	3	2	3	1	already used or upgrade from dedicated SNP panel, more detailed estimates of popgen parameters, higher power in reconstructing pedigrees
② Microsatellite genotyping by HTS	1	2	5	3	1	Data exchangability, faster, cheaper, lower workload
③ Whole Genome Sequencing	0	3	2	3	3	Already used, or upgrade from genome-wide SNP (mainly academics)
Other: Dedicated SNP panel	1	3	0	0	0	Data exchangability, faster, cheaper, more reliable with non-invasive samples, better migrant detection
None	1	0	0	0	0	Preference to rely on current method for data compatability

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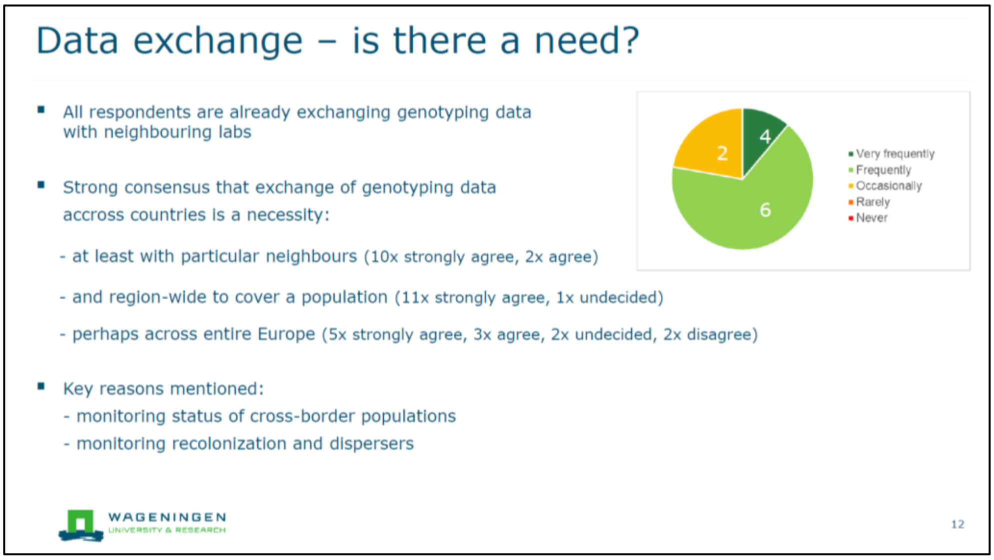

Data exchange – is there a need?

- All respondents are already exchanging genotyping data with neighbouring labs
- Strong consensus that exchange of genotyping data accross countries is a necessity:
  - at least with particular neighbours (10x strongly agree, 2x agree)
  - and region-wide to cover a population (11x strongly agree, 1x undecided)
  - perhaps across entire Europe (5x strongly agree, 3x agree, 2x undecided, 2x disagree)
- Key reasons mentioned:
  - monitoring status of cross-border populations
  - monitoring recolonization and dispersers

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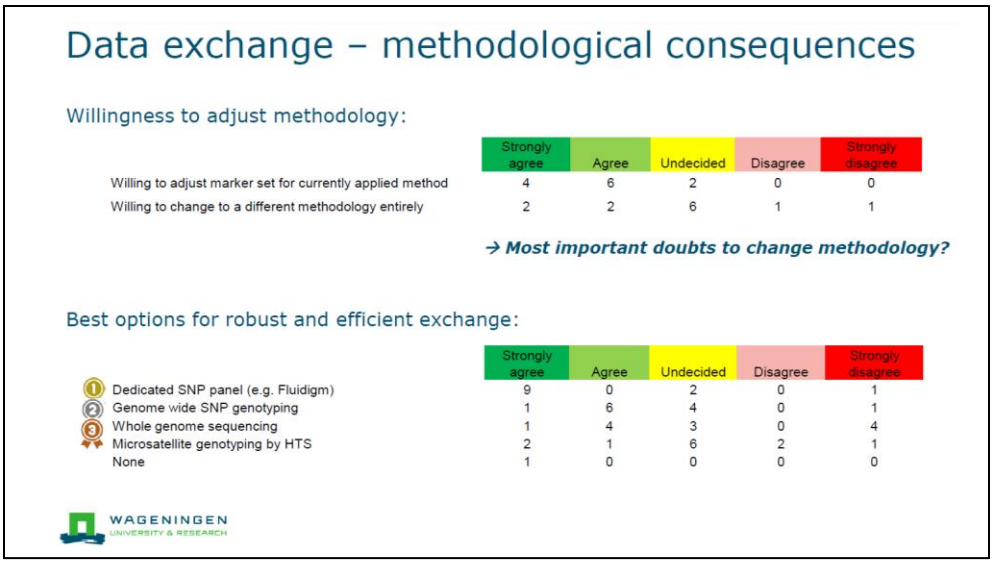

Data exchange – methodological consequences

Willingness to adjust methodology:

	Strongly agree	Agree	Undecided	Disagree	Strongly disagree
Willing to adjust marker set for currently applied method	4	6	2	0	0
Willing to change to a different methodology entirely	2	2	6	1	1

→ Most important doubts to change methodology?

Best options for robust and efficient exchange:

		Strongly agree	Agree	Undecided	Disagree	Strongly disagree
①	Dedicated SNP panel (e.g. Fluidigm)	9	0	2	0	1
②	Genome wide SNP genotyping	1	6	4	0	1
③	Whole genome sequencing	1	4	3	0	4
	Microsatellite genotyping by HTS	2	1	6	2	1
	None	1	0	0	0	0

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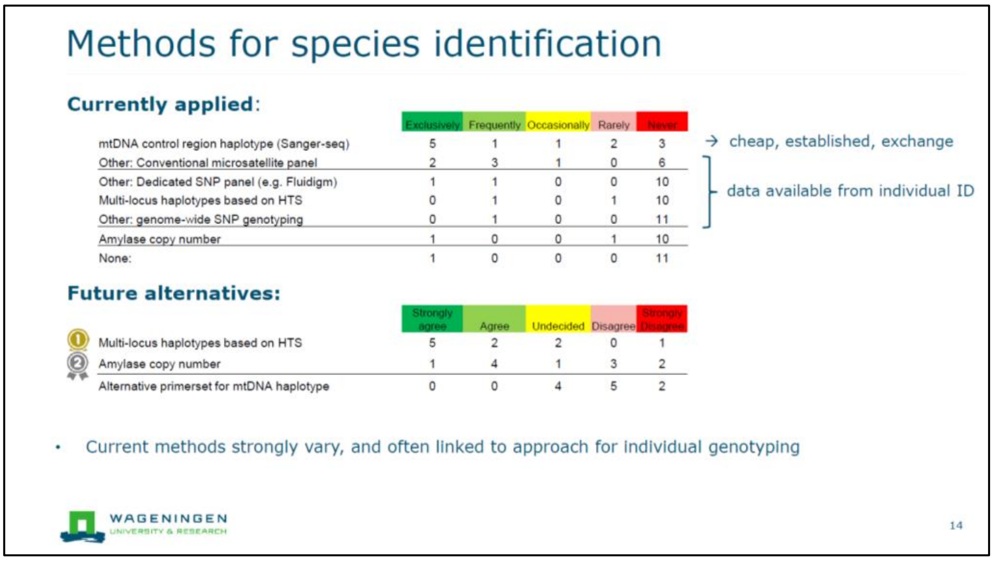

Methods for species identification

Currently applied:

	Exclusively	Frequently	Occasionally	Rarely	Never
mtDNA control region haplotype (Sanger-seq)	5	1	1	2	3
Other: Conventional microsatellite panel	2	3	1	0	6
Other: Dedicated SNP panel (e.g. Fluidigm)	1	1	0	0	10
Multi-locus haplotypes based on HTS	0	1	0	1	10
Other: genome-wide SNP genotyping	0	1	0	0	11
Amylase copy number	1	0	0	1	10
None:	1	0	0	0	11

→ cheap, established, exchange

data available from individual ID

Future alternatives:

		Strongly agree	Agree	Undecided	Disagree	Strongly Disagree
①	Multi-locus haplotypes based on HTS	5	2	2	0	1
②	Amylase copy number	1	4	1	3	2
	Alternative primerset for mtDNA haplotype	0	0	4	5	2

- Current methods strongly vary, and often linked to approach for individual genotyping

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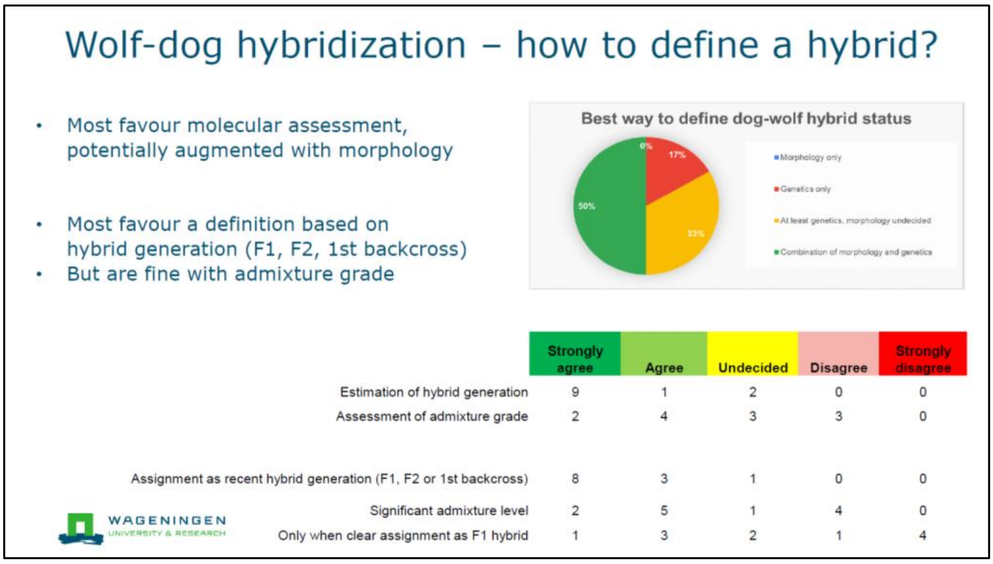

Wolf-dog hybridization – how to define a hybrid?

- Most favour molecular assessment, potentially augmented with morphology
- Most favour a definition based on hybrid generation (F1, F2, 1st backcross)
- But are fine with admixture grade

Best way to define dog-wolf hybrid status

	Strongly agree	Agree	Undecided	Disagree	Strongly disagree
Estimation of hybrid generation	9	1	2	0	0
Assessment of admixture grade	2	4	3	3	0
Assignment as recent hybrid generation (F1, F2 or 1st backcross)	8	3	1	0	0
Significant admixture level	2	5	1	4	0
Only when clear assignment as F1 hybrid	1	3	2	1	4

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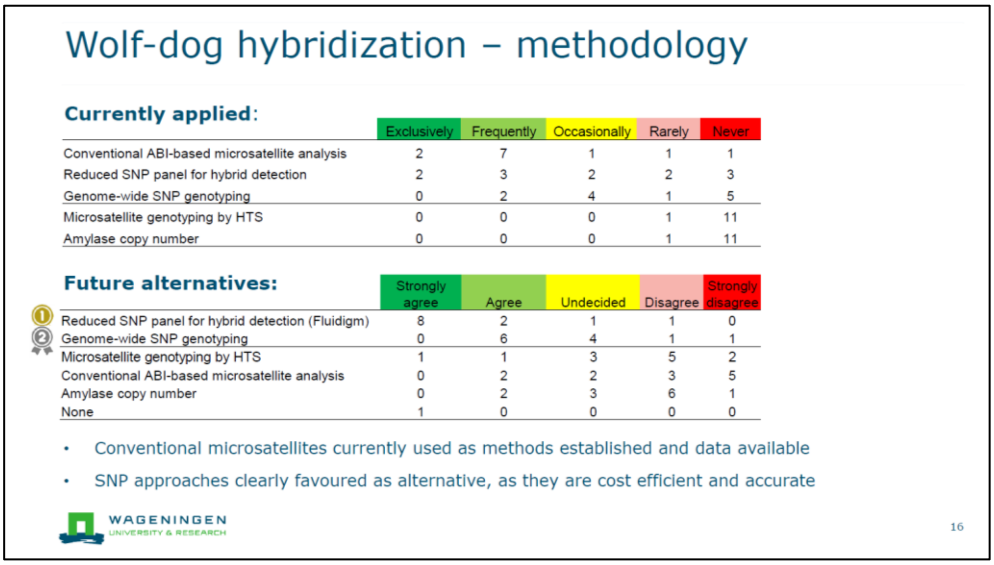

Wolf-dog hybridization – methodology

Currently applied:

	Exclusively	Frequently	Occasionally	Rarely	Never
Conventional ABI-based microsatellite analysis	2	7	1	1	1
Reduced SNP panel for hybrid detection	2	3	2	2	3
Genome-wide SNP genotyping	0	2	4	1	5
Microsatellite genotyping by HTS	0	0	0	1	11
Amylase copy number	0	0	0	1	11

Future alternatives:

	Strongly agree	Agree	Undecided	Disagree	Strongly disagree
① Reduced SNP panel for hybrid detection (Fluidigm)	8	2	1	1	0
② Genome-wide SNP genotyping	0	6	4	1	1
Microsatellite genotyping by HTS	1	1	3	5	2
Conventional ABI-based microsatellite analysis	0	2	2	3	5
Amylase copy number	0	2	3	6	1
None	1	0	0	0	0

- Conventional microsatellites currently used as methods established and data available
- SNP approaches clearly favoured as alternative, as they are cost efficient and accurate

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Thank you for joining!

Any further remarks, suggestions, information: welcome!

Arjen de Groot (g.a.degroot@wur.nl / +31-317485926)

Hugh Jansman (hugh.jansman@wur.nl)

Joachim Mergeay (joachim.mergeay@inbo.be)

Carsten Nowak (carsten.nowak@senckenberg.de)

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Appendix 3 CEwolf consortium

CEwolf is a consortium of scientific institutions working on a harmonized genetic monitoring of the Central European wolf population. Founded in 2015 our tasks are to:

- Standardize genetic marker systems for a harmonized trans-border genetic wolf monitoring. For this we perform regular ring tests, share common samples of wolves, domestic dogs and other canid species and exchange genotype data.
- Provide high standard genetic analyses that support and inform the legal wolf monitoring of the CEwolf member countries. Our laboratories are involved in the official wolf monitoring of Austria, Germany, Denmark, Czech Republic, the Netherlands, Luxemburg, Poland, and Belgium.
- Perform rigorous scientific assessment of the wolf recolonization process. For this, CEwolf members regularly publish the results of their analyses in national and international, peer-reviewed journals. See the website for a publication list.
- Inform the public. There is a considerable amount of misinformation regarding wolves in recently occupied areas, also regarding genetic aspects, such as the appropriateness of methods used in genetic wolf monitoring or the extent of hybridization between wolves and dogs. CEwolf provides solid scientific information on wolf genetics.

Figure B3.1 *Countries and partners involved within the CEwolf-consortium.*

CEwolf currently consists of 14 scientific institutions from eight countries (Figure B3.1). CEwolf members involve i) the laboratories that are in charge of genetic wolf monitoring in their respective countries, ii) institutions that are centrally involved in genetic sampling and closely cooperate with those central laboratories.

More information regarding the CEwolf-consortium, its partners, used genetic marker systems, results and publications can be found at:
www.senckenberg.de/CEwolf

Appendix 4 Project partners

Wageningen Environmental Research (WENR)
Wageningen Environmental Research (WENR) contributes by qualified and independent research to the realisation of a high quality and sustainable green living environment. WENR offers a combination of practical, innovative and interdisciplinary scientific research across many disciplines related to the green world around us and the sustainable use of our living environment. Aspects of our environment on which WENR focuses include soil, water, the atmosphere, the landscape and biodiversity – on a global scale as well as regionally. On request of policy makers WENR is since 2011 involved in the (budding) return of wolves to the Netherlands. Amongst other things this is done by writing fact finding studies (Groot Bruinderink et al., 2012; Jansman et al, 2021) and a proposition of a plan how to be prepared for the return of wolves (Groot Bruinderink & Lammertsma, 2013). Next to scientific advice regarding wolves, WENR conducts post mortem examinations on dead wolves and the genetical monitoring of wolves in the Netherlands on request of the Dutch authorities.

Websites:
https://www.wur.nl/en/research-results/research-institutes/environmental-research.htm
www.wageningenur.nl/wolven

Instituut voor Natuur- en Bosonderzoek (INBO)
The Research Institute for Nature and Forest (INBO) is the independent research institute of the Flemish government, which underpins and evaluates biodiversity policy and management by means of applied scientific research, data and knowledge sharing. INBO is the focal point for the ecological and genetic monitoring of wolves in Flanders, and collaborates closely with regional stakeholders and with international partners from the CEwolf consortium and the IUCN Species Survival Commission Specialist group Large Carnivore Initiative for Europe.

Websites:
www.inbo.be
www.natuurenbos.be/de-wolf-in-vlaanderen

Senckenberg Gesellschaft für Naturforschung (SGN)
SGN is part of the German Federal Documentation and Consultation Centre on Wolves (Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf) which, in addition to advising the federal states, compiles all wolf monitoring data collected in Germany. This is used by policymakers for monitoring and management purposes. SGN was recommended by the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz) as the national reference centre for the genetical monitoring of wolves in Germany. Since 2010, all samples collected in the frame of the German-wide wolf monitoring are analysed at the Senckenberg Centre for Wildlife Genetics. More than 27.000 DNA samples have been genetically analysed to date. Internationally SGN participates in multiple consortia, such as the CEwolf-consortium (see attachment 3) and the Wolf Alpine Group (https://www.kora.ch/index.php?id=330).

Website:
https://www.senckenberg.de/en/institutes/senckenberg-research-institute-natural-history-museum-frankfurt/division-river-ecology-and-conservation/center-for-wildlife-genetics/national-reference-center-for-genetic-analysis-of-wolf-and-lynx/#content-0002_4

Wageningen Environmental Research
P.O. Box 47
6700 AA Wageningen
The Netherlands
T +31 (0)317 48 07 00
wur.eu/environmental-research

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Wageningen Environmental Research
P.O. Box 47
6700 AB Wageningen
The Netherlands
T +31 (0) 317 48 07 00
www.wur.eu/environmental-research

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