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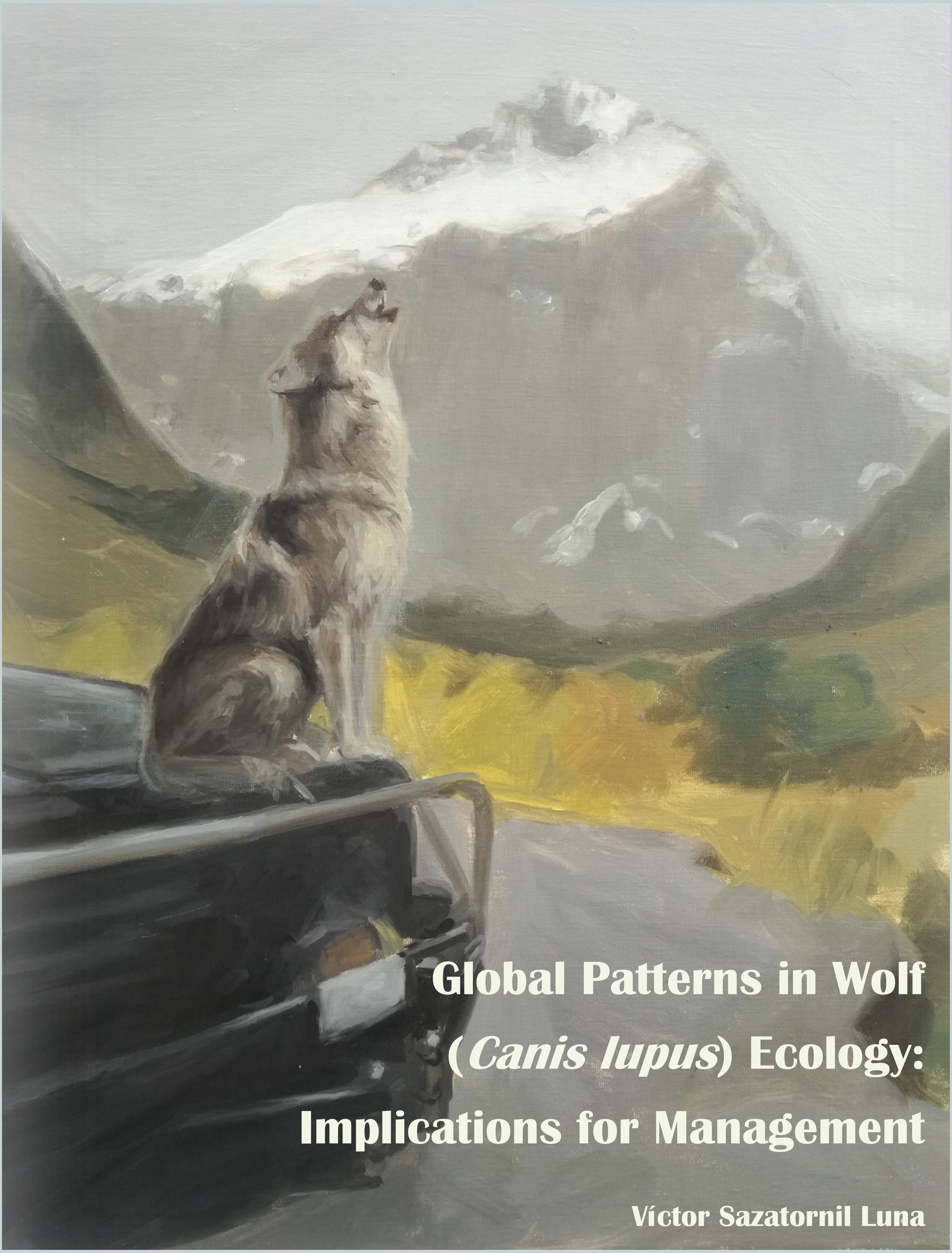
Patrons globals en l'ecologia del llop: Implicacions en la gestió

Victor Sazatornil i Luna



Global Patterns in Wolf (*Canis lupus*) Ecology: Implications for Management

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Memòria presentada per **Víctor Sazatornil i Luna**
per optar al grau de Doctor per la Universitat de Barcelona

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A la Idoia, el Fèlix i l'Eloi,

els altres tripulants de la nau

Agraïments

Aquesta tesi és el fruit d'un seguit d'anys durant els quals he tingut la sort de treballar i estudiar el llop, un animal fascinant (com tants altres), que m'ha permès conèixer llocs i gent meravellosa. Al llarg d'aquests anys son moltes les persones amb qui he tingut la sort de compartir bons moments i a les que estic profundament agraït. Amb algunes d'elles he forjat una gran amistat.

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Summary

Environmental authorities, conservation professionals, and several other social sectors frequently demand scientifically sound information to inform policy and decision-making processes. Beyond national or subnational conservation laws, biodiversity conservation increasingly relies on international agreements and commitments, through which sovereign nations commit to share part of their duties and responsibilities in conservation issues. In this pyramidal structure of multi-governance layers, the use of the best available evidence is of paramount importance to effectively adapt general statements contained in general laws or regulations into specific contexts. Using wolves (*Canis lupus*) as case study, this thesis explores the interface between ecology and policy-making in wildlife conservation and management at different spatial and governance scales. The thesis combines empirical evidence, focused on wolf breeding site attributes and livestock depredations by wolves, literature reviews and in-deep analyses of conservation and management instruments in order to critically assess how evidence is used to develop site-specific management actions, and the way forward to improve policy implementations and effectiveness. We provide an illustrative example of how unveiling general ecological patterns and sources of variation from empirical datasets can provide valuable information to policy decision-makers. In particular, Chapter 1 analyzes global patterns in breeding site selection by wolves regarding their vulnerability to humans. By identifying global patterns and context-dependent sources of variability on this issue, Chapter 2 explores whether current mandates to protect wolf breeding sites at the European level are translated effectively into domestic management instruments. Chapter 3 explores the widely assumed positive relationship between the number of wolves and the number of livestock attacks, and shows that the history of coexistence can explain remarkable differences between territories, undermining the general assumption that the increase in wolf population size will translate

into higher levels of human-wolf conflict. Chapter 4 goes further with the impact of wolves on livestock conducting a critical test of the frequently used assumption of the existence of a negative correlation between wild prey abundance and the number of livestock depredations. This thesis calls the attention on the importance of local knowledge and contexts when implementing management and conservation interventions, in order to avoid a lack of effectiveness or undesired outcomes when local management actions are grounded on general assumptions. Nonetheless, when local evidence is not available, compiling systematically data from multiple, representative sites can provide valuable information to managers and policy-makers.

Resum

Les autoritats ambientals, els professionals de la conservació i altres sectors socials, demanen freqüentment informació científica fiable per a l'elaboració de polítiques i la presa de decisions. Més enllà de la normativa ambiental a nivell dels estats o regions, la conservació de la biodiversitat recau cada cop més en acords i compromisos internacionals, a través dels quals les sobiranies acorden repartir-se part dels seus deures i responsabilitats en matèria de conservació. En aquest sistema piramidal de governança amb diversos nivells, l'ús de la millor evidència a l'abast és fonamental a l'hora d'adaptar els mandats generals continguts en lleis o regulacions als contextos específics. A partir del llop (Canis lupus) *com a model d'estudi, aquesta tesi explora la interfície entre ecologia i la definició de polítiques en matèria de conservació i gestió de la natura a diferents escales espacials i de governança. La tesi combina l'evidència empírica focalitzada en les característiques dels llocs de reproducció dels llops i els danys a la ramaderia, la revisió de literatura científica i l'anàlisi dels instruments en què es basa la gestió i conservació del llop, amb la finalitat de fer una revisió crítica de com l'evidència fonamenta l'actual gestió de l'espècie en contextos específics i la manera en què la implementació i eficàcia d'aquestes polítiques es podria millorar. Aquesta tesi representa un exemple de com el fet d'explorar patrons ecològics generals i la seva variabilitat a partir de dades empíriques pot proporcionar informació valuosa als gestors implicats. Concretament, el Capítol 1 analitza els patrons globals en la selecció dels llocs de reproducció dels llops en relació a la seva vulnerabilitat enfront els humans. A partir de la identificació de patrons globals i fonts de variabilitat en aquest àmbit, el Capítol 2 es planteja si els mandats de protegir els llocs de reproducció dels llops, existents a nivell europeu, son transferits de manera efectiva als instruments de gestió a escala local. El capítol 3 explora l'estesa assumpció d'una relació positiva entre el nombre de llops i el nombre de danys al bestiar, i mostra*

com la història de la coexistència pot explicar diferències destacables entre territoris. El Capítol 4 va més enllà en l'impacte dels llops sobre el bestiar domèstic i fa una anàlisi crítica d'una altra assumpció freqüentment utilitzada, que suggereix una correlació negativa entre l'abundància de preses salvatges *i els danys a la ramaderia. Finalment, aquesta tesi destaca la importància del coneixement dels contextos locals a l'hora d'implementar intervencions de conservació i gestió per tal d'evitar una falta d'efectivitat o efectes indesitjats quan la gestió es basa en assumpcions generals. No obstant això,, quan aquesta informació no és a l'abast, la compilació sistemàtica de dades de múltiples contextos representatius també pot proporcionar informació valuosa per als gestors.*

Introduction

With the time passing within the 21st century, the impacts of the ever increasing human pressure on the planet are becoming more evident than ever, and prospects are not optimistic (Jenkins 2003; Jordan *et al.* 2013; Urban 2015). There is now a remarkable amount of evidence showing that the planet has entered in what is considered the 6th Mass Extinction (Barnosky *et al.* 2011; Ceballos *et al.* 2015). Some authors point out that we are probably approaching tipping points towards a global collapse led by overconsumption of resources, habitat transformation and climate change (Barnosky *et al.* 2012; Ehrlich & Ehrlich 2013). Indeed, biodiversity is one of the planetary boundaries that are over-stepped (Rockström *et al*. 2009).

Beyond reducing the number of extant species and disrupting ecosystem functions, paradoxically the biodiversity crisis is expected to affect human wellbeing (Duffy *et al.* 2009; Isbell *et al*. 2011). Nonetheless, despite most forecasts are pessimistic and the challenges are overwhelming, it is also true that awareness among societies has increased in the last decades and that environmental concern is gaining political recognition (Rands *et al.* 2010; Tittensor *et al.* 2014). There is an increasing number of international initiatives aiming at ambitious environmental commitments. A growing consensus has emerged amongst the world's approximately 200 sovereign states regarding the need to minimize, halt, or reverse biodiversity loss and law and conservation regulations have a key role to play in achieving these aims (Chapron *et al.* 2017). In terms of biodiversity conservation, some notable examples are the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Washignton DC, 1973) and the United Nations Convention on Biological Diversity (Nairobi, 1992). However, to date, the objectives of most international agreements have not been fully achieved; awakening doubts about the feasibility of mainstreaming biodiversity across other sectoral policies (Tittensor *et al*. 2014; Tinch *et al.* 2015).

An illustrative example of failure despite broad commitment is the ratification of the Convention on Biological Diversity (CBD; Rio de Janeiro, 1992), through which 193 parties committed to achieve a significant reduction of the current rate of biodiversity loss by 2010 (Decision VI/26 of the Conference of the Parties of the Convention on Biological Diversity, 2002). It was extended to 2020 in the Aichi targets once the objectives were proven to be far from fulfilment (Butchart *et al*. 2010). Currently, even the 2020 horizon seems unrealistic, which indicates that governments and economies are not on track regarding their obligations (Tittensor *et al*. 2014).

Towards a holistic view to preserve biodiversity

The wide international consensus reached under the umbrella of the Convention on Biological Diversity, leading among others to the "*Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets*" (Decision X/2 of the Conference of the Parties of the Convention on Biological Diversity; 2010) illustrates one of the substantial changes in modern times regarding the way nations deal with environmental problems. As other environmental issues, biodiversity has been characterized as a *Common Concern of Humankind* (Biermann 1996), a legal concept originally restricted to climate (UN General Assembly Resolution 43/53, 1988) and later extended to other issues considered basic to all humans, such as biological diversity, as recognized by the CBD itself.

A move to a holistic approach in biodiversity conservation is of paramount importance as it introduces biodiversity into the legal sphere at international level, and recognizes that all nations have an interest in biodiversity and a commitment in cooperating in its conservation. This process acknowledges the necessity to tackle this issue from a global perspective, setting aside, at least partially, self-interests of states and sovereignties. Consequently, almost all nations in the world have in practice relinquished part of their sovereignty in biodiversity conservation at ratifying binding and non-binding international agreements on biodiversity while sovereign rights of the states over their natural resources remain untouched in most cases.

Biodiversity has a spatial dimension that differs from other environmental issues of common and public concern, such as the atmosphere, since it occurs (mainly) within national borders (Soltau 2016). This fact has substantial implications regarding the implementations of management and conservation strategies, which usually rely on domestic regulations, despite countries can coordinate their conservation strategies and regulations (see Kark *et al*. 2015; Lim 2016). Integrating the conservation of biodiversity at local scales within the holistic perspective and global targets provided by international agreements is a matter of concern (Butchart *et al.* 2015; Hill *et al.* 2015). Some international organisms, such as the International Union for the Conservation of Nature (IUCN), the Global Environment Facility (GEF) or the CBD provide instrumental assessment and financial assistance to implement conservation actions (e.g., Biagini *et al.* 2014; Bax *et al.* 2016). The CBD itself also enables cooperation between contracting parties within its statements as a mean to achieve the global targets (Iwu 1996).

Moreover, some nations have also reached substantial agreements at intermediate regional multistate levels, posing additional obligations to its members. The environmental policy framework in Europe (European Union - EU - and the Council of Europe) is an illustrative example of such multi-level hierarchical structure of legally and non-legally binding nature. In this case, governance is largely exerted at the multistate level, especially in the EU, where supranational governmental structures are designated by states to delineate environmental laws and to enforce compliance by member states. Since the acquisition of international obligations has become generalized, it has turned out that the transposition of commitments from international statements to domestic legal, social and ecological contexts is not straightforward and have multiple pitfalls (Ledoux 2000; López-Bao *et al.* 2015; Murcia *et al.* 2016; López-Bao & Margalida 2018; Mateo-Tomás *et al.* 2018), and can also entail undesired outcomes on people's livelihoods if not properly contextualized (López-Bao *et al.* 2013; Brondizio & Le Tourneau 2016). It can also collide with strategic goals from other sectoral policies (Rosendal 2001; López-Bao & Margalida 2018; Mateo-Tomás *et al*. 2018).

The pyramidal structure of multi-governance layers in conservation necessarily requires that general statements and obligations committed at higher levels are enunciated in vague terms since they have to be suitable for a larger number of taxa, situations and contexts. In this step, the critical evaluation of conservation and management action using sound scientific approaches and evidence is fundamental in order to adapt policy decision-making processes, accommodating such general statements contained in international agreements into practical, effective conservation interventions on the ground.

The need of transferable evidence in biodiversity conservation

The policy-making process related to conservation and management of biodiversity and natural resources is aided by multiple sources of information, such as scientific or traditional knowledge (Cook *et al*. 2012). Nonetheless, it is widely acknowledged that the best available science should inform the policy-making process, to predict the likely response of the ecosystems with acceptable accuracy, optimize the allocation of limited resources, and in the end improving the chances of success after implementing interventions (Pullin *et al.* 2004; Sutherland *et al*. 2004). Some authors, though, argue that despite being desirable and necessary in certain situations, not all the conservation action needs to rely on quantitative data and claim that policy-making under certain circumstances can be more flexible regarding the use of sources outside formal research (Adams & Sandbrook 2013).

Although performing experimental research to inform policy-making would be desirable in every situation, it is often unfeasible. In most situations, site-specific evidence does not exist or, it is difficult to obtain, and decisions have to rely on external knowledge produced under situations and ecological conditions frequently differing than the ones at site. In order to build trust in the policy-making decision process and the transferability of conservation actions, some remarkable initiatives have been put into practice in an attempt to summarize quantitative outcomes and deliver previous knowledge in a useful manner for conservation and management practitioners (Eklund *et al*. 2017; Sutherland *et al.* 2018). Finally, despite adopting successful external experiences, in-site evaluation is also key to conservation practice, in order to assess its effectiveness, address possible pitfalls (Ferraro

& Pattanayak 2006) and to improve the evidence base from useful precedents (Salafski *et al.* 2002).

In spite of the amount and quality of available evidence, the natural systems are generally shaped by complex interactions, and ecological processes are largely influenced by intrinsic and extrinsic factors that can only be estimated under a reductionist, probabilistic approach. This inherent uncertainty associated with observational research can compromise conservation outcomes (Cooke *et al*. 2017). The use of systematic reviews, compilation of primary data, and meta-analysis techniques, however can help to remove a significant portion of the variance posed by contextual constraints, reducing uncertainty (Pullin & Knight 2009; Haddaway & Pullin 2014; Mengersen *et al.* 2015). It can be a useful approach to discriminate true from random context-specific effects (Jackson *et al*. 2015; Gutzat & Dormann 2018), as well as to unveil general patterns (e.g. Chamberlain *et al.* 2014).

Context-dependent responses refer to site-specific observed effects attributable to intrinsic (physiological, genetic, etc.) or extrinsic (environment) characteristics affecting individuals, populations or communities. Identifying and quantifying the effect of context-specific constraints can provide valuable information to decision-makers and may help to increase the effectiveness of conservation and management interventions (e.g.: Barral *et al.* 2015; Meli *et al.* 2014). On the contrary, evidence that do not capture and account for contextual variance, can lead to misinterpretation of the observed effects, the prevalence of preconceived ideas and, ultimately, influence on the process of effective policy and decision-making if blindly transferred. Some authors warn about the misuse of anecdotal observations or traditional knowledge without proper evaluation (Pullin *et al*. 2004; Sutherland *et al.* 2004). Also, the mismatch between research topics and conservation needs (Balme *et al.* 2013) or the use of misconceptions as dogma (Dybing *et al.* 2018, Primack *et al*. 2018) can seriously compromise the outcomes and success of interventions. For example, Florida panther (*Puma concolor couguar*) conservation was performed under misguided assumptions until an independent scientific team detected that critical flaws existed in the supposed evidence guiding the species conservation action (Gross 2005). In another example the suitability of no-take marine zones in marine reserves in Australia is challenged by Kearney *et al.* (2012), who claim that they have been designated after an inappropriate use of fisheries data.

Thus, in conservation science, a critical evaluation of implemented conservation and management actions is of paramount importance to inform the policy-making process and move towards an adaptive conservation and management approach (McCarthy & Possingham 2007).

The wolf as an example of multi-level policy-making in biodiversity conservation and management

Large terrestrial mammals (megafauna) illustrate the current biodiversity crisis since most species are being threatened, and their populations declining worldwide (Ripple *et al.* 2016). These negative trends prevail despite remarkable signs of resilience and population recovery exist, mainly in developed countries (Madhusudan 2004; Chapron *et al.* 2014). Habitat loss, persecution and competition for resources are the main threats to the survival of these species (Ripple *et al*. 2016). To counteract most of the existing pressures requires a high capability of authorities and competing organisms to implement and enforce conservation commitments and actions.

Within large mammals, the large carnivore group is represented by 31 species of the order Carnivora (excluding *Pinnipeda*) with an average adult body mass above 15 kg. This group includes members of the families *Canidae*, *Felidae*, *Hyaenidae*, *Mustelidae* and *Ursidae* (Ripple *et al.* 2014). Large carnivores generally share in common large body sizes, long lifespans, low reproduction rates, large spatial requirements and, therefore low densities (Ripple *et al*. 2014). These species play substantial roles in ecosystem functioning, such as those related with trophic cascades and mesopredator control (Beschta & Ripple 2009; Estes *et al*. 2011; Ripple *et al.* 2014). Besides, their ecological significance can be partially set aside in some contexts of coexistence with humans, such as exploited populations (Ordiz *et al*. 2013).

Beyond their benefit to ecosystems, many large carnivore species have further relevance as conservation assets because they can play a prevailing role in engaging society (individuals, stakeholders, authorities, etc.) in conservation awareness and action (e.g. Ran *et al.* 2009). In fact, some of the most charismatic species for the general public belong to this group (Clucas *et al.* 2008). Their high marketing potential can ultimately help to scale up sustainability and biodiversity conservation in societal priorities and governmental agendas, despite their suitability has been also called into question in certain contexts (e.g. Linnell *et al*. 2000).

However, the conservation and management of these species is not exempt from challenges. Notwithstanding, what brings enormous complexity to the management of these species, especially in human-dominated landscapes, is their predatory behaviour on livestock, game, pets or even humans (Treves & Karanth 2003). This behaviour often triggers retaliatory persecution and killing. Attitudes towards carnivores often reflect a strong polarization, which adds even more complexity to effectively delineate successful coexistence frameworks (Keller *et al*. 1996; Kleiven *et al*. 2004).

The strategies adopted to cope with large carnivore coexistence vary largely among territories (Treves & Karanth 2003; Packer *et al.* 2009; Chapron *et al*. 2014). The degrees of coexistence go from strict contention of carnivores within reserves (Woodroffe & Ginsberg 1998) to tight coexistence, where landscapes are generally heterogeneous in a manner that provide large carnivores refuge areas within a multi-use human-dominated matrix (Oriol-Cotterill *et al.* 2015b). To manage large carnivores in these particular contexts is challenging when it comes to mitigate conflicts and reach acceptable levels of tolerance (Packer *et al.* 2009; Dickman *et al*. 2010).

The gray wolf (*Canis lupus*, 1758 L.) has the largest distribution range of all the extant terrestrial mammals in the world (excepting non-native populations). Wolves currently expand throughout an estimated area of ca. $51 x 10^6$ km^2, accounting for 35% of the emerged land on Earth, all of it in the Northern Hemisphere in America and Eurasia (considering apart the recently described African wolf *Canis lupus lupaster;* Rueness *et al.* 2011). Wolf occurrence encompasses from above Parallel 75ºN in the Arctic to below Parallel 20ºN in the Tropics. Within this huge portion of land, wolves share the landscape with roughly 1.29 billion humans and, perhaps more significant, with ca. 330 million sheep, 210 million goats, 170 million cattle[1] and several millions of other livestock, wild ungulates and smaller potential prey.

Wolves are capable to thrive in human-dominated landscapes (Agarwala 2009; Llaneza *et al.* 2012; Chapron *et al*. 2014), persisting in some of the most populated regions of the world (Fig.1). It is easy to imagine the panoply of ecological and social contexts where wolves can be found. Because of this fact, together with its wide dietary spectrum, the wolf has been widely considered an opportunistic and highly adaptable species (Mech & Boitani 2010). Wolves rely on wild prey in large areas of their distribution range while in others they feed mainly on livestock (Newsome *et al*. 2016), with the consequent differences in the levels of conflicts across contexts.

Although the wolf has been globally assessed as of Least Concern by the IUCN (Mech & Boitani 2010), regional assessments from Europe denote different conservation status depending on the populations, or portions of populations (LCIE 2007). Wolf protection is granted at different levels according to supranational (e.g. Europe), national and subnational legislations. It is precisely in Europe that wolf is regarded in legally binding and non-binding international agreements, namely the Bern Convention on the Conservation of European Wildlife and Natural Habitats (Council of Europe, 1979), and EU Habitats Directive of 1992 (Directive 92/43/EEC). These agreements establish duties and obligations to contracting parties and member countries of the EU, respectively, and represent a good opportunity to delve into potential pitfalls of implementation in multi-level legislation systems.

Wolf management in the US attains also remarkable complexity. Wolves in the lower 48 states have also been granted federal protection since their listing in the Endangered Species Act in 1974. Today, wolves from the Great Lakes region (after being delisted and

[1] Data on human population: Center for International Earth Science Information Network - CIESIN - Columbia University. 2017. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 10. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).
Data on livestock, Gridded Livestock of the word v.2.0. - Robinson T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I and Gilbert, M. (2014) Mapping the global distribution of livestock. *PLoS ONE* 9(5):e96084.
Data on wolf distribution: IUCN (International Union for Conservation of Nature) 2010. Canis lupus. The IUCN Red List of Threatened Species. Version 2018-1.

relisted again), the Pacific Northwest, and the Mexican wolf population remain listed in the Endangered Species Act while the population from the Northern Rockies has been delisted and now is managed at the state level.

Figure 1. An Indian wolf (*Canis lupus pallipes*) near the outskirts of Pune (Maharashtra, India) a conurbation inhabited by over 5 million people. The densely populated grasslands of the Deccan Plateau are one of the last strongholds of this subspecies in India. (Photo courtesy of Mihir Godbole).

At the global scale, the complexity of wolf management has motivated guidance and coordination from several international organisms. For example, the IUCN stated a *Manifesto and Guidelines on Wolf Conservation* (Pimlott 1975) containing a set of principles and suggestions to guide wolf conservation and management. Among others, the *Manifesto* pointed out the convenience to develop management strategies for wolf populations. In fact, wolf management at supranational (e.g. Boitani 2000), national and subnational levels largely relies on specifically designed plans or strategies (especially in Europe and North America) aimed to delineate guidelines, regulations and instrumental aids to manage and conserve wolf populations. The existence of these plans makes information on wolf management clearly defined and easy to access.

The aspects of wolf ecology and conservation above mentioned justify the selection of this species as an appropriate case study to delve into the interface between ecology and decision-making at a global scale. Widely distributed in very diverse scenarios, the gray wolf also receives broad attention as a management subject from international to (sub) national levels. The wolf therefore brings a good opportunity to assess if and how evidence lies at the core of its management.

In this thesis, we conducted research on global patterns of wolf ecology and possible sources of variability in order to scrutinize the implementation of suitable management and conservation interventions at different levels, focusing on two major aspects of wolf ecology: behavioural strategies to cope with humans and attacks to livestock.

Objectives

This thesis combines systematic review and primary research with a twofold purpose: 1) to build evidence on general patterns of wolf breeding and trophic ecology, and 2) to conduct a critical evaluation on how current wolf conservation and management instruments integrate the best available knowledge and put it into practice. The thesis focuses on two aspects of wolf ecology with important implications for the management of this species, which draw considerable reaching attention not only by researchers, managers or conservationists, but also the general public.

First, it examines general patterns in the use of habitat by wolves in the breeding period, when the location of wolves is spatially and temporally predictable over several months, making them especially vulnerable to humans. How these general patterns in wolf habitat use are integrated in habitat protection obligations and explicit actions within wolf conservation and management instruments is also examined.

Second, the thesis explores the issue of livestock depredation by wolves, one of the major drivers of the wolf-human conflict worldwide. It performs a critical review of wolf conservation and management instruments regarding measures undertaken to reduce livestock losses.

The thesis is structured in two blocks, composed of two chapters each, dealing with the topics mentioned above. Chapters 1 and 3 provide a strong empirical basis for wolf habitat use and livestock depredation across large portions of its vast geographic range. Chapters 2 and 4, are designed as practical analogues which focus on effective implementation of management interventions and maximizing outcomes for wolf conservation.

Chapter 1 explores patterns of habitat selection by wolves during the breeding period at a global scale in relation to risk from humans. The objective is to put into context the idea of the wolf as a habitat generalist species. To do so, the research dealt with habitat selection reducing the spatio-temporal window to breeding sites during the breeding period. As it is assumed that during this period (up to 6 months) and at these places wolves are highly vulnerable to humans, a strong and evident response is expected. Large-scale drivers of variation in the patterns of breeding site selection are also explored. Systematic literature research and primary data were used to gather information on breeding sites and conduct meta-analysis.

Chapter 2 is a critical evaluation of the implementation of breeding site protection by international agreements (Bern Convention) and laws (EU Habitats Directive) in Europe. The case study is presented as an example to illustrate potential pitfalls in the transposition of general norms into domestic regulations and management if species and context particularities are not thoroughly considered in the policy-making process.

Chapter 3 deals with the patterns of wolf depredation on livestock from an international perspective. Specifically, it examines whether the frequently used assumption that wolf numbers determine the number of livestock killed is supported by the empirical evidence. This fundamental assumption is used to justify population interventions (e.g. population caps, hunting, culling) in order to deal with livestock losses and the resulting wolf-human conflict. This chapter explores the general relationship between wolf numbers and livestock depredations from a global perspective, together with possible sources of variation.

Chapter 4 continues with the management of livestock depredation by wolves. Increasing the abundance of wild prey is recurrently adduced in some wolf management guidelines and instruments as a measure to decrease the number of kills. We combine a literature review, a review of wolf management and conservation strategies, and primary research to address the tenet that enhancing wild prey decreases wolf attacks on livestock. We also examine this assumption in a context of changes in the abundance of wild and domestic prey in a wolf population of northwestern Spain over a 12-year time period.

Chapter 1

The role of human-related risk in breeding site selection by wolves[1]

ABSTRACT

Large carnivores can be found in different scenarios of cohabitation with humans. Behavioural adaptations to minimize risk from humans are expected to be exacerbated where large carnivores are most vulnerable, such as at breeding sites. Using wolves as a model species, along with data from 26 study areas across the species´ worldwide range, we performed a meta-analysis to assess the role of humans in breeding site selection by a large carnivore. Some of the patterns previously observed at the local scale become extrapolatable to the entire species range provided that important sources of variation are taken into account. Generally, wolves minimised the risk of exposure at breeding sites by avoiding human-made structures, selecting shelter from vegetation and avoiding agricultural lands.

Our results suggest a scaled hierarchical habitat selection process across selection orders by which wolves compensate higher exposure risk to humans within their territories via a stronger selection at breeding sites. Dissimilar patterns between continents suggest that adaptations to cope with human-associated risks are modulated by the history of coexistence and persecution. Although many large carnivores persisting in human-dominated landscapes do not require large-scale habitat preservation, habitat selection at levels below occupancy and territory should be regarded in management and conservation strategies aiming to preserve these species in such contexts. In this case, we recommend providing shelter from human interference at least in small portions of land in order to fulfil the requirements of the species to locate their breeding sites.

[1] A version of this chapter has been published in *Biological Conservation*.
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Introduction

Despite the fact that large carnivores are focal species for biodiversity conservation their predatory behaviour leads to their persecution (both legal hunting and poaching) worldwide. Different perceptions and interests contribute to controversy on their conservation and management, including whether or how to coexist with these species (Packer *et al*. 2013; Chapron *et al*. 2014). Mitigating conflicts and promoting coexistence have become cornerstones of large carnivore conservation in modern times. Consequently, a comprehensive knowledge of the different human and carnivore factors that make coexistence possible is required. Understanding the adaptive behaviours of large carnivores favouring their persistence in human-dominated landscapes is pivotal for delineating effective conservation measures.

Apart from persecution, sharing the landscape has traditionally driven both humans and large carnivores to adopt adaptive strategies in order to coexist. While humans have historically implemented damage prevention measures (e.g., livestock guarding dogs, shepherds, enclosures; Woodroffe *et al*. 2007; Linnell *et al*. 2012), large carnivores have adopted different behavioural adaptations to minimise risks (e.g., temporal or fine-scale spatial segregation; Theuerkauf *et al*. 2003; Habib & Kumar 2007; Zedrosser *et al*. 2011; Ahmadi *et al.* 2014). On a global scale, historical and human determinants seem to lie behind dissimilar outcomes in such competitive scenarios given, for instance, the persistence of large carnivores in densely populated landscapes in Europe as compared to their absence in similarly populated regions of North America (Chapron *et al*. 2014).

Many large carnivore populations can be found outside of protected areas and can breed and thrive in human-dominated landscapes with few or negligible portions of natural habitats (Abay *et al.* 2011; Athreya *et al*. 2013; Ahmadi *et al.*,2014; López-Bao *et al,* 2015). Wolves (*Canis lupus*) are the most widely distributed large carnivore species with which humans share the landscape (Mech & Boitani 2003). However, coexistence is largely variable in terms of interaction attributes and conflict intensity (e.g., Agarwala & Kumar 2009; López-Bao *et al*. 2013; Chapron *et al*. 2014). Wolves are resilient and able to thrive under a wide spectrum of biotic and abiotic conditions (Mech & Boitani 2003). As a consequence, they have traditionally been considered habitat generalists, being habitat tolerance mainly shaped by food availability and mortality risk (Mech & Boitani 2003). Such constraining factors of habitat tolerance are the same for most large carnivore species (Woodroffe & Ginsberg 1998; Fuller & Sievert 2001). Therefore, wolves are a good model species for gaining a better understanding of the behavioural adaptations of large carnivores to humans.

Human impacts (e.g., persecution, disturbance) result in different behavioural responses of large carnivores, such as wolves, to minimise their interactions with humans and their effects (e.g., Whittington *et al*. 2005; Llaneza *et al*. 2012; Lesmerises *et al.* 2013; Ahmadi *et al.* 2014). Factors influencing exposure risk, such as the availability of refuge habitat, are also modulated by human activity and impact at the landscape level (Thurber *et al.* 1994; Llaneza *et al*. 2012). During the pup rearing season, when large carnivores are more vulnerable, these species are expected to strengthen avoidance behaviour from humans.

In the case of wolves, during the breeding period (April - early autumn in temperate regions; Mech 1970; Carbyn *et al*. 1993), pack members, especially the breeding female and the pups, become temporally and spatially predictable (Ruprecht *et al.* 2012) around den and rendezvous sites (known together as homesites; Joslin 1967). This predictability increases their exposure risk. Wolves are known to compensate for their intrinsic vulnerability during this period by selecting areas with low human activity or adjusting their temporal use in response to human activities (Theuerkauf *et al.* 2003; Capitani *et al.* 2006; Habib & Kumar 2007; Person & Russell 2009; Ahmadi *et al.* 2014; Iliopoulos *et al.* 2014; but see Mech *et al.* 1988; Thiel *et al.* 1998). However, the constancy and generality of the behavioural adaptations of wolves to humans remain unclear (e.g., available literature shows contrasting patterns on the influence of roads on wolf behaviour; Thiel 1985; Mech 1989; Thurber *et al.* 1994; Jędrzejewski *et al*. 2004; Whittington *et al.* 2005; Zimmermann *et al.* 2014).

Herein, we explored how perceived exposure risk to humans affects the selection patterns of breeding sites in wolves. By gathering wolves' homesite data across its worldwide distribution range (Fig.1.1), we compiled the most comprehensive dataset to date about the breeding site selection patterns of a large carnivore on a global scale. The large distribution range of wolves is comprised by a wide arrange of local environmental constraints for the species. Such heterogeneity poses a risk of misleading generalisation on the general behavioural response of wolves to humans from context-specific observations (Levin 1992). Therefore, we sought to de-contextualise the general patterns of homesite selection by wolves through a meta-analysis.

First, we hypothesised a global common pattern in the signal of the behavioural response of wolves towards the same source of mortality risk and disturbance, humans. We assessed whether the direction and magnitude of selection in relation to vulnerability to humans coincided between den and rendezvous sites. Second, we hypothesised that the response to avoid human-related risk at homesites would be stronger where a longer history of coexistence has allowed wolves to adapt and persist under continued persecution. Accordingly, we expected to find continental-scale effects due to major differences in the coexistence nature between North America and Eurasia. For example, whereas it took many centuries to eliminate large carnivores from most of Western Europe, they were eradicated from most of the American West within a few decades (Frank and Woodroffe 2001). Finally, we hypothesised that the strength of this behavioural response would be proportional to the intensity of context-specific, human-related, environmental constraints. We predicted that wolves that are more exposed to people (i.e. closely cohabiting with humans and/or using anthropogenic resources, such as livestock) should compensate human-related risk by being more averse to human activities, locating their homesites in less accessible areas and with higher availability of refuge. Identifying global patterns of homesite selection provides valuable information to develop transferrable tools to be applied in wolf and possibly other large carnivore conservation, conciliating the persistence of these species with human activities.

Material and Methods

We carried out a systematic literature review to compile published data on homesites and primary data sources to build a combined dataset of homesite characteristics in relation to 16 predefined variables (Table 1.1) associated to human impacts, refuge habitat and topographic attributes. We focused on the impact of perceived risk of mortality or disturbance at homesites. Our initial assumption was that avoidance of human-made structures and accessible areas would be a common response across the entire distribution range of the species.

Systematic review and primary data

Systematic review was carried out using search terms of the type "*Canis lupus* AND ["den" OR "homesite" OR "rendezvous"]", in Google Scholar (scholar.google.com) and Scopus (scopus.com) literature search databases. We also searched in the literature-cited sections of all retrieved articles. We retained only those studies from which basic statistics (mean and s.d.) were available for any of the variables of interest for this meta-analyses (Table 1.1), both for homesites and control groups. In exceptional cases, we contacted corresponding authors in order to get raw data. Data from 8 study areas were obtained from literature review (Fig. 1.1). In addition, we compiled original data from a total of 449 geo-referenced homesites distributed across 18 study areas (Fig.1.1; mean of 25 homesites per study area, s.d.= 10.6, range 4-41).

All homesites were categorized as den or rendezvous sites. For primary data, we classified homesites depending on the estimated age of the pups (criterion also used in most published papers, Appendix 1.1). Thus, we considered den sites those where the breeding female gave birth and kept the pups during the first 6 weeks of life. Den sites were determined by telemetry or direct observation of the den. Sites used by pups approximately between 6 weeks and 5 months of age were classified as rendezvous sites. Rendezvous sites were located by telemetry, direct observation of the pups and/or howling surveys (Capitani *et al.* 2006; Llaneza *et al*. 2014). We set a den cut-off at June 15^{th} if direct observation of the den was not possible. We considered rendezvous sites those sites used from June 15^{th} until October 31^{st} when original data were not obtained using direct observation (Theuerkauf et al. 2003; Mech & Boitani 2003). Primary data only for den or rendezvous sites were available for nine and five areas, respectively, with both being available in four study areas (Fig.1.1). Den and rendezvous sites were geo-referenced in the field or calculated using the centre of the clusters of GPS-positions of collared wolves. We assumed that our method for locating homesites did not influence our results because we were not interested in micro-scale patterns of homesite selection.

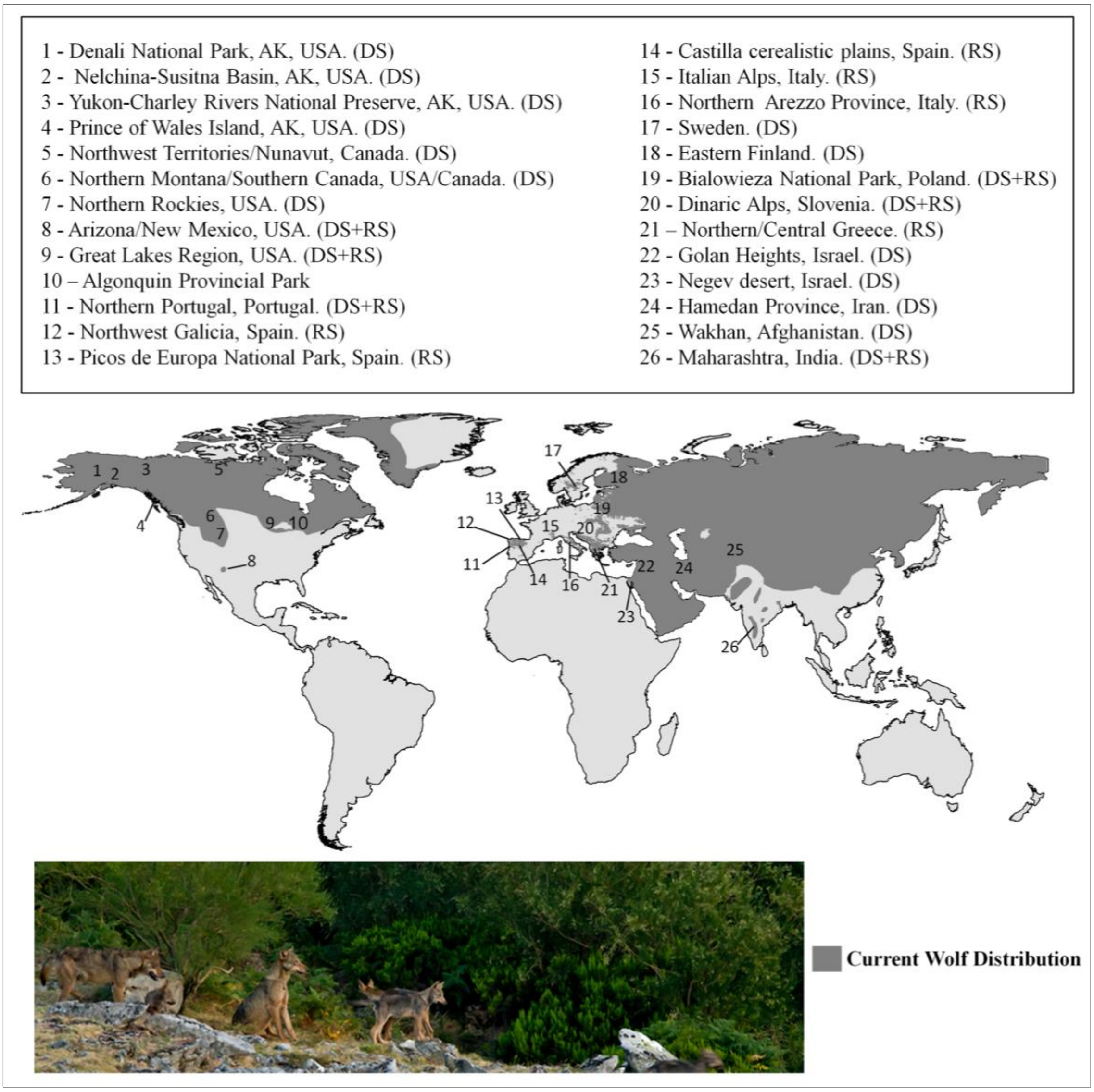


Figure 1.1. Study areas included in the meta-analysis on global patterns of homesite selection by wolves. (Wolf distribution: IUCN (International Union for Conservation of Nature) 2010. *Canis lupus*. The IUCN Red List of Threatened Species. Version 2014.3; DS= den sites data; RS= rendezvous sites data) (Photo credit: ©Artur Oliveira/CIBIO).

From the systematic review, we used variable measurements for homesites and random locations derived directly from the studies. However, for primary data, we characterised homesites using available environmental datasets and geographical information sources (Appendix 1.2). We considered two spatial resolutions for variables on land cover and terrain ruggedness, 100 and 900 ha around homesites (Table 1.1). When the mean value of a variable was 0 for homesites or control group it was excluded from the final dataset.

To prevent auto-correlation in our primary homesite dataset, when two homesite locations were separated by less than 2,500 m from each other, we randomly excluded one of them. In addition, when possible (date of use and pack identification was not always available), we selected only one location per homesite type per year for every pack. Control points were randomly generated within an estimated home range around homesites.

Home-ranges were estimated from telemetry when possible (Slovenia, Sweden), or as a buffer around homesites covering an area of variable size according to home-range sizes described for the corresponding or neighbouring wolf populations (n=15) (Appendix 1.3; unpublished data). We generated three random points for each homesite. When both den and rendezvous sites were available in a study area, this procedure was carried out separately. We used ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA) and Google Earth 5.0 (Google Inc., Mountain View, CA) to process all geographic information data. Information used to characterize homesites from primary data was generated using contemporary layers and dates were adjusted between homesites and the measurements of the indicators of human-related disturbance and mortality risks as much as possible using the *"Historic images tools"* of Google Earth.

Human-made infrastructures were assumed to represent human presence and pressure (Table1.1). Topographical variables were used as indicators for the accessibility of the homesites. Higher elevations, steeper slopes and rougher terrain around homesites were considered to reduce human access and to be positively correlated with remoteness. Refuge habitat around homesites was classified into four categories according to their ability to provide visual and physical protection to wolves (Table1.1). Although most agricultural land would fit into the definition of Open Areas, we considered Agriculture separately because such areas are often areas with higher levels of human activity. Refuge habitat included those vegetation types that provided protection by visual obstruction, as well as impeded access of people to homesites. Terrain Ruggedness and refuge habitat categories were measured at 100 and 900 ha around homesites (Table 1.1).

Table 1.1. Description of the variables used in the meta-analysis analysing homesite selection patterns by wolves in relation to human-related risk. (Scale=0: scale independent; 1: ≤ 100 ha; 2: ≤900 ha).

Scale	Variable	Factor	Description
0	Distance to Settlements	Direct Vulnerability	Distance to the nearest human settlement (m), including villages but also isolated constructions and facilities such as farms, ranches, mine camps, park's visitor centres etc. composed by 2-9 buildings.
0	Distance to Villages	Direct Vulnerability	Distance to the nearest village (m) (aggregation of 10 or more buildings, or when explicitly considered as village in the original study or dataset).
0	Distance to Roads	Direct Vulnerability	Distance to the nearest road of any type (m), including gravel and forestry roads. When able to be discriminated, roads with evident signs of abandonment were not considered.
0	Distance to Main Roads	Direct Vulnerability	Distance to the nearest first or second-class road (m), usually paved roads but depending on the local context some unpaved roads were also included when represented the main transportation infrastructure connecting 2 villages (e.g. India-Maharashtra).
0	Elevation	Topography	Elevation above sea level (m).
1	Terrain Ruggedness	Topography	Vector Ruggedness Measure (VRM index) calculated according to Sappington *et al*. (2007).
2	Terrain Ruggedness	-	VRM index calculated according to Sappington *et al*. (2007).
0	Slope	Topography	Slope (degrees) obtained from Digital Elevation Model (DEM) surface analysis
1	Refuge	-	Area within buffer around site occupied by forests and scrubland (except creeping scrubs)
2	Refuge	-	Area within buffer around site occupied by forests and scrubland (except creeping scrubs)
1	Open Areas	-	Area within buffer around site occupied by land uses corresponding to bare soil or open vegetation such as natural grasslands, pastures, moors, tundra, dwarf scrubland, etc.
2	Open Areas	-	Area within buffer around site occupied by land uses corresponding to bare soil or open vegetation such as natural grasslands, pastures, moors, tundra, dwarf scrubland, etc.
1	Agriculture	-	Area within buffer around site occupied by agricultural land.
2	Agriculture	-	Area within buffer around site occupied by agricultural land.
1	Urban	Direct Vulnerability	Area within buffer around site occupied by residential, industrial or commercial uses.
2	Urban	-	Area within buffer around site occupied by residential, industrial or commercial uses.

Variables of human-made structures and topography were also grouped into two factors named *Direct Vulnerability* and *Topography* (Table 1.1) according to our interpretation regarding wolves' exposure to humans. *Direct Vulnerability* represented the risk of human-caused disturbance and/or mortality, while *Topography* accounted for variables related with accessibility based on topographical features and terrain characteristics that potentially would facilitate or prevent wolf-human interactions. We used these factors to test if the selection was influenced by constraints at the study-area level.

Data Analyses

Within each study area, data on descriptive variables corresponding to homesites and random points were transformed to a measure of the specific response (direction and magnitude) of wolves towards the risk of interaction with humans. For each variable within each study area, we calculated *Hedge's g* and its associated variance as an independent and comparable effect size estimate using the package *"compute.es"* in R (Del Re 2013). For simplicity, coherence among variables, and illustrative purposes, we shifted the sign of the effect size in those variables representing distance to human-made infrastructures, with negative values representing avoidance.

We built an individual random-effects model for each variable and grouping factor, assuming heterogeneity among study areas beyond sampling error, and estimated the average effect size, variance and heterogeneity among the true effects (Koricheva *et al.* 2013). Models were adjusted weighting individual effect sizes, according to variance within study areas as a bias correction of the true effects in the set of study areas (Viechtbauer 2010). Confidence intervals (95%) of the mean effect size across study areas were calculated for every variable alone and grouped by factors. Those variables and factors that included zero in their 95% confidence intervals were considered as non-significant effects. Between-study area variance for each random-effects model was assessed calculating the statistic T^2 by the restricted maximum-likelihood estimator method (Viechtbauer 2005). In addition, we calculated the statistic I^2 (%) as a measure of the amount of variability in the effect size estimates that can be attributed to heterogeneity among the true effects. Individual random-effects models were constructed separately for all homesites indistinctly of their class as well as separated as den or rendezvous sites and were computed using the package "*metaphor*" in R (Viechtbauer 2010).

In a second step, we analysed the relationship between the effect sizes estimated for the different indicators of human-related risk at the level of homesites and a moderator considering the continental level - representing different persecution histories - (two levels: America, Eurasia; Appendix 1.4). We built a Generalized Linear Model (GLM) with Gaussian distribution errors and identity link function to evaluate the influence of the continent on the effect sizes (*Hedge´s g*) of variables and factors.

Finally, to test whether the strength of the homesite selection patterns was proportional to the intensity of context-specific human-related environmental constraints, we explored the influence of three cofactors representing different human-related traits of the study areas (human population density, wolf diet and livestock biomass density). Within each study area, we accounted for variability in the ecological context in relation to humans, which will affect the strength of the selection patterns (effect size) by calculating: i) human population density (inhabitants/km^2), ii) a categorical description of the predominant items in the diet of the wolf population (three levels: wild prey, livestock, or mix) and iii) an estimation of livestock biomass density (kg/km^2) (Appendix 1.4). We then built a set of GLMs with Gaussian distribution errors and identity link function to evaluate the influence of each moderator independently on the effect sizes (*Hedge´s g*) of variables and factors. Due to limited sample size, we only ran individual univariate GLM models for each variable and factor to avoid overparameterizing our models. All analyses were carried out in the R software (R Core Team 2014).

Results

We gathered data from 26 study areas, 10 in North America and 16 in Eurasia (Fig. 1.1, Appendix 1.1). The overall dataset contained information from a total of 728 homesites (457 den sites and 271 rendezvous sites; mean number of homesites per study area (±s.d.): 28±14). On average, we obtained valid information of 10.0±5.4 variables per study area.

In combination, significant effects were observed across study areas in homesite (joined), den and rendezvous site selection patterns by wolves (Figs. 1.2 and 1.3), indicating a consistent behavioural response of wolves towards human-related risk regardless of the local context. Wolves showed avoidance of human-made structures (Fig. 1.2); placing their homesites significantly further from linear infrastructures (all-kind roads, main roads) and human settlements (settlements, villages) compared to random points. This avoidance tended to be stronger for main roads and villages than for all-kind roads and settlements (Fig. 1.2). The strength of the observed response towards these variables was stronger for rendezvous sites compared to den sites, although significant differences were only detected for the distance to settlements (Fig. 1.2). Variables associated with topography (Elevation, Slope, Terrain Ruggedness) did not show a consistent pattern. We detected a significant selection only to locate rendezvous sites at higher altitudes (Fig. 1.2).

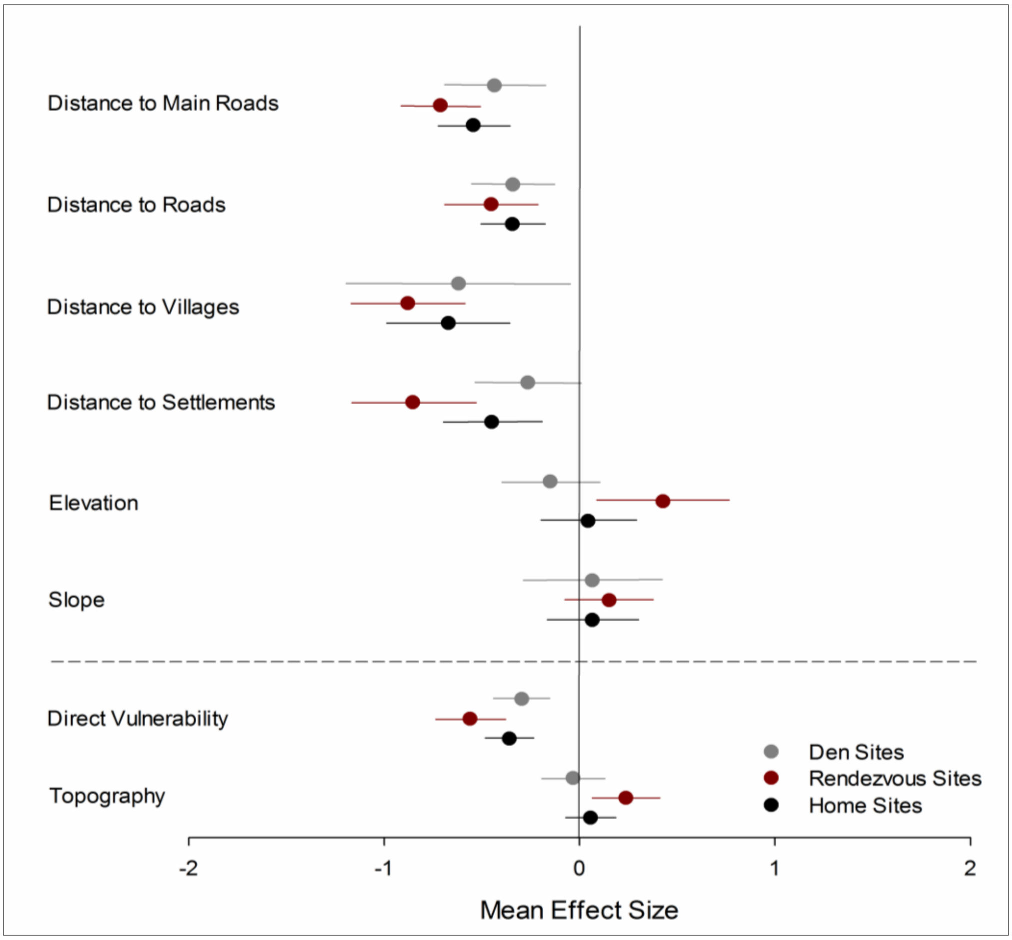


Figure 2. Results of the meta-analysis on homesite selection patterns by wolves regarding scale-independent variables (above dashed line) and factors (below dashed line). The summary effect size of every variable/factor (points) across study areas and ± 95% confidence intervals (lines) are shown. Summary effect sizes are shown for homesites, den and rendezvous sites. Confidence intervals containing zero were interpreted as non-significant and no general effect was considered to be plausible regarding the corresponding variable. Sign of distance-based variables has been shifted for better representation (i.e. negative values represent avoidance).

Individual univariate random-effects models for Elevation and Slope, including the all-class homesites dataset, retained a high amount of between-study heterogeneity representing 83% and 79% of the observed variability (Table 1.2). When we grouped the selected variables into factors, we found that *Direct Vulnerability* was negatively selected by wolves while *Topography* showed a pattern of selection only for rendezvous sites, towards the most inaccessible areas (Fig. 1.2).

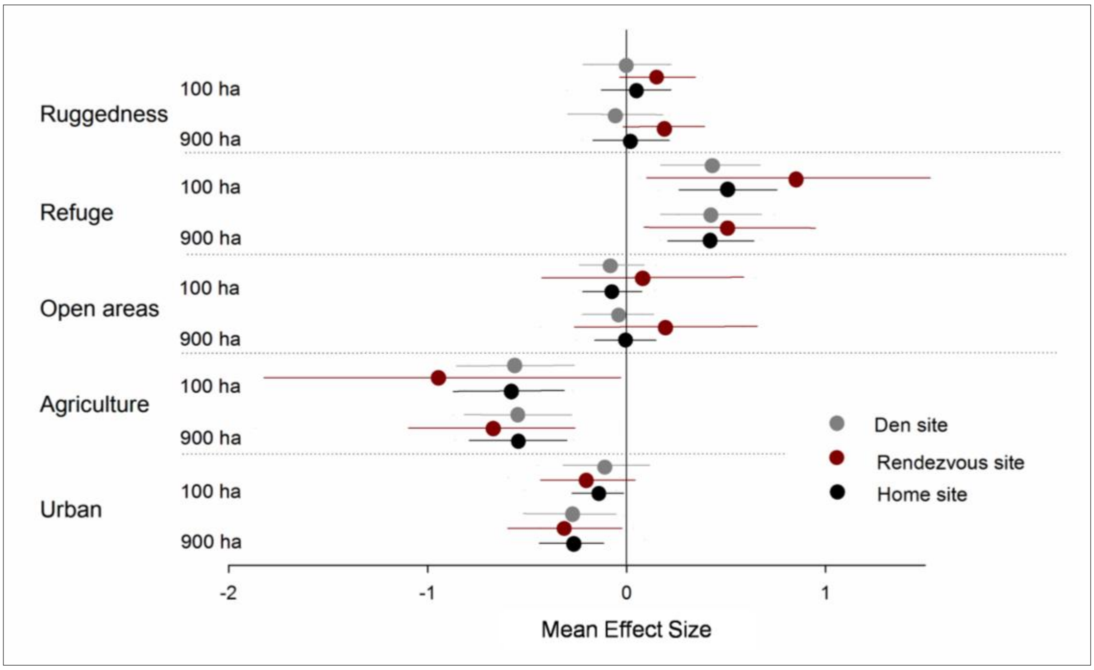


Figure 3. Results of the meta-analysis of homesite selection regarding variables measured at two spatial resolutions, 100 and 900 ha around homesites. The summary effect size for every variable/factor (points) across study areas and ± 95% confidence intervals (lines) are shown. Summary effect sizes are shown for homesites, den and rendezvous sites. Confidence intervals containing zero were interpreted as non-significant and no general effect was considered to be plausible regarding the corresponding variable.

Wolves located their homesites in areas with significantly higher availability of Refuge habitat, while avoided agricultural lands (Fig. 1.3); with these patterns being consistent across spatial resolutions regardless of homesite type (Fig. 1.3). Moreover, we found a general avoidance of Urban areas around homesites, although such a pattern was not significant when we evaluated den and rendezvous sites separately at the 100ha resolution (Fig. 1.3). No clear effect of Open Areas was observed (heterogeneity T^2 remained well below of the mean value -0.127 across all the variables; Table 1.2). We did not find significant differences between spatial resolutions regarding Refuge habitat or Terrain

Ruggedness, suggesting non-independence in the observed patterns across the spatial resolutions considered (Fig. 1.3).

Table 1.2: Sample size, total heterogeneity (T^2) and heterogeneity among true effects (I^2) of random-effects models of joint (den and rendezvous) homesite dataset.

Variable/Factor	**n**	T^2**(SE)**	I^2 **(%)**
Distance to Main roads	16	0.08 (0.05)	61.0
Distance to Roads	22	0.09 (0.09)	62.1
Distance to Villages	13	0.28 (0.14)	83.6
Distance to Settlements	17	0.20 (0.10)	76.5
Elevation	23	0.28 (0.10)	83.1
Slope	22	0.23 (0.09)	79.7
Ruggedness 100 ha	17	0.06 (0.04)	51.9
Ruggedness 900 ha	17	0.10 (0.06)	62.6
Agriculture 100 ha	11	0.17 (0.10)	75.9
Agriculture 900 ha	10	0.10 (0.07)	65.9
Open Areas 100 ha	17	0.04 (0.04)	41.1
Open Areas 900 ha	17	0.04 (0.03)	37.6
Refuge habitat 100 ha	18	0.20 (0.09)	77.4
Refuge habitat 900 ha	16	0.14 (0.07)	70.4
Urban 100 ha	10	0.00 (0.02)	0.3
Urban 900 ha	11	0.04 (0.04)	42.0
Direct Vulnerability (factor)	50	0.13 (0.04)	70.3
Topography (factor)	62	0.19 (0.05)	77.0

We detected a significant continental-scale pattern in homesite selection (Fig. 1.4; Appendix 1.5). We found significant differences in the selection of topography-related variables either alone (Elevation, Slope) or pooled as a factor (*Topography*) between continents (Appendix 1.5 and 1.6). *Topography* was positively selected in Eurasia, indicating that wolves minimize exposure risk locating their homesites in less accessible areas, while the opposite pattern was observed in North America (Fig. 1.4; Appendix 1.6). *Direct vulnerability*, on the other hand, showed consistent negative mean effect size at the continental scale, though only significant in Eurasia (Fig. 1.4; Appendix 1.6). Distance to settlements was the variable included in this factor for which Continent explained the highest amount of deviance (38%; Appendix 1.5). The only variable with significantly different effects between continents was Refuge habitat within 100ha (Appendix 1.5). Again, we detected a stronger selection towards vegetation providing refuge to wolves in Eurasia compared to North America (mean effect size = 0.73±0.29 and 0.09±0.18, respectively). Such continental differences were in accordance with the amount of heterogeneity observed in the corresponding random-effects models for factors (Table 1.2).

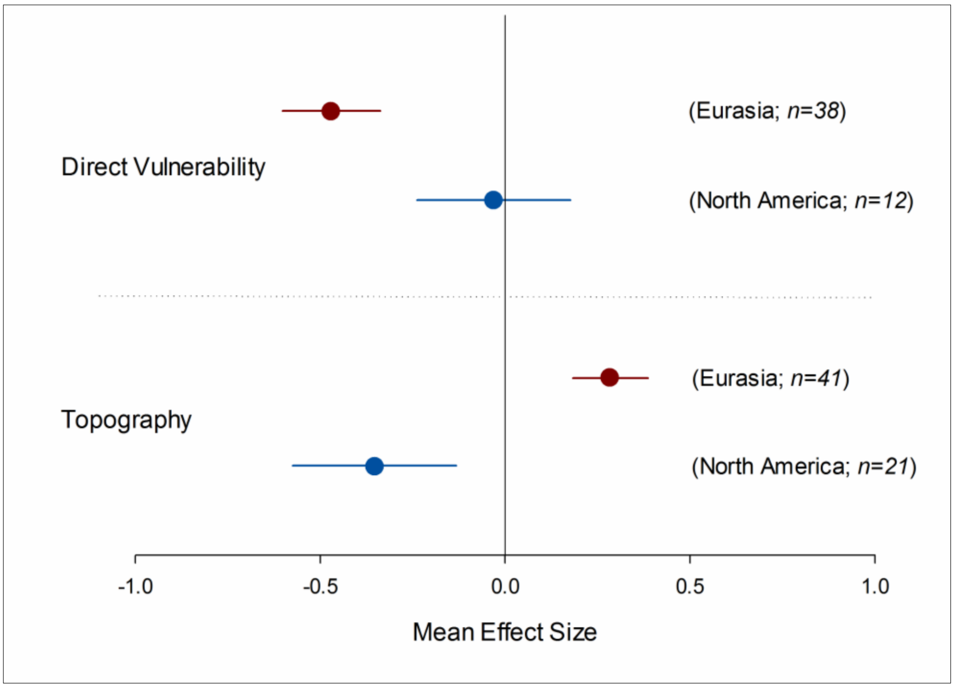


Figure 4: Comparison between the continents of the mean effect size (points) and ± 95 % confidence intervals (lines) of factors grouping variables associated with *Direct Vulnerability* and *Topography* (see methods for details). All homesites pooled.

Finally, when we evaluated the influence of cofactors related to human activity and the potential for human-wolf conflict (human population density, wolf diet and livestock biomass density) on homesite selection, we found an important contribution of these to the variance observed in Elevation (Appendix 1.7), as well as a significant effect on the mean effect sizes related to different land uses around homesites. Selection for Refuge habitat and avoidance for Agriculture further increased along with human population density (Fig. 1.5; Appendix 1.7) and the same pattern was observed for livestock biomass density and wolf diet (Appendix 1.7). Similar patterns were observed when variables were pooled into factors (Appendix 1.8).

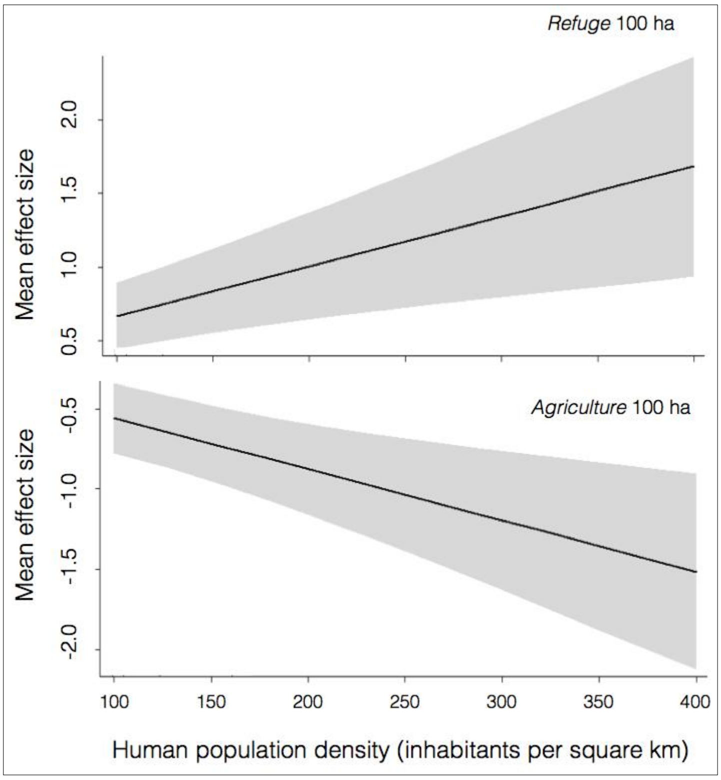


Figure 1.5. Variation of the mean effect size of *Refuge habitat* and *Agriculture* within 100 ha around homesites in relation to the human population density (inhabitants/km^{-2}).

Discussion

Our dataset covered a high proportion of the diversity of ecological contexts in which wolves live, with most of the data used being original (18 out of 26 study areas and 449 out of 728 total homesites in the dataset were primary data). Most of the latitudinal range of the species was represented in our meta-analysis, from the southernmost tips of the species´ distribution range in India to the Northwest Territories/Nunavut area of Canada (Fig. 1.1). On the other hand, a wide range of human impact in the landscape was also covered. Therefore, this study represents the most comprehensive review of the breeding site selection of a large carnivore on a global basis so far. The number of studies (26) is within the mean range of sample sizes found in ecological meta-analyses (between 20-30; Koricheva *et al.* 2013).

Our findings show how homesite selection by wolves is strongly influenced by their perception of risk of interaction with humans. Despite the fact that different local behavioural adaptations to reduce human-related risk at homesites have previously been observed (e.g., Habib and Kumar 2007; Ahmadi *et al.* 2014; Iliopoulos *et al*. 2014), segregation from humans at homesites is a general pattern in wolves regardless of the context-dependent particularities of human pressure. This generalisation reveals that many of such behavioural adaptations are predictable and thus extrapolatable at least at the species level. Minimizing exposure to humans when choosing homesites is fundamental for promoting the survival of pups and other pack members. The observed patterns seem to be common across the entire wolf range regardless of the type of homesite considered, thus supporting the idea of functional similarity between them. Furthermore, similar behavioural responses observed in other large carnivore species (e.g., Linnell *et al*. 2000, Wilmers *et al.* 2013, White *et al*. 2015) suggest that some of the observed patterns in this meta-analysis could be common across the large carnivore guild. Because humans are the main predator of wolves, the homesite selection patterns observed would fit with some of the predictions made for risk effects from humans on wolves (e.g. Creel & Christianson 2008; Ordiz *et al*. 2013).

Despite these general patterns, the magnitude of the behavioural response depended largely on the context and the perceived risk of interaction. The importance of the availability of safe places for wolves and the strength of the avoidance of human-made structures increased with human pressure, with a significant distinction in avoidance intensity between continents (Fig. 1.4). The observed risk-mediated behavioural response suggests that vulnerability should prevail over other factors in homesite selection (e.g. soil characteristics, prey availability) because the influence of these factors is observable in areas with low human use (McLoughlin *et al.* 2004; Ausband *et al*. 2010; Kaartinen *et al*. 2010).

Behavioural response of wolves to human-made infrastructures (Fig. 1.2) seems to vary in relation to road or settlement characteristics; which are related to the level of human activity and its predictability (Thurber *et al.* 1994; Jędrzejewski *et al.* 2004; Blanco *et al*. 2005; Kaartinen *et al.* 2005; Ahmadi *et al.* 2014; Iliopoulos *et al*. 2014; Zimmermann *et al*. 2014). Wolves are probably able to discriminate between different intensities of traffic and its associated risk (Kaartinen *et al.* 2005; Whittington *et al.* 2005). The strength of such behavioural response seems to be stronger where wolves share the landscape more intensely with human activities (Eurasia). For example, in Eurasia, threshold values for settlements and roads from which wolves are absent are remarkably higher compared to North America (Thiel 1985; Mech *et al.* 1988; Mladenoff *et al.* 1995; Woodroffe 2000; Blanco and Cortés 2007; Llaneza *et al*. 2012).

Although it has been reported that wolves are able to persist in agro-ecosystems in some contexts (Blanco & Cortés 2007; Agarwala & Kumar 2009; Ahmadi *et al*. 2014), wolves generally avoid agricultural lands around homesites. Agricultural lands are usually connected with increased human frequentation and vegetation cover is extremely variable year round (depending on the cultivated crops and harvest periods). Observed increases in the selection of refuge habitat and the avoidance of agricultural land around homesites along a gradient of human pressure (Fig. 1.5) reflect that wolves cope with variations in exposure risk accordingly. The role of open areas remains unclear, and this category probably includes a wide range of habitats differing in protective visual structure at a wolf's height. The pastoralist use of these habitats in some areas can also have a significant influence on homesite selection (Habib & Kumar 2007), without an accurate characterisation in our analyses.

Our results suggest a hierarchical habitat selection process by which wolves compensate for higher exposure risk within their territories via stronger selection against this risk at homesites (see Basille *et al*. 2013 for a similar process in Eurasian lynx, *Lynx lynx*). Although wolves coexisting with humans are expected to be more tolerant of humans (Mech & Boitani 2003), the strength of risk avoidance at different orders of selection (Johnson 1980) may be dependent on the history of coexistence and persecution. In this regard, stronger human avoidance at the first and second selection orders (occupancy and territory) in North America (Mladenoff *et al*. 1995; Woodroffe 2000; Wydeven *et al*. 2001; Oakleaf *et al.* 2006) could explain the lower magnitude of the response observed at the third selection order (homesites). On the contrary, in Eurasia, a higher tolerance of human-made structures at lower selection orders (Woodroffe 2000; Jędrzejewski *et al*. 2004; Blanco *et al*. 2005; Llaneza *et al*. 2012), may force wolves to be more cautious at critical places within their territories, such as homesites. Continental patterns have been previously exemplified by divergent adaptations and tolerance thresholds in large carnivores and ungulates (Woodroffe 2000; Sand *et al*. 2006).

Differences in life-history traits associated with a different history of persecution have been reported for brown bears (*Ursus arctos*) (Zedrosser *et al*. 2011), but no such large-scale (continental level) differences have been previously reported regarding behavioural adaptations in large carnivores.

Wolves in Eurasia are more prone to inhabit cultural landscapes and share their territories with humans in a closer proximity than in North America (Chapron *et al*. 2014). A social and political willingness for coexistence has been suggested to be an important factor that may shape intrinsic behavioural characteristics (Chapron *et al.* 2014). The stronger selection of homesites at inaccessible places (e.g. due to *Topography*) in Eurasia compared to North America appears to be a behavioural adaptation of wolves to persist in human-dominated landscapes, contributing to the coexistence pattern observed in Europe (Chapron *et al*. 2014). Wolves occurring in areas with low human population density have greater availability of valley bottoms and lower slopes compared to wolves in human-dominated landscapes, where agricultural land and urban development dominate (Llaneza *et al.* 2012). Milder climate conditions, increased water availability and/or prey abundance could partly explain the preference for valley bottoms in areas with low human population density (Ausband *et al*. 2010).

Historically, the intensity of large carnivore persecution in Eurasia increased in parallel with the expansion of livestock husbandry after domestication around 11 000 yrs BP (Vigne 2011). As a consequence, Eurasian large carnivore populations have been subjected to human persecution for millennia, and the effectiveness of techniques to kill wolves has become gradually more sophisticated over time. On the other hand, North American large carnivore populations were severely depleted shortly after European settlers expanded westwards and intensive persecution began during the 18th century (Frank & Woodroffe 2001). Thus, a gradual long-term co-adaptation between persecution techniques and anti-predator behaviour in Eurasia compared to North America may be the mechanism behind the observed continental pattern. Livestock biomass density and livestock as the primary component of the wolf diet were positively correlated with selection towards refuge vegetation and likely reflect the adaptive behaviour of wolves to be more secretive in areas where livestock represent the primary prey item of wolves and where human animosity is presumed to be higher.

Despite the renowned habitat plasticity of wolves (Mech & Boitani 2003), we have identified strict habitat requirements for wolves at a small spatial scale during a critical period for the species. Large carnivore conservation is often hindered by the remarkable spatial requirements and the need to preserve large areas of suitable habitats (Weber & Rabinowitz 1996; Woodroffe & Ginsberg 1998; but see Chapron *et al*. 2014; López-Bao *et al*. 2015). Although many large carnivores do not necessarily require such large-scale habitat preservation, the issue of habitat protection for these species should not be disregarded but rather identified at the proper scale. Habitat selection at levels (orders) below occupancy and territory, along with the interaction with human-related risks should be regarded in the management and conservation of large carnivores in human-dominated landscapes.

Wolves repeatedly using the same homesites and vocalising in their vicinity are vulnerable to humans, especially those actively searching for litters or aiming to eradicate entire wolf packs. Although the protection of the breeding sites of large carnivores is mandatory in some legal contexts (e.g. European Union and the Council of Europe), such as for populations listed in Annex II of the EU Habitats Directive 92/43/EEC of 1992, the enforcement of their effective protection is still lacking in many areas. When management and conservation goals aim to preserve large carnivores in human-dominated landscapes, providing insights on the general patterns of breeding site selection patterns is a valuable tool for guiding decision-making processes. In this case, we recommend that managers should be focused on providing shelter from human interference in the small portions of land that fulfil the characteristics of the places that wolves in particular and large carnivores in general select as breeding sites, in order to encourage their persistence.

References

Abay, G.Y., Bauer, H., Gebrihiwot, K., & Deckers, J. (2011). Peri-urban spotted hyena (*Crocuta crocuta*) in northern Ethiopia, diet, economic impact, and abundance. *European Journal of Wildlife Researc*h 57: 759-765.

Agarwala, M., & Kumar, S. (2009). Wolves in agricultural landscapes in western India. Tropical Resources, *Bulletin of the Yale Tropical Resources Institute* 28: 48–53.

Ahmadi, M., López-Bao, J.V., & Kaboli, M. (2014). Spatial heterogeneity in human activities favours persistence of wolves in agroecosystems. *PLoS ONE* 9: e108080.

Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J., & Karanth, U. (2013). Big cats in our backyards, persistence of large carnivores in a human dominated landscape in India. *PLoS ONE* 8: e57872.

Ausband, D.E., Mitchell, M.S., Doherty, K., Zager, P., Mack, C.M., & Holyan, J. (2010). Surveying predicted rendezvous sites to monitor gray wolf populations. *Journal of Wildlife Management* 74: 1043–1049.

Basille, M., Van Moorter, B., Herfindal, I., Martin, J., Linnell, J.D.C., Odden, J., Andersen, R., & Gaillard, J.M. (2013). Selecting habitat to survive, the impact of road density on survival in a large carnivore. *PLoS ONE* 8: e65493.

Blanco, J.C., Cortés, Y., & Virgós, E. (2005). Wolf response to two kinds of barriers in an agricultural habitat in Spain. *Canadian Journal of Zoology* 83: 312-323.

Blanco, J.C., & Cortés, Y. (2007). Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. *Journal of Zoology* 273: 114-124.

Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A., & Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica* 51: 395-404.

Carbyn, L.N., Oosenbrug, S.M., Anions, & D.W. (1993). Wolves, bison, and the dynamics related to the Peace-Athabasca delta in the Canada's Wood Buffalo National Park. Circumpolar Research Series 4, Canadian Circumpolar Institute, University of Alberta, Edmonton.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517-1519.

Creel, S. & Christianson, D.A. (2008). Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23: 194–201.

Del Re, A.C. (2013). Compute.es, Compute effect sizes. R package version 0.2-2.

Frank, L.G., & Woodroffe, R. (2001). Behaviour of carnivores in exploited and controlled populations. Pp. 419-442 *In*: Gittleman, J.L., Funk, S.M., Macdonald, D.W., & Wayne, R.K. (Eds.). Carnivore conservation. Conservation Biology Series, Cambridge University Press, Cambridge, UK.

Fuller, T.K., & Sievert, P.R. (2001). Carnivore demography and the consequences of changes in prey availability. Pp. 163-178 *In:* Gittleman, J.L., Funk, S.M., Macdonald D., & Wayne, R.K. (Eds.). Carnivore conservation. Conservation Biology Series, Cambridge University Press, Cambridge, UK.

Habib, B., & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *Journal of Zoology* 272: 259–265.

Iliopoulos, Y., Youlatos, D. & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *European Journal of Wildlife Research* 60: 23-34.

Jędrzejewski, W., Niedziałkowska, M., Nowak, S., & Jędrzejewska, B. (2004). Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity and Distributions* 10: 225–233.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.

Joslin, P.W.B. (1967). Movements and homesites of timber wolves in Algonquin Park. *American Zoologist* 7: 279-288.

Kaartinen, S., Kojola, I., & Colpaert, C. (2005). Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici* 42: 523-532.

Kaartinen, S., Luoto, M., & Kojola, I. (2010). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology* 281: 99-104.

Koricheva, J., Gurevitch, J., Mengersen, K. (Eds.). (2013). Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton.

Lesmerises, F., Dussault, C., & Saint-Laurent, M.H. (2013). Major roadwork impacts the space use behaviour of gray wolf. *Landscape and Urban Planning* 112: 18–25.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Linnell, J.D.C., Swenson, J.E., Andersen, R., & Barnes, B. (2000). How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28: 400-413.

Linnell, J.D.C., Odden, J., & Mertens, A. (2012). Mitigation methods for conflicts associated with carnivore depredation on livestock. Pp. 314-332 *In:* Boitani, L. & Powell, R.A (Eds.). Carnivore ecology and conservation: A handbook of techniques. Oxford University Press, Oxford.

Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions* 18: 459-469.

Llaneza, L., García, E.J., & López-Bao, J.V. (2014). Intensity of territorial marking predicts wolf reproduction: Implications for wolf monitoring. *PLoS ONE* 9: e93015.

López-Bao, J.V., Sazatornil, V., Llaneza, L., & Rodríguez, A. (2013). Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters* 6: 448-455.

López-Bao, J.V., Kaczensky, P., Linnell, J.D., Boitani, L., & Chapron, G. (2015). Carnivore coexistence: Wilderness not required. *Science* 348: 871-872.

McLoughlin, P.D., Walton, L.R., Cluff, H.D., Paquet, P.C., & Ramsay, M.A. (2004). Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy* 85: 576–580.

Mech, L.D. (1970). The wolf, the ecology and behavior of an endangered species. Natural History Press, Doubleday Publishing Co., New York.

Mech, L. D. (1989). Wolf population survival in an area of high road density. *American Midland Naturalist* 121: 387-389.

Mech, L.D., Boitani, L. (Eds.), 2003. Wolves, behavior, ecology, and conservation. The University of Chicago Press, Chicago.

Mech, L.D., Fritts, S.H., Radde, G., & Paul, W.J. (1988). Wolf distribution in Minnesota relative to road density. *Wildlife Society Bulletin* 16: 85-88.

Mladenoff, D., Sickley, T.A., Haight, R.G., & Wydeven, A.P. (1995). A regional landscape analysis and prediction of favourable gray wolf habitat in the northern great lakes region. *Conservation Biology* 9: 279–294.

Oakleaf, J.K., Murray, D.L., Oakleaf, J.R., Bangs, E.E., Mack, C.M., Smith, D.W., Fontaine, J.A., Jimenez, M.A., Meier, T.J., & Niemeyer, C.C. (2006). Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. *Journal of Wildlife Management* 70: 554-563.

Ordiz, A., Bischof, R., & Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation* 168: 128-133.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., Maclennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O. and Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters* 16: 635–641.

Person, D.K., & Russell, A.L. (2009). Reproduction and den site selection by wolves in a disturbed landscape. *Northwest Science* 83: 211-224.

R Core Team. (2014). R, a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/.

Ruprecht, J.S., Ausband, D.E., Mitchell, M.S., Garton, E.O., & Zager, P. (2012). Homesite attendance based on sex, reproductive status and number of helpers in gray wolf packs. *Journal of Mammalogy* 93: 1001-1005.

Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Cross-continental differences in patterns of predation, will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society of London B* 273: 1421-1427.

Sappington, J.M., Longshore, K.M., & Thompson, D.B. (2007). Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. *Journal of Wildlife Management* 71:1419-1426.

Theuerkauf, J., Rouys, S., & Jędrzejewski, W. (2003). Selection of dens, rendezvous and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology* 81: 163–167.

Thiel, R.P. (1985). The relationship between road densities and habitat suitability in Wisconsin. *American Midland Naturalist* 113: 404-407.

Thiel, R.P., Merrill, S., & Mech L.D. (1998). Tolerance by denning wolves, *Canis lupus,* to human disturbance. *Canadian Field Naturalist* 122: 340-342.

Thurber, J.M., Peterson, R.O., Drummer, T.D., & Thomasma, S.A. (1994). Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22: 61–68.

Viechtbauer, W. (2005). Bias and efficiency of meta-analytic variance estimators in the random-effects model. *Journal of Educational and Behavioral Statistics* 30: 261–293.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* 36: 1-48.

Vigne, J.D. (2011). The origins of animal domestication and husbandry, A major change in the history of humanity and the biosphere. *Comptes Rendus Biologies* 334: 171-181.

Weber, W., & Rabinowitz, A. (1996). A global perspective on large carnivore conservation. *Conservation Biology* 10: 1046–1054.

White, S., Briers, R.A., Bouyer, Y., Odden, J., & Linnell, J.D.C. (2015). Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway. *Journal of Zoology* 297: 87–98.

Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., & Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the Puma. *PLoS ONE* 8: e60590.

Whittington, J., St. Clair, C.C., & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15: 543–553.

Woodroffe, R. (2000). Predators and people, using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165-173.

Woodroffe, R., & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.

Woodroffe, R., Frank, L.G., Lindsey, P.A., Ranah, S.M.K., & Romañach S. (2007). Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: A case–control study. *Vertebrate Conservation and Biodiversity* 5: 419-434.

Wydeven, A.P., Mladenoff, D.J., Sickley, T.A., Kohn, B.E., Thiel, R.P., & Hansen, J.L. (2001). Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. *Endangered Species Update* 18: 110-114.

Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., & Swenson, J.E. (2011). Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144: 2163-2170.

Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., & Liberg, O. (2014). Behavioral responses of wolves to roads: Scale-dependent ambivalence. *Behavioral Ecology* 25: 1353-1364.

APPENDIX CHAPTER 1

(*The role of human-related risk in breeding site selection by wolves*)

APPENDIX 1.1: Available data from publications on homesites and their characteristics used in Chapter 1 (numbers denote the study area in Fig. 1.1 (Chapter 1); note that some studies may refer to the same area).

[1]Ballard, W.B., Dau, J.R. (1983). Characteristics of gray wolf (*Canis lupus*) den and rendezvous sites in south central Alaska. *Canadian Field Naturalist* 97: 299-302.

[2]Matteson, M.Y. (1992). Denning ecology of wolves in northwest Montana and southern Canadian Rockies. MSc thesis, University of Montana, Missoula.

[3] Trapp, J.R., Beier, P., Mack, C., Parsons, D.R., Paquet, P.C. (2008). Wolf, *Canis lupus*, den site selection in the Rocky Mountains. *Canadian Field-Naturalist* 122: 49-56.

[4]Unger, D., Keenlance, P., Kohn, B., Anderson, E. (2009). Factors influencing homesite selection by grey wolves in Northwestern Wisconsin and east-central Minnesota. Pp:175-189 *In:* Wydeven, A.P., Deelen, T.R. and Heske, E. (Eds.). Recovery of gray wolves in the Great Lakes Region of the United States, an endangered species success story. Springer, New York,

[4] Keenlance, P.W. (2002). Resource selection of recolonizing gray wolves in northwest Wisconsin. PhD thesis. Michigan State University, East Lansing, Minnesota.

[5] Benson, J.F., Mills, K.J., Patterson, B.R. (2015). Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation* 182: 223-232.

[6] Capitani C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A., Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica* 51: 395-404.

[7] Kaartinen, S., Luoto, M., Kojola, I. (2010). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology* 281: 99-104.

[8] Theuerkauf, J., Rouys, S., Jędrzejewski, W. (2003). Selection of dens, rendezvous and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology* 81: 163–167.

APPENDIX 1.2. Data sources to calculate the variables used from primary data in the meta-analysis analysing homesite selection patterns by wolves in relation to human-related risk.

1. Distance to Roads, Main Roads, Settlements and Villages.

General sources:

Google Earth 5.0 (Google Inc., Mountain View, CA).

Spain:

Transportation Infrastructures Strategic Plan, 2005. National Center of Geographic Information, Ministry Public Works and Transport. Government of Spain.

National Topographical Base and National Cartographical Base (BCN/BTN 25). National Center of Geographic Information, Ministry Public Works and Transport. Government of Spain.

USA:

Dollison, R.M. (2010). The National Map*:* New viewer, services, and data download: U.S. Geological Survey Fact Sheet 2010–3055, 2 pp.

Slovenia:

Geodetska uprava Republike Slovenije (www.gu.gov.si).

Israel:

Mapcruzin (www.mapcruzin.com).

Italy:

Mapcruzin (www.mapcruzin.com).

France:

Mapcruzin (www.mapcruzin.com).

Sweden:

Swedish Corine land cover map, Geographical Data Sweden, road map (1:100000) Lantmäteriet.

Canada:

Department of Environment and Natural Resources, Government of the Northwest Territories.

2. Topography (Elevation, Slope, Terrain Ruggedness)

General sources:

Google Earth 5.0 (Google Inc., Mountain View, CA).

NASA Land Processes Distributed Active Archive Center (LP DAAC). ASTER Global Digital Elevation Model. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, 2001.

3. Land Cover (Refuge habitat, Open Areas, Agriculture, Urban)

General:

Google Earth 5.0 (Google Inc., Mountain View, CA).

Afghanistan:

Food and Agriculture Organization of the United Nations. Global Land Cover Network. Himalaya Region Land Cover Mapping.

Canada

Matthews, S., Epp, H., Smith, G. (2001). Vegetation Classification for the West Kitikmeot/Slave Study Region, Final Report. Government of the Northwest Territories. 42 pp.

Europe (except Spain)

Corine Land Cover 2000 (European Environment Agency (EEA), Copenhagen, Denmark).

USA:

National Land Cover Database (see Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., Van Driel, J.N., Wickham, J,(2007). Completion of the 2001 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337-341).

Iran:

Forest, Range and Watershed Management Organization I. R. of Iran, (FRWMO) 2010. Iranian Forests, Range and Watershed Management Organization National Land use/Land cover map. Iran.

India:

National Remote Sensing Centre. 2006. Land Use / Land Cover database on scale 1: 50,000. Natural Resources Census Project, LUCMD, LRUMG, RS & GIS AA, National Remote Sensing Centre, ISRO, Hyderabad.

Spain:

Spanish Forest Map. Ministry of Agriculture, Food and Environment. Government of Spain.

APPENDIX 1.3: References used to define buffer distances around homesites as an estimate of home ranges to calculate random points.

Álvares, F. (2011). Ecology and conservation of the wolf (*Canis lupus*, L.) in Northwest Portugal. PhD thesis. University of Lisbon, Portugal (in Portuguese).

Blanco, J.C., Cortés, Y., Virgós, E. (2005). Wolf response to two kinds of barriers in an agricultural habitat in Spain. *Canadian Journal of Zoology* 83: 312-323.

Burch, J. (2011). Annual report on vital signs monitoring of wolf (*Canis lupus*) distribution and abundance in Yukon-Charley Rivers National Preserve, Central Alaska Network. Natural Resource Technical Report NPS/CAKN/NRTR-2011/485. National Park Service, Fort Collins, Colorado.

García, E.J., Llaneza, L., Palacios, V., López-Bao, J.V., Sazatornil, V., Rodríguez, A., Rivas, O., Cabana, M. (2012). First data on the spatial ecology of the wolf in Galicia. Abstracts of the III Iberian Wolf Congress, Lugo (Spain), November 23-25. (in Spanish).

García, E.J., Llaneza, L., Palacios, V., López-Bao, J.V. (2013). Spatial ecology of wolves (*Canis lupus signatus*) in the Picos de Europa National Park. Technical Report. Organismo autónomo de Parques Nacionales, Ministerio de Medio Ambiente, Rural y Marino, Madrid, Spain. (in Spanish).

Habib, B. (2007). Ecology of Indian wolf (*Canis lupus pallipes*, Sykes 1831) and modelling its potential habitat in the Great Indian Bustard Sanctuary, Maharashtra, India. PhD thesis. Aligarh Muslim University, Aligarh, India.

Marucco, F., McIntire E.J.B. (2010). Predicting spatio-temporal recolonization of large carnivore populations and livestock depredation risk, wolves in the Italian Alps. *Journal of Applied Ecology* 47: 789–798.

Mech, L.D, Adams, L.G., Meier, T.J., Burch, J.W., Dale, B.W. (1998). The wolves of Denali. University of Minnesota Press, Minneapolis.

Reichmann, A., Saltz, D. (2005). The Golan wolves, the dynamics, behavioral ecology and management of an endangered pest. *Israel Journal of Zoology* 51: 87-133.

USFWS (United States Fish and Wildlife Service) (2011). Mexican wolf recovery program: Progress report #14. 63 pp.

APPENDIX 1.4: Summary of the study area-specific cofactors. Livestock biomass density was calculated as an index of livestock biomass (kg x km^{-2}) from data of individuals x km^{-2} as: *"60 sheep + 45 goats + 250 cattle"*.

Study area	Human pop. density (inhab/km^2)	Continent	Diet	Livestock biomass density[1]
Afghanistan-Wakhan	1.02[2]	Eurasia	Mix[3]	0.188
Alaska Denali	0.05[4]	N. America	Wild[5]	0.033
Alaska-Nelchina basin	0.28[4]	N. America	Wild[6]	0.003
Alaska-Prince of Wales Island	0.55[4]	N. America	Wild[7]	0.007
Alaska-Yukon-Charley NR	0.11[4]	N. America	Wild[8]	0.006
Arizona-N Mexico	2.03[4]	N. America	Wild[9]	0.369
Canada-NWT	0.03[10]	N. America	Wild[11]	0
Canada-Algonquin	0.08[10]	N. America	Wild[12]	0.051
Eastern Finland	5[13]	Eurasia	Mix	0.566
Greece	39.99[14]	Eurasia	Livestock[15]	7.430
India-Maharashtra	431.46[16]	Eurasia	Mix[17]	17.892
Iran-Hamadan	88[18]	Eurasia	Mix[19]	7.439
Israel-Golan	104.67[20]	Eurasia	Mix[21]	15.777
Israel-Negev	46.64[20]	Eurasia	Livestock[22]	1.304
Italy-N Arezzo Province	66[23]	Eurasia	Mix[24]	7.353
Italy-W Alps	99.29[23]	Eurasia	Mix[24]	7.941
N Montana/S Canada	3.44[4,10]	N. America	Wild[25]	0.583
N Portugal	123.60[26]	Eurasia	Livestock[27]	14.411
N Rocky Mountains	1.96[4,10]	N. America	Wild[24, 28]	0.869
Poland-Bialowieza forest	70[29]	Eurasia	Wild[30]	4.948
Slovenia-Dinaric Mts.	57.42[31]	Eurasia	Wild[32]	4.570
Sweden	25.72[33]	Eurasia	Wild[34]	0.886
Spain-Castilla	37.34[35]	Eurasia	Livestock	5.054
Spain-Picos de Europa	66.24[35]	Eurasia	Mix[36]	8.898
Spain-W Galicia	160.68[35]	Eurasia	Livestock[37]	10.479
Upper Great Lakes	6.89[4]	N. America	Wild[38]	1.998

DATA SOURCES AND REFERENCES FOR APPENDIX 1.4

[1]Gridded Livestock of the World v.2 (Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I and Gilbert, M. (2014). Mapping the global distribution of livestock. *PLoS ONE* 9(5):e96084.

[2] United Nations Environment Programme, Food and Agriculture Organization of the United Nations - FAO. (2003). Afghanistan Wakhan mission. Technical Report. Geneva, Switzerland.

[3] Habib, B. (2006). Status of large mammals in proposed Big Pamir Wildlife Resrerve, Wakhan, Afghanistan. Technical report. Wildlife Conservation Society, New York.

[4] US Census Bureau. URL http://www.census.gov

[5]Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., Dale, B.W. (1998). The wolves of Denali. University of Minnesota Press. Minneapolis.

[6]Van Ballenberghe, V. (1985). Wolf predation on caribou: the Nelchina herd case history. *The Journal of Wildlife Management* 49:711-720.

[7]Person, D.K., Kirchhoff, M., Van Ballenberghe, V., Iverson, G.C., Grossman, E. (1996). The Alexander Archipelago wolf: a conservation assessment. Technical Report PNW-GTR-84 of the U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland.

[8]Hayes, R.D., Baer, A.M., Wotschikowsky, U., Harestad, A.S. (2000). Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology* 78: 49-59.

[9]Reed, J.E., Ballard, W.B., Gipson, P.S., Kelly, B.T., Krausman, P.R., Wallace, M.C., Wester, D.B. (2006). Diets of free-ranging Mexican gray wolves in Arizona and New Mexico. *Wildlife Society Bulletin* 34: 1127-1133.

[10]Statistics Canada.URL http://www.statcan.gc.ca/

[11]Musiani, M., Leonard, J.A., Cluff, H.D., Gates, C.C., Mariani, S., Paquet, P.C., Vilà, C., Wayne, R.K. (2007). Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Molecular Ecology* 16: 4149-4170.

[12]Forbes, G.J., Theberge, J.B. (1996). Response by wolves to prey variation in central Ontario. *Canadian Journal of Zoology* 74: 1511-1520.

[13]Kaartinen, S., Luoto, M., Kojola, I. (2010). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology* 281: 99-104.

[14]Hellenic Statistical Authority.www.statistics.gr/portal/page/portal/ESYE

[15]Papageorgiou, N., Vlachos, C., Sfougaris, A., Tsachalidis, E. (1994). Status and diet of wolves in Greece. *Acta Theriologica* 39: 411-416.

[16]Census of India, Ministry of Home affairs. URL- http://censusindia.gov.in/

[17]Maurya, K.K., Habib, B., Kumar, S. (2011). Food habits of Indian Wolf (*Canis lupus pallipes*) in Deccan Plateau of Maharashtra, India. *World Journal of Zoology* 6: 318-322.

[18]Reyahi-Khoram, M., Fotros, M.H. (2011). Land use planning of Hamadan province by means of GIS, in International conference on chemical, biological and environment sciences (ICCEBS). Bangkok, Thailand, 2011.

[19]Hosseini-Zavarei, F., Farhadinia, M.S., Beheshti-Zavareh, M., Abdoli, A. (2013). Predation by grey wolf on wild ungulates and livestock in central Iran. *Journal of Zoology* 290: 127–134.

[20]Central Bureau of Statistics of Israel. www.cbs.gov.il/reader/cw_usr_view_Folder?ID=141

[21] Reichmann, A., Saltz, D. (2005). The Golan wolves: the dynamics, behavioral ecology and management of an endangered pest. *Israel Journal of Zoology* 51: 87-133.

[22]Shalmon, B. (1986). Wolves in the southern Arava. *Re'em* 5: 60–74.

[23] Italian National Institute of Statistics. www.istat.it/it/

[24]Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., Milanesi, P. (2011). Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology, Ecology & Evolution* 23: 195-210.

[25]Derbridge, J. (2010). Summer wolf diet in northwestern Montana. MSc thesis. The University of Montana, Missoula.

[26]Instituto Nacional de Estatística de Portugal.

[27]Álvares, F. (2011). Ecology and conservation of the wolf (*Canis lupus*, L.) in Northwest Portugal. PhD thesis. University of Lisbon, Portugal (in Portuguese).

[28]Oakleaf, J.K., Mack, C., Murray, D. (2003). Effects of wolves on livestock calf survival and movements in central Idaho. *The Journal of Wildlife Management* 67: 299-306.

[29]Theuerkauf, J., Rouys, S., Jędrzejewski, W. (2003). Selection of dens, rendezvous and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology* 81: 163–167.

[30]Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M. (2000). Prey selection and predation by wolves in Białowieża primeval forest, Poland. *Journal of Mammalogy* 81: 197-212.

[31]Statistical Office of the Republic of Slovenia. www.stat.si/statweb/en/home

[32]Krofel, M., Kos, I. (2010). Scat analysis of gray wolves (*Canis lupus*) in Slovenia. *Acta Silvae et Ligni* 91: 85-88.

[33]Statistics Sweden. www.scb.se

[34]Sand, H., Wabakken, P., Zimmermann, B., Johansson, O., Pedersen, H.C., Liberg O. (2008). Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* 156: 53–64.

[35]Instituto Nacional de Estadística (Spanish Statistical Office). URL http://www.ine.es/

[36]García, E., Llaneza, L., López-Bao, J.V. (2014). Livestock and livestock damages by wolves in the Picos de Europa National Park. Report to Organismo autónomo de Parques Nacionales, Ministerio de Medio Ambiente, Rural y Marino. 64 pp. (in Spanish).

[37]López-Bao, J.V., Sazatornil, V., Llaneza, L., Rodríguez, A. (2013). Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters* 6: 448-455.

[38] Del Giudice, G.D., McCaffery, K.R., Beier, D.E., Nelson, M.E. (2009). Prey of wolves in the Great Lakes Region, in: Wydeven, A.P., Deelen, T.R. and Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes Region of the United States, an endangered species success story. Springer, New York.

APPENDIX 1.5. Summary of the Generalized Linear Models analysing the influence of the Continent of the study area on the effect sizes estimated for the different variables at the level of homesites. The level "*Eurasia*" (continent) is included in the intercept. Variables not tested because of small sample size are not included. R^2 is the variance explained by the model and P is the significance level (* P < 0.05; ** P < 0.01; *** P < 0.001; n.s. no significant effects).

		Distance to Roads			Distance to Settlements			Elevation			Slope		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2	*Estimate (±SE)*	*P*	R^2	*Estimate (±SE)*	*P*	R^2
CONTINENT	Model		n.s.	0.07		**	0.38		***	0.58		*	0.19
	Intercept	-0.38(±0.1)	***		-0.60(±0.12)	**		0.39(±0.11)	**		0.27(±0.16)		
	$\beta_{America}$	0.24(±0.18)	*		0.72(±0.24)	**		-0.9(±0.17)	***		-0.57(±0.27)	*	

		Terrain Ruggedness(≤ 100 ha)			Open Areas(≤100 ha)			Refuge habitat(≤ 100 ha)		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2	*Estimate (±SE)*	*P*	R^2
CONTINENT	Model		n.s.	0.17		n.s.	0.04		**	0.38
	Intercept	0.17(±0.12)			-0.23(±0.13)			0.75(±0.13)	***	
	$\beta_{America}$	-0.4(±0.23)			0.2(±0.25)			-0.67(±0.22)	**	

		Terrain Ruggedness(≤ 900 ha)			Open Areas(≤ 900 ha)			Refuge habitat(≤ 900 ha)		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2	*Estimate (±SE)*	*P*	R^2
CONTINENT	Model		n.s.	0.18		n.s.	0.00		n.s.	0.19
	Intercept	0.12(±0.11)			-0.08(±0.12)			0.58(±0.13)	***	
	$\beta_{America}$	-0.40(±0.22)			0.02(±0.21)			-0.41(±0.23)		

APPENDIX 1.6. Summary of the Generalized Linear Models analysing the influence of the geographical location (Continent) of the study area associated to the history of human-wolf coexistence on the effect sizes estimated for the different factors at the level of homesites. The level "*Eurasia*" is included in the intercept. R^2 is the variance explained by the model and P is the significance level (* P < 0.05; ** P < 0.01; *** P < 0.001; n.s. no significant effects).

		Direct Vulnerability			Topography		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2
CONTINENT	Model		***	0.19		***	0.31
	Intercept	-0.45(±0.06)	***		0.28(±0.07)	***	
	β_{America}	0.44(±0.13)	**		-0.65(±0.13)	***	

APPENDIX 1.7. Summary of the Generalized Linear Models analysing the influence of the cofactors representing different human-related traits of the study areas associated to human-wolf conflicts on the effect sizes estimated for the different variables at the level of homesites. The level *"Livestock"* (Diet) is included in the intercept. R^2 is the variance explained by the model and P is the significance level (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s. no significant effects).

		Distance to Roads			Distance to Main Roads			Distance to Settlements		
		Estimate (±SE)	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*
HUMAN POP. DENSITY	Model		n.s.	0.03		n.s.	0.12		n.s.	0.13
	Intercept	-0.27(±0.11)	*		-0.43(±0.12)	**		-0.29(±0.16)		
	β	-0.001(±0.001)			-0.001(±0.001)			-0.002(±0.001)		
LIVESTOCK BIOMASS	Model		n.s.	0.13		n.s.	0.13		**	0.38
	Intercept	-0.17(±0.12)			-0.37(±0.14)	*		-0.10(±0.15)		
	β	-0.03(±0.02)			-0.02(±0.02)			-0.05(±0.02)	**	
DIET	Model		n.s.	0.23		n.s.	0.01		n.s.	0.15
	Intercept	-0.45(±0.18)	*		-0.58(±0.17)	**		-0.64(±0.23)	**	
	β (Mix)	0.25(±0.23)	*		0.05(±0.23)			0.13(±0.31)		
	β (Wild)	0.12(±0.22)			0.08(±0.24)			0.47(±0.31)		

		Distance to Villages			Elevation			Slope		
		Estimate (±SE)	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*
HUMAN POP. DENSITY	Model		n.s.	0.06		*	0.20		n.s.	0.02
	Intercept	-0.54(±0.24)	*		-0.13(±0.13)			0.002(±0.17)		
	β	-0.001(±0.002)			0.003(±0.001)	*		0.001(±0.002)		
LIVESTOCK BIOMASS	Model		n.s.	0.17		***	0.43		n.s.	0.05
	Intercept	-0.25(±0.32)			-0.31(±0.13)			-0.07(±0.19)		
	β	-0.05(±0.03)			0.07(±0.02)	***		0.03(±0.03)		
DIET	Model					**	0.39		n.s.	0.17
	Intercept				0.37(±0.22)			0.52(±0.28)		
	β (Mix)				-0.13(±0.31)			-0.467(±0.37)		
	β (Wild)				-0.71(±0.26)	*		-0.68(±0.34)		

		Terrain Ruggedness (≤ 100 ha)			Agriculture (≤ 100 ha)			Open Areas (≤100 ha)		
		Estimate (±SE)	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*	*Estimate (±SE)*	*P*	*R^2*
HUMAN POP. DENSITY	Model		n.s.	0.15		***	0.61		n.s.	0.12
	Intercept	-0.04(±0.12)			-0.24(±0.13)			-0.27(±0.13)		
	β	0.02(±0.01)			-0.003(±0.001)	**		0.001(±0.001)		
LIVESTOCK BIOMASS	Model		n.s.	0.09		*	0.37		n.s.	0.10
	Intercept	-0.05(±0.15)			-0.15(±0.22)			-0.31(±0.15)		
	β	0.02(±0.02)			-0.05(±0.02)			0.02(±0.02)		
DIET	Model		***	0.34					n.s.	0.07
	Intercept	0.36(±0.11)	**					-0.06(±0.33)		
	β (Mix)	-0.30(±0.15)						-0.26(±0.38)		
	β (Wild)	-0.58(±0.15)	***					-0.03(±0.37)		

(*Appendix 1.7 continued*)

		Refuge habitat (≤100ha)			Urban (≤100 ha)		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2
HUMAN POP. DENSITY	Model		***	0.42		n.s.	0.32
	Intercept	0.33(±0.12)	*		-0.06(±0.07)		
	β	0.003(±0.001)	**		-0.001(±0.000)		
LIVESTOCK BIOMASS	Model		**	0.31		**	0.55
	Intercept	0.27(±0.14)			0.02(±0.07)		
	β	0.05(±0.02)	*		-0.02(±0.01)	*	
DIET	Model		**	0.47			
	Intercept	0.57(±0.24)	*				
	B (Mix)	0.42(±0.29)					
	β (Wild)	-0.37(±0.28)					

		Terrain Ruggedness(≤ 900 ha)			Agriculture(≤900 ha)			Open Areas(≤ 900 ha)		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2	*Estimate (±SE)*	*P*	R^2
HUMAN POP. DENSITY	Model		n.s.	0.13		*	0.39		n.s.	0.12
	Intercept	-0.08(±0.12)			-0.31(±0.15)			-0.16(±0.11)		
	β	0.001(±0.001)			-0.002(±0.001)			0.001(±0.001		
LIVESTOCK BIOMASS	Model		n.s.	0.10		n.s.	0.20		n.s.	0.17
	Intercept	-0.11(±0.14)			-0.25(±0.25)			-0.23(±0.12)		
	β	0.02(±0.02)			-0.03(±0.023)			0.03(±0.02)		
DIET	Model		n.s.	0.27					n.s.	0.07
	Intercept	0.28(±0.17)						0.15(±0.29)		
	β (Mix)	-0.20(±0.23)						-0.33(±0.33)		
	β (Wild)	-0.51(±0.23)	*					-0.21(±0.32)		

		Refuge habitat (≤ 900 ha)			Urban (≤ 900 ha)		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2
HUMAN POP. DENSITY	Model		**	0.36		n.	0.36
	Intercept	0.28(±0.11)	*		-0.15(±0.11)		
	β	0.003(±0.001)	*		-0.001(±0.001)		
LIVESTOCK BIOMASS	Model		n.s.	0.13		n.	0.33
	Intercept	0.29(±0.15)			-0.09(±0.12)		
	β	0.03(±0.02)			-0.03(±0.01)		
DIET	Model		***	0.5			
	Intercept	0.24(±0.19)					
	B (Mix)	0.69(±0.24)	*				
	β (Wild)	-0.02(±0.23)					

APPENDIX 1.8. Summary of the Generalized Linear Models analysing the influence of the cofactors representing different human-related traits of the study areas associated to human-wolf conflicts on the effect sizes estimated for the different factors at the level of homesites. The level "*Livestock*" (diet) is included in the intercept. R^2 is the variance explained by the model and P is the significance level (* P < 0.05; ** P < 0.01; *** P < 0.001; n.s. no significant effects).

		Direct Vulnerability			Topography		
		Estimate (±SE)	*P*	R^2	*Estimate (±SE)*	*P*	R^2
HUMAN POP. DENSITY	Model		n.s.	0.06		*	0.09
	Intercept	-0.26(±0.08)	**		-0.06(±0.08)		
	β	-0.001(±0.001)			0002(±0.001)	*	
LIVESTOCK BIOMASS	Model		**	0.18		***	0.16
	Intercept	-0.14.(±0.08)			-0.16(±0.09)		
	β	-0.03(±0.01)	**		0.04(±0.01)	**	
DIET	Model		n.s.	0.03		***	0.26
	Intercept	-0.47(±0.13)	***		0.45(±0.13)	***	
	B (Mix)	0.15(±0.16)			-0.28(±0.17)		
	β (Wild)	0.19(±0.16)			-0.69(±0.16)	***	

Chapter 2

Top-down dilution of conservation commitments in Europe: An example using breeding site protection for wolves

ABSTRACT

In Europe, decision-making power related to biodiversity conservation has been partly, and voluntarily, relinquished by countries to superior levels. In this hierarchical top-down scenario, the Bern Convention and the EU Habitats Directive grant protection to a considerable number of taxa, and determine underlying conservation actions at (sub)national levels. The protection precepts emanating from these legal instruments are expected to be transferred effectively to lower levels, adapting general obligations to species-specific contexts.

We assessed the implementation of general obligations from international agreements through local regulations, using as illustrative example the European requirement of protecting the breeding sites of protected species, and the conservation of grey wolves (*Canis lupus*) in Europe.

After reviewing 43 wolf management and conservation plans across Europe, overall, we found only seven actions or guidelines designed to ensure breeding site protection/availability for wolves (from six countries). None of the plans contained a comprehensive set of measures to preserve breeding sites or guarantee their availability. Our results suggest that transposition of general obligations from international agreements into local legislation systems may be a critical point of weakness in the biodiversity conservation policy process. We recommend additional scrutiny to ensure that ambitious conservation goals are not diluted, but enforced, along its way from high-tier laws to local regulations, in accordance with the letter and spirit of international agreements.

Introduction

The conservation of biodiversity is mandated by commitments and obligations to sovereign states at the international level. A growing consensus has emerged amongst the world's approximately 200 sovereign states regarding the need to minimize, halt, or reverse biodiversity loss. Law has a key role to play in achieving these aims (Chapron *et al.* 2017). Given the multifold international dimensions of the challenges involved, multiple international legal instruments have been adopted (Kelly 1997; Bowman *et al.* 2010). In terms of biodiversity conservation, some notable examples are the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Washigngton DC, 1973) and the UN Convention on Biological Diversity (Nairobi, 1992). However, to date, the objectives of most international agreements have not been fully achieved, as the failure of the specific targets committed in 2002 to substantially reduce global biodiversity loss by 2010 exemplifies (Butchart *et al.* 2010).

In Europe, legal milestones for biodiversity conservation are the Bern Convention (BC) on the Conservation of European Wildlife and Natural Habitats (Council of Europe, 1979), the EU Birds Directive (BD) of 1979 (Directive 2009/147/EC) and the EU Habitats Directive (HD) of 1992 (Directive 92/43/EEC). These legal tools have proven instrumental for protecting habitats (Trouwborst, *et al.* 2017), and the conservation status of many species has improved since their enactment, such as large carnivores and bird species (e.g., Fleurke & Trouwborst 2014; Chapron *et al.* 2014; Sanderson *et al.* 2015). Even so, compliance and enforcement failures remain an issue (López-Bao *et al.* 2015; Trouwborst *et al.* 2017).

Although compliance is pivotal for international legislations to be effective, because transforms obligations into better prospects for species and habitats (Weiss & Jackobson 2000; Chape *et al*. 2005), it can be hindered in a variety of ways (Kelly 1997; Bennett & Ligthart 2001; Epstein *et al*. 2016). Besides enforcement and practical application, the degree of compliance is determined by the accuracy of the transposition and integration of obligations and goals contained in international agreements into domestic law (López-Bao & Margalida 2018, Mateo-Tomás *et al.* 2018).

National authorities are responsible for ensuring that domestic regulations conform to international obligations (Bennett & Ligthart 2001). If transposition and integration are adequate, no loss of strength of objectives and obligations should be observed across a hierarchical legal system and their associated tenets, which in a biodiversity preservation context, take often the form of conservation and management plans. Besides, the interpretation of the general principles of international agreements, in order to convert them into specific obligations at the local level, emerges as another issue. Such principles are necessarily stated in vague terms, as they should embrace a panoply of taxa and multiple situations, and adapting them to concrete obligations concerning a single species in each of the many physical, environmental, and socioeconomic contexts is not always straightforward. In spite of these potential problems, little attention has been paid to top-down dilution of conservation obligations through hierarchical, multilevel legal systems, and the impact of generalization on the functionality of conservation obligations that encompass multiple taxa.

Here, we show how the strength of ambitious international conservation instruments, such as the BC and the HD, can be diluted in the successive transposition from general, multi-taxa commitments, to specific conservation and management instruments concerning single or similar taxa at local levels. To illustrate this point, we use the European obligation of protecting the breeding sites of protected species (explicitly and implicitly required by the BC and HD) and the conservation of the grey wolf (*Canis lupus*). The wolf is a widely distributed species across Europe (Chapron *et al.* 2014), generally protected under the Appendices or Annexes of the BC and the HD (Fig. 1; Appendix 2.1). Because of its conservation status and the numerous conflicts often associated with the presence of the species (e.g., livestock depredation, land use, competition for game), multiple legal instruments, delineated by the BC and the HD, have been devoted to conserve and manage wolf populations in Europe.

Habitat requirements of wolves: setting the focus on breeding sites

Wolves are considered a generalist species, given their ability to persist in a wide range of habitats (Mech & Boitani 2010), including human-dominated landscapes (Llaneza *et al.* 2012; Chapron *et al.* 2014). Viewed from this perspective, it seems reasonable to argue that wolves' habitat conservation doesn't need to be steered toward preserving large tracts of habitat with low human presence. This does not imply that the issue of habitat protection for wolves should be disregarded; rather it should be mainly focused on those places and periods in which wolves are vulnerable. Wolf breeding sites (encompassing both den and rendezvous sites; Joslin 1967) restrict spatio-temporal vulnerability of wolf packs (Sazatornil *et al*. 2016) within a fraction of their home ranges (a few hectares; e.g., Iliopoulos *et al*. 2014) until pups reach approximately 6-7 months of age (Mech & Boitani 2010).

Wolves have developed different behavioural tactics to reduce the interference with humans at breeding sites (e.g., Habib & Kumar 2007; Ahmadi *et al.* 2014). Generally, wolves avoid humans either by placing breeding sites away from human activity or by increasing the strength of selection towards protective cover (*see* Chapter 1). This pattern of habitat selection raises the question whether the availability of suitable places to be used as breeding sites by wolves may become a limiting factor in some scenarios, determining, for instance, their persistence in human-dominated landscapes. Moreover, wolves frequently reuse breeding sites or establish them at close distance from previous ones (Ballard & Dau 1983; Capitani *et al*. 2006), indicating either optimal conditions for pup raising (Ciucci *et al.* 1997), or lack of alternative sites (Mech & Packard 1990).

Breeding site protection under the Bern Convention and the Habitats Directive

The critical role of breeding sites for species conservation is acknowledged in BC and HD (Appendix 2.2). For strictly protected species (BC Appendix II, HD Annex IV; Appendix 2.1), these provisions require the authorities to explicitly prohibit the damage to breeding sites, as well as the disturbance of individuals at those places (Appendix 2.2). Importantly, it has been stressed by the Court of Justice of the EU (CJEU) that member states must take all necessary measures to ensure that these terms are not violated in practice (e.g., CJEU 30 January 2002, Case C-103/00).

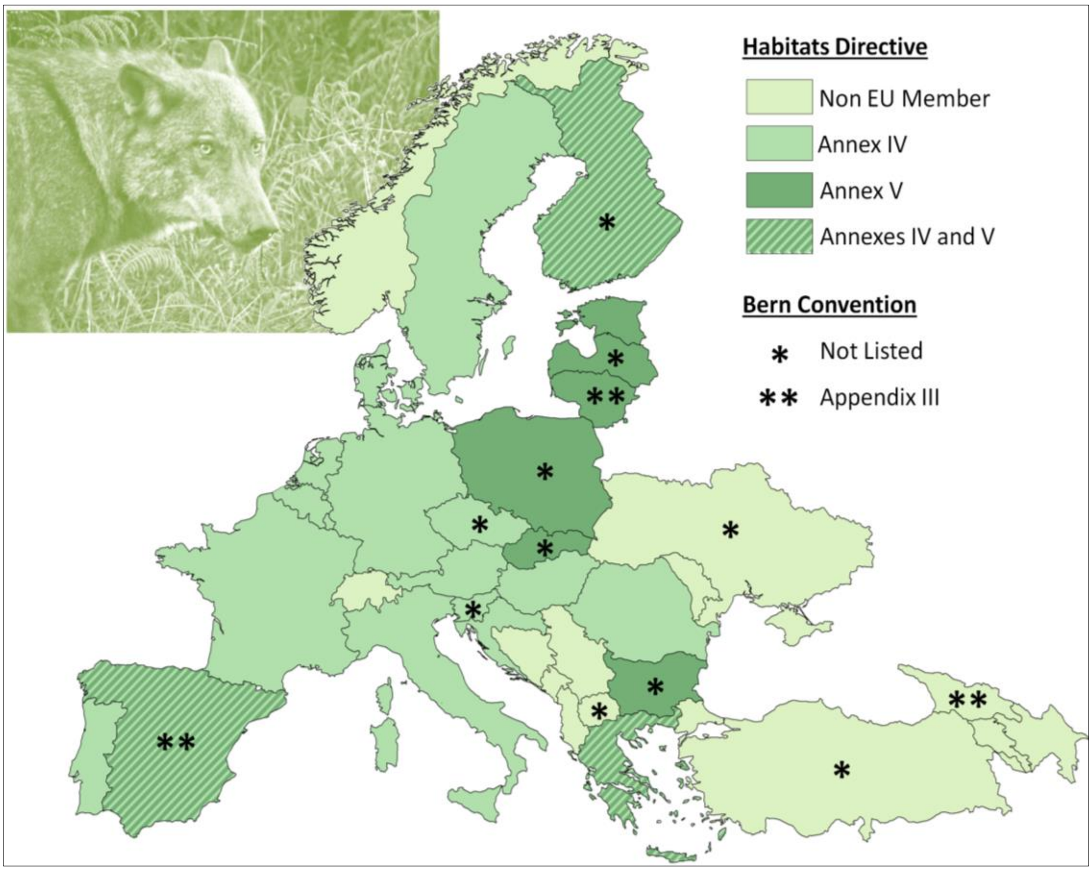


Figure 2.1. Wolf protection under the Bern Convention (BC) and the European Union Habitats Directive (HD) within non-insular countries of the Council of Europe (except Russia). HD Annex IV: Species of community interest in need of strict protection. HD Annex V: Species of community interest whose taking in the wild and exploitation may be subject to management measures. For HD, out of the 24 non-insular Member States, nine list wolf populations in the Annex V. In three cases (Greece, Spain, Finland) the exceptions are partial, with sections of their wolf populations remaining strictly protected under Annex IV. For BC, out of the 41 non-insular members of the Council of Europe (excluding Russia), three countries keep wolves out of Appendix III of the BC (protected fauna species) and 10 countries did not list the species in any Appendix. Photo courtesy of F.J. Lema.

For more flexible protection regimes (BC Appendix III, HD Annex V; Appendix 2.1), the BC requires authorities to ensure the 'protection' of species included in its Appendix III, but not necessarily implementing the prohibitions associated with strict protection

(Appendix 2.2). Under the HD, member states are required to ensure a favourable conservation status for species in Annex V (Fig. 1; Trouwborst 2014; Appendix 2.1).

How can species protection be ensured without forbidding damage or disturbance to breeding sites is left to the interpretation of local administrations or legislative bodies. Given the vulnerability of wolves during the breeding period, protecting wolf breeding sites may be necessary to comply with BC and HD, particularly in human-dominated landscapes. Regarding area protection rules, the HD provides an additional layer of protection for breeding sites inside Special Areas of Conservation under the 'Natura 2000' network, through the strict site protection requirements laid down in HD Article 6, whereas broadly similar considerations apply with regard to the BC equivalent of the Natura 2000 network, known as the 'Emerald Network'.

Species covered by the BC and HD include a high diversity of taxa, organism sizes, life history traits, and breeding behaviours. Both instruments list, for example, species: i) breeding in colonies (e.g., *Miniopterus schreibersii*), ii) with extremely restricted habitat -that facilitates monitoring- (e.g., *Valencia hispanica*), iii) building conspicuous structures to breed (e.g., most large birds of prey, all of them included in BC Appendix II), iv) showing high fidelity to breeding sites (e.g., *Chelonia mydas*), or v) species that may find many suitable sites to breed (e.g., *Lynx lynx*). Under such a diversity of traits covered by the same general requirements (Appendix 2.2), there is a risk that generalization plays down the effectiveness of breeding site protection regarding particular taxa. The "*means and measures*" (Appendix 2.2) to which BC Article 6 and HD Article 12 appeal should foresee potential gaps in effectiveness for specific taxa in particular contexts.

In the case of wolves, low detectability and recognition of breeding sites poses a constraint to effectively reduce disturbance to the species during the breeding period, as well as to preserve breeding sites via reactive measures.

Wolf breeding sites within conservation and management plans

In 1989, the Standing Committee of the BC made a recommendation to contracting parties that set specific guidelines regarding wolves, including drawing up wolf management plans ensuring viable populations at appropriate levels (Rec. No.17/1989). Such guidelines were in accordance with the principles and suggestions included in the Manifesto and Guidelines on Wolf Conservation from 1973 (Appendix 2.2). Despite the absence of explicit references to breeding site protection in this manifesto, the issues of protection of suitable areas for wolves and ecological restoration arose. The convenience of developing and implementing wolf management plans was subsequently endorsed by the Action Plan for the conservation of wolves in Europe (Boitani 2000), and a new recommendation from the BC Standing Committee No.74/1999. Finally, the Recommendation of the BC Standing Committee No.59/1997 appeals to take into account habitat requirements and habitat preservation in action plans (Appendix 2.2).

Species-specific plans are a suitable, or even required, means of implementing the obligations of EU member states under HD Article 12, that requires '*not only to adopt a comprehensive legislative framework but also to implement concrete and specific protection measures*' whereas likewise the provision presupposes the '*adoption of coherent and coordinated measures of a preventive nature*' (CJEU 11 January 2007, Case C-183/05). Species action or recovery plans are recommended, '*on condition that they are correctly established and applied*', as effective means of implementing HD Article 12, as without such plans or similarly comprehensive and species-specific measures, '*the system of strict protection contains gaps*' amounting to a violation of the HD (Case C-183/05). As an illustrative example, in a case concerning the European hamster (*Cricetus cricetus*) in France, the CJEU held that '*by failing to establish a programme of measures to ensure strict protection of hamsters, the French Republic has failed to fulfil its obligations under HD Article 12(1)(d) regarding breeding sites and resting places*' (CJEU 9 June 2011, Case C-383/09).

Along these lines, we assessed the degree to which wolf breeding site protection and restoration is considered by contracting parties of the BC and EU member states. We reviewed instruments (plans and strategies legally and non-legally binding) aiming to regulate wolf conservation and management at national and subnational levels across the Council of Europe (CoE, except Russia), in search of references to wolf habitat and specific protection actions regarding breeding sites (Appendix 2.3).

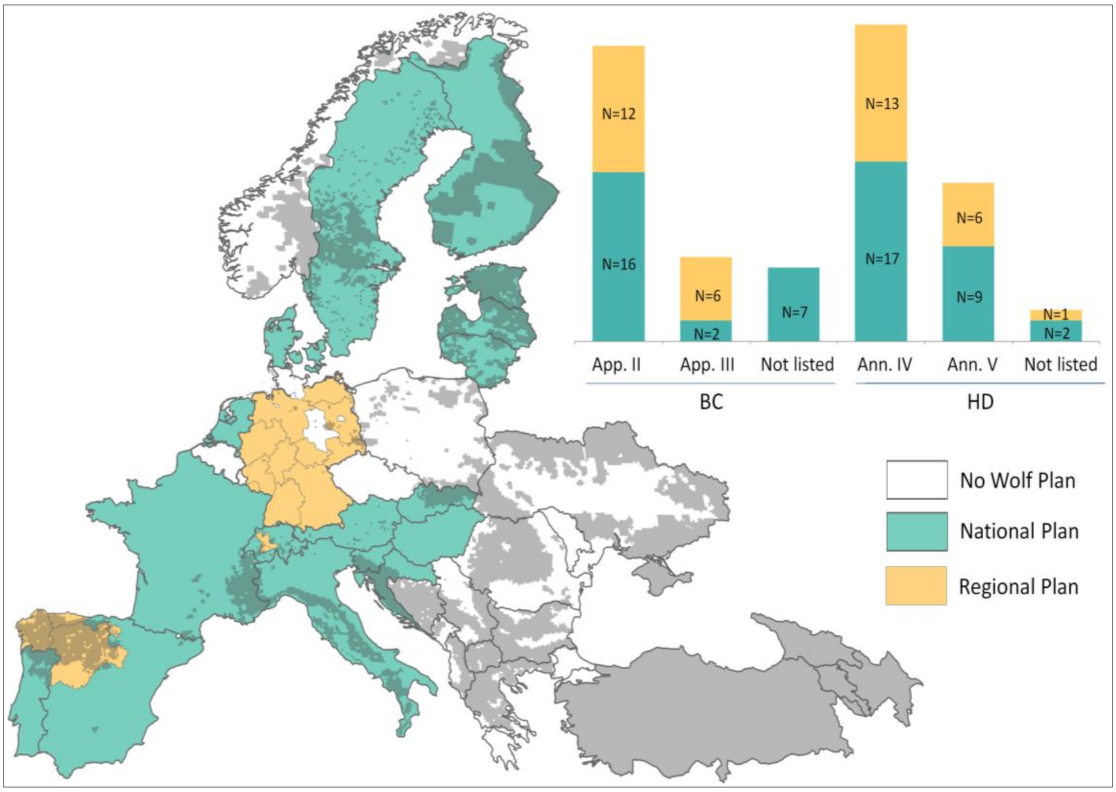


Figure 2.2 Distribution and number of wolf action plans or conservation strategies in countries within the Council of Europe, and number of plans at the national or regional level, amongst Appendices or Annexes of the Bern Convention (BC) and the European Union Habitats Directive (HD). Partitioned territories in which wolves are listed under Annexes IV and V of HD, have been counted in both cases. Wolf range (grey area) was extracted from the IUCN Red List of Threatened Species (www.iucnredlist.org).

We examined 43 wolf plans and strategies (hereafter plans) from 18 countries and 16 regions (Appendix 2.3). Twenty-five and 18 plans were issued at the national and subnational level, respectively (in some countries, wolf management is fully or partially decentralized to a sub-national level: 6 plans in Spain, 11 plans in Germany and 1 plan in Switzerland). We reviewed all sections of the plans in search of references to habitat and breeding sites (Appendix 2.3), and identified whether these were merely descriptive or included actions to guarantee breeding sites' protection and suitability.

We found 91 references to wolf habitat in 26 plans (60%, n=43, Fig. 3, Appendix 2.3). Forty-eight references (53%) were related to actual conservation actions, or guidelines intended to design effective actions on wolf habitat; whereas the remaining 43 references had no associated actions. Most of these non-action references (91%) appeared in the non-binding, background sections of plans.

Overall, eight national (32%) and one subnational (6%) plans contained 15 explicit references to breeding habitat. But only seven of such references, belonging to six countries, corresponded to actions designed to ensure breeding site protection and/or availability (Fig. 2.3). Interestingly, three of these countries are situated in southern Europe where wolves occupy human-dominated landscapes, while a fourth country (The Netherlands) has the densest human population in the continent and no re-established wolf population yet. Out of the seven actions detected, two were aimed at carrying out a diagnosis in order to create further actions, while the remaining five actions proposed explicit restrictions to human intrusion at breeding sites, preventing disturbance (e.g., selective forest management, restrictions of access and protection of refuge patches).

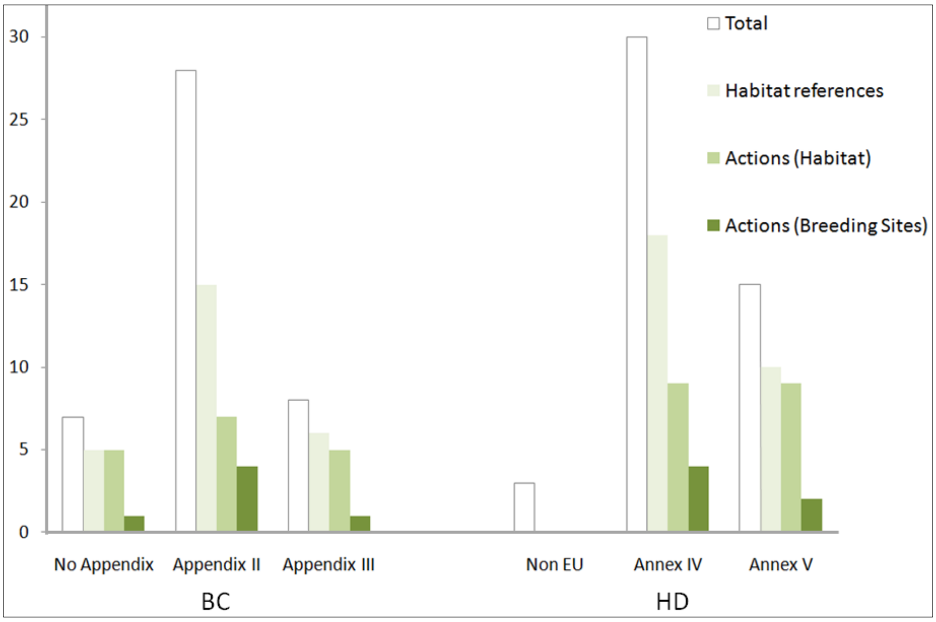


Figure 2.3. Number of wolf plans in Europe classified under each Appendix or Annex of BC and HD, respectively ("Total" = Total number of plans within each law or convention), and the corresponding number of plans within each category that include references to wolf habitat, actions or guidelines on wolf habitat, and actions or guidelines intended to protect and provide breeding sites for wolves. Partitioned territories in which wolves are listed under Annexes IV and V of HD, have been counted in both cases.

While less than half (33%) of the plans included measures other than monitoring or diagnosis to guarantee habitat availability, plans showing actions to protect breeding sites were even fewer (14%). None of them contained a comprehensive set of actions; although this would often be required in order to fully transpose and integrate obligations under the BC and HD into local instruments.

These results reveal a dysfunctional top-down transfer system that ultimately compromises an adequate enforcement of international agreements (the European biodiversity conservation legislation in our case).

Towards a better implementation and compliance of European commitments

The wolf is arguably one of the species whose conservation and management raises most concern in Europe, considering the number of single-species plans (43) ultimately devoted to provide frameworks of sustainable coexistence with humans (Fig. 2). However, these plans pay little attention or neglect the most critical aspects of wolf vulnerability in space (habitat requirements at small scale for breeding sites) and through time (long breeding periods). The enforcement of wolf breeding site protection through proactive management is still generally missed.

Practitioners should find in local plans unequivocal descriptions of habitat features allowing wolves to establish breeding sites, which sources of disturbance wolves might be sensitive to, which responses are expected from wolves facing different kinds of disturbance, and which forms of human activity might be compatible with wolf reproductive success at small spatial scales. This background, regularly updated by the input of emerging knowledge, should be translated into a spatially explicit allocation of permitted and forbidden activities.

The general assumption of habitat plasticity may drive a biased perception concerning the ecological requirements of wolves. This mechanism may be behind the weak efforts devoted to habitat and breeding site preservation contained in wolf plans. The availability of suitable areas for wolf breeding may have been taken for granted in those areas where large forested tracts remain, or where wolf populations are not declining.

Habitat protection for wolves should be better implemented through effective breeding site protection at fine spatial scales. In human-dominated Europe, managers need to improve the protection of suitable sites for wolves to breed and raise pups. This recommendation should be specially regarded in those areas where wolves coexist closely with humans. We argue that to be in line with BC and HD obligations, (sub)national plans and strategies should provide preventive protection of breeding sites. Extensive monitoring to identify used and potential breeding sites, protection of known breeding sites, ensuring the availability of patches of refuge vegetation within wolf territories, and temporally restricting human activities around breeding sites could be effective measures to be implemented at local scales.

Figure 2.4. Wolf breeding (*Rendezvous*) site in NW Spain. The low detectability and recognition of wolf breeding sites by the general public poses a constraint to effectively reduce disturbance to the species during the breeding period. Photo by V. Sazatornil.

Plans and lower-level regulatory texts alike should fill the interpretation gap, that is, the realization of the necessarily vague principles dictated in international legislation within an idiosyncratic socioeconomic and environmental reality. Overlooking the interpretation gap in local instruments represents an illustrative example of weak compliance with international agreements. Simplifying compliance to literal transposition of specific general obligations into local legislation (e.g., local wildlife protection laws) may limit the potential effectiveness of international agreements. Providing guidance from international bodies (in our case the EU and the CoE) could be a useful initiative for an effective transposition and implementation of general commitments contained in international agreements into a specific taxon and context. Disentangling general patterns of the ecology of the concerning species (wolves in our case; Sazatornil *et al.* 2016) and integrating them into general management guidelines would help improve compliance and effectiveness of international agreements. Moreover, such integration would reduce the heterogeneity in the implementation of regulations among territories, being only limited to contextual particularities and not misinterpretations of the norm (Mateo-Tomás *et al.* 2018).

Conservation obligations contained in international legislation and agreements aiming to preserve multiple taxa cannot avoid a certain generalisation due to the diversity of ecological, behavioural and life history traits of the species of concern, as well as the particular contexts where each species occurs. In order for these overarching instruments to attain their conservation objectives, the general obligations they impose on parties must be duly translated into species-specific plans and strategies at lower levels. In this regard, our findings regarding wolves are relevant for other species protected under the BC and HD (more than 1,500 species are protected under the European Directives). In our example, the low detectability of the breeding sites of wolves (Fig. 4) may increase the likelihood of involuntary infringements of international obligations (e.g., prohibit the damage to breeding sites or the disturbance of individuals at those places). Such assumption, and our call for proactive management in order to prevent breeding site disturbance or deterioration, is applicable to other protected taxa under the BC and HD, such as many small mammals and reptiles, or biological traits (e.g., hibernation dens in brown bears *Ursus arctos*). The active detection and protection of breeding sites has already been implemented for some species which populations would not be viable without such proactive management actions (e.g., Montagu's harrier *Circus pygargus* conservation in agricultural areas; Arroyo *et al*. 2002).

Our results suggest that transposition of general obligations from international agreements into local legislation systems may be a critical point of weakness in the biodiversity conservation policy process. We recommend additional scrutiny to ensure that ambitious conservation goals are not diluted but implemented into local legislation systems in accordance with the letter and spirit of the agreements at the international level.

References

Ahmadi, M., López-Bao, J.V., & Kaboli, M. (2014). Spatial heterogeneity in human activities favors the persistence of wolves in agroecosystems. *PloS ONE* 9: e108080.

Arroyo, B., García, J., & Bretagnolle, V. (2002). Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Animal Conservation* 5: 283-290.

Ballard, W.B., & Dau J.R. (1983). Characteristics of gray wolf (*Canis lupus*) den and rendezvous sites in south-central Alaska. *Canadian Field Naturalist 97*: 299–302.

Bennett, G., & Ligthart, S. (2001). The implementation of international nature conservation agreements in Europe: the case of the Netherlands. *European Environment* 11: 140–150.

Boitani, L. (2000). Action plan for the conservation of Wolves (*Canis lupus*) in Europe. Strasbourg Cedex, Council of Europe (85pp).

Bowman, M., Redgwell, C., & Davies, P. (2010). Lyster's International Wildlife Law. 2nd edition. Cambridge University Press, Cambridge.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., & Bruno, J. (2010). Global biodiversity: indicators of recent declines. *Science* 328: 1164-1168.

Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A., & Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica* 51: 395-404.

Chape, S., Harrison, J., Spalding, M., & Lysenko, I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society* B 360: 443–455.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., &

Boitani, L. (2014). Recovery of large carnivores in Europe’s modern human-dominated landscapes. *Science* 346: 1517-1519.

Chapron, G., Epstein, Y., Trouwborst, A., & López-Bao, J.V. (2017). Bolster legal boundaries to stay within planetary boundaries. *Nature Ecology & Evolution* 1: 0086.

Ciucci, P., Boitani, L., Francisci, F., & Andreoli, G. (1997). Home-range, activity and movements of a wolf pack in central Italy. *Journal of Zoology* 243: 803–819.

Epstein, Y., López-Bao, J.V., & Chapron, G. (2016). A Legal-Ecological Understanding of Favorable Conservation Status for Species in Europe. *Conservation Letters* 9: 81-88.

Fleurke, F.M., & Trouwborst, A. (2014). European regional approaches to the transboundary conservation of biodiversity: The Bern Convention and the EU Birds and Habitats Directives. Pp: 128-162 *In*: Kotze, L. & Marauhn, T. (Eds.) Transboundary governance of biodiversity. Martinus Nijhoff, Leiden/Boxton.

Habib, B., & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *Journal of Zoology* 272: 259-265.

Iliopoulos, Y., Youlatos, D., & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *European Journal of Wildlife Research* 60: 23-34.

Joslin, P.W.B. (1967). Movements and homesites of timber wolves in Algonquin Park. *American Zoologist* 7: 279-288.

Kelly, M.J. (1997). Overcoming obstacles to the effective implementation of international environmental agreements. *Georgetown International Environmental Law Review* 9: 447-488.

Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions* 18: 459-469.

López-Bao, J.V., Blanco, J.C., Rodríguez, A., Godinho, R., Sazatornil, V., Álvares, F., García, E.J., Llaneza, L., Rico, M., Cortés, Y., Palacios, V., & Chapron, G. (2015). Toothless wildlife protection laws. *Biodiversity and Conservation* 24: 2105-2108.

López-Bao, J.V., & Margalida, A. (2018). Slow transposition of European environmental policies. *Nature Ecology & Evolution* 2: 914.

Mateo-Tomás, P., Olea, P.P., & López-Bao, J.V. (2018). Europe's uneven laws threaten scavengers. *Science* 360: 612-613.

Mech, L.D., & Packard, J.M. (1990). Possible use of wolf, *Canis lupus*, den over several centuries. *Canadian Field Naturalist* 104: 484-485.

Mech, L.D., & Boitani, L. (2010). Wolves, Behavior, Ecology, and Conservation. 2nd edn. The University of Chicago Press, Chicago.

Sanderson, F.J., Pople, R.G., Ieronymidou, CH., Burfield, I.J., Gregory, R.D., Willis, S.G., Howard, C., Stephens, P.A., Beresford, A.E., Donald, P.F. (2015). Assessing the performance of EU nature legislation in protecting target bird species in an era of climate change. *Conservation Letters* 9: 172–180.

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand H., Unger, D., Wabakken, P., & López-Bao, J.V. (2016). The role of human-related risk in breeding site selection by wolves. *Biological Conservation* 201: 103-110.

Trouwborst, A. (2014). The EU Habitats Directive and wolf conservation and management on the Iberian Peninsula: a legal perspective. *Galemys* 26: 15-30.

Trouwborst, A., Chapron, G., Fleurke, F., Epstein, Y., & López-Bao, J.V. (2017). Europe's biodiversity avoids fatal setback. *Science* 355: 140.

Weiss, E.B., & Jackobson, H.K (Eds.). (2000). Engaging countries: strengthening compliance with international environmental accords. The MIT Press. Cambridge, MA.

APPENDIX CHAPTER 2

(*Top-down dilution of conservation commitments in Europe: An example using breeding site protection for wolves)*

APPENDIX 2.1: Wolves under the Bern Convention (BC) and the Habitats Directive (HD).

The BC and HD provide the predominant international legal frameworks for wolf conservation in Europe (Fleurke & Trouwborst 2014). However, due to reservations submitted by some countries under the BC, and country-specific differences recorded under the HD, the applicability and nature of the obligations these instruments impose vary from one country to the other, or indeed between parts of the same country (Fig. 1; main text). All European states with wolves, except Russia, are bound by the general obligation in BC Article 2 to ensure a wolf population level that corresponds to, *inter alia*, ecological requirements (Trouwborst *et al.* 2017), and to implement habitat conservation measures (BC Article 4). Under the HD, which applies only in the 28 EU member states, wolves have Annex II status in most of those, entailing an obligation to designate and protect the most suitable habitat as Special Areas of Conservation (SACs) under the 'Natura 2000' network (HD Articles 4 and 6). Moreover, where BC Appendix II and/or HD Annex IV apply (Fig. 1; main text), national authorities must ensure special protection, including the prohibition of killing wolves, destroying or damaging their breeding sites, and disturbing them during the breeding season (BC Article 6; HD Article 12). These prohibitions are subject to the possibility of limited, strictly defined exceptions (BC Article 9; HD Article 16). Finally, BC Appendix III and HD Annex V represent more flexible regimes, but requiring states to ensure healthy wolf populations – i.e., to ensure a '*favourable conservation status*' under the HD – (BC Article 7; HD Article 14).

REFERENCES FOR APPENDIX 2.1

Fleurke, F.M. & Trouwborst, A. (2014). European regional approaches to the transboundary conservation of biodiversity: The Bern Convention and the EU Birds and Habitats Directives. Pp: 128-162 *In:* Kotze, L. & Marauhn, T. (Eds.) Transboundary governance of biodiversity. Martinus Nijhoff, Leiden/Boxton.

Trouwborst, A., Fleurke, F.M. & Linnell, J.D.C. (2017). Norway's wolf policy and the Bern Convention on European Wildlife: avoiding the 'manifestly absurd'. J. Int. Wild. Law Policy, 20, 155-167.

APPENDIX 2.2: Selected excerpts from international laws, agreements, or strategies for biodiversity preservation used in Chapter 2.

A) Bern Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention, Council of Europe, 1979):

(Art.6) "*Each contracting party shall take appropriate and necessary legislative and administrative measures to ensure the special protection of the wild fauna species specified in Appendix II. The following will in particular be prohibited for these species:*"

(Art.6§b) "*The deliberate damage to or destruction of breeding or resting sites*".

(Art.6§c) "*The deliberate disturbance of wild fauna, particularly during the period of breeding, rearing, and hibernation, insofar as disturbance would be significant in relation to the objectives of this Convention*".

(Art.7§1) *"Each contracting party shall take appropriate and necessary legislative and administrative measures to ensure the protection of the wild fauna species specified in Appendix III"*.

B) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (Habitats Directive):

(Art. 12) "*Member States shall take the requisite measures to establish a system of strict protection for the animal species listed in Annex IV (a) in their natural range, prohibiting:*

(Art.12§b) *"Deliberate disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration"*.

(Art.12§d) *"Deterioration or destruction of breeding sites or resting places"*.

C) Recommendation No.17/1989 of the Standing Committee of the Bern Convention on the protection of the wolf (*Canis lupus*) in Europe:

"Draw up management plans for the species in view of assuring viable populations at appropriate levels;"

"Assess the impact on wolf populations of projects for public works, reafforestation, touristic uses or other developments in areas known to be of importance for wolves;"

"1. Identify within their territories the areas with different potential value to wolf conservation, mainly of three kinds:"

"(1.a). zones where the wolf would be fully protected,"

"2. Give full legal protection or enforce existing protection of the wolf in zones referred to in paragraph 1.a. above."

D) Manifesto and Guidelines on Wolf Conservation of the Wolf Specialist Group of the International Union for the Conservation of Nature and Natural Resources (adopted by the IUCN/SSC Wolf Specialist Group at its meeting in Stockholm, Sweden on 5-7 September 1973, and incorporated as appendix to the Recommendation No. 17/1989 of the Standing Committee of the Bern Convention on the protection of the wolf (*Canis lupus*) in Europe).

"Each country should define areas suitable for the existence of wolves and enact suitable legislation to perpetuate existing wolf populations or to facilitate reintroduction. These areas would include zones in which wolves would be given full legal protection e.g. as in national parks, reserves or special conservation areas, and additionally zones within which wolf populations would be regulated according to ecological principles to minimise conflicts with other forms of land use."

"Sound ecological conditions for wolves should be restored in such areas through the rebuilding of suitable habitats and the reintroduction of large herbivores."

"In specifically designated wolf conservation areas, extensive economic development likely to be detrimental to the wolf and its habitat should be excluded."

E) Recommendation No. 59/1997 of the Standing Committee of the Bern Convention on the Drafting and Implementation of Action Plans of Wild Fauna Species (Section: Guidelines on the Drafting and Implementation of Action Plans of Wild Fauna Species/Contents)

(4.2)*"Ensure that the plan takes into consideration the following aspects:"*

(4.2.1.)*"Biological data, including distribution, habitat, population size estimates, trend, and other demographic data, migratory and dispersal patterns (if applicable), genetics, taxonomy, and ecological and ethological studies;"*

(4.2.3.)*"Evaluation of the habitat requirements of the species, including the assessment of whether present areas occupied by the species are able to support genetically viable populations;"*

(4.2.4.)*"Habitat conservation and habitat restoration in the natural range of the species (including present sites and those in which the species was present in recent times); while designing areas for conservation, corridor areas permitting genetic flow among neighboring populations should to be taken into account;"*

APPENDIX 2.3: Review of management instruments (plans, see more details in the main text of Chapter 2). Methods (Appendix 2.3.1), Sources (Appendix 2.3.2) and Results (Appendix 2.3.3).

APPENDIX 2.3.1 (METHODS)

We searched documents available in literature search engines (Google – www.google.com -, Google Scholar – www.scholar.google.com -), but also contacted at least one expert for each member country of the BC and HD with presence of the species, in order to get all the existing plans and strategies.

We classified as references on wolf habitat those related to "*human presence*" (human density, human frequentation, accessibility, disturbance), "*human infrastructures*" (specially transportation infrastructure as a source of risk and fragmentation), "*land uses/forest management*" (accounting for vegetation structure and landscape configuration), and "*general habitat*" (referred to general considerations on habitat as well as action aiming to assess habitat use and suitability maps).

APPENDIX 2.3.2 (DATA SOURCES). Plans and strategies reviewed and used in the analyses.

Austria

Wolfs management in Österreich. Grundlagen und Empfehlungen (2012). Koordinierungsstelle für den Braunbären, Luchs und Wolf. Forschungsinstitut für Wildtierkunde und Ökologie, Veterinärmedizinische Universität Wien.

Croatia

Wolf Management Plan for Croatia. Towards understanding and addressing key issues in wolf management planning in Croatia (2005). State Institute for Nature Protection, Zagreb.

Denmark

Forvaltningsplan for ulv i Danmark (2013). Miljøministeriet Naturstyrelsen, København.

Estonia

Status of Large Carnivore Conservation in the Baltic States: Large Carnivore Control and Management Plan for Estonia, 2002-2011 (2001). Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg.

Action plan for conservation and management of large carnivores (wolf *Canis lupus*, lynx *Lynx lynx*, brown bear *Ursus arctos*) in Estonia in 2012–2021 (2012). Estonian Ministry of the Environment, Tartu.

Finland

Management plan for the wolf population in Finland (2005). Ministry of Agriculture and Forestry, Helsinki.

Suomen susikannan hoitosuunnitelma (2015). Maa-ja metsätalousministeriö, Helsinki.

France

Plan d'Action Sur le Loup 2004-2008 (2004). Ministère de l'Ecologie et du Développement Durable/Ministère de l'Agriculture, de l'Alimentation, de la Pêche et des Affaires Rurales.

Plan d'Action National Sur Le Loup 2008-2012, dans le contexte Français d'une activité importante et traditionnelle d'élevage (2008). Ministère de l'Ecologie, de l'Energie, du Développement durable et de l'Aménagement du territoire/Ministère de l'Agriculture et de la Pêche.

Plan d'Action National Loup 2013-2017(2013). Ministère de l'Ecologie et du Développement Durable et de l'Énergie/Ministère de l'Agriculture, de l'Agroalimentaire et de la Forêt.

Germany

Die Rückkehr des Wolfs nach Baden-Württemberg. Handlungsleitfaden für das Auftauchen einzelner Wölfe. (2013). Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg.

Managementplan Wölfe in Bayern-Stufe 2: Stand April 2014 (2014). Bayerisches Landesamt für Umwelt, Augsburg.

Managementplan für den Wolf in Brandenburg 2013 – 2017 (2012). Ministerium für Umwelt, Gesundheit und Verbraucherschutz, Brandenburg.

Wolfsmanagement für Hessen (2015). Hessisches Ministerium für Umwelt, Klimaschutz, Landwirtschaft und Verbraucherschutz, Wiesbaden.

Managementplan für den Wolf in Mecklenburg-Vorpommern (2010). Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz, Schwerin.

Der Wolf in Niedersachsen. Grundsätze und Maßnahmen im Umgang mit dem Wolf (2010) Niedersächsisches Ministerium für Umwelt, Energie und Klimaschutz. Hannover.

Wolfsmanagementplan für NRW. Handlungsleitfaden für das Auftauchen einzelner Wölfe (2016). Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, Recklinghausen.

Managementplan für den Umgang mit Wölfen in Rheinland-Pfalz (2015). Ministerium für Umwelt, Landwirtschaft, Ernährung, Weinbau und Forsten, Mainz.

Managementplan für den Umgang mit Wölfen im Saarland (2015) Ministerium für Umwelt und Verbraucherschutz Saarland. 2015.

Managementplan für den Wolf in Sachsen (2014). Staatministerium für umwelt und Landwirtschaft, Dresden.

Managementplan für den Wolf in Thüringen (2014). Thüringer Ministerium für Umwelt, Energie und Naturschutz, Erfurt.

Hungary

Farkas (*Canis lupus*) (2004). Környezetvédelmi és Vízügyi Minisztérium, Természetvédelmi Hivatal.

Italy

Piano d'azione nazionale per la conservazione del lupo (*Canis lupus*) (2002). Ministero dell'Ambiente e della Tutella del Territorio/Istituto Nazionale per la fauna selvatica "Alessandro Ghigi".

Latvia

Status of Large Carnivore Conservation in the Baltic States: Action Plan for the Conservation of Wolf (*Canis lupus*) in Latvia (2001). Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg.

Wolf (*Canis lupus*) conservation plan (2008). Latvian State Forestry Institute "Silava".

Lithuania

Wolf (*Canis Lupus*) Protection Plan (2014). Ministry of Environment of the Republic of Lithuania.

Netherlands

Voorstel voor een wolvenplan voorNederland; versie 2.0. (2013). Alterra Wageningen UR (University & Research centre), Wageningen.

Portugal

Plano de Ação para a Conservação Lobo-ibérico em Portugal (2015, *preliminary version*). Instituto da Conservação da Natureza e das Florestas.

Slovakia

Program starostlivosti o vlka dravého (*Canis lupus*) na Slovensku (2016). State Nature Conservation of the Republic of Slovakia.

Slovenia

Strategija ohranjanja volka (*Canis lupus*) v Sloveniji in trajnostnega upravljanja z njim (2009).

Akcijski načrt za upravljanje Populacije volka (*Canis lupus*) v sloveniji Za obdobje 2013–2017 (2013). Ministry of Agriculture and the Environment.

Spain

Estrategia para la conservación y gestión del lobo (*Canis lupus*) en España (2005). Ministerio de Medio Ambiente, Madrid.

Plan de Gestión del Lobo (*Canis lupus*) para afrontar el conflicto con la ganadería extensiva en el Territorio Histórico de Álava (2010). Departamento de Medio Ambiente de la Diputación Foral de Álava, Vitoria.

Plan de Gestión del Lobo en el Principado de Asturias (2002). Consejería de Medio Ambiente del Principado de Asturias, Oviedo

II Plan de Gestión del Lobo en el Principado de Asturias (2015). Consejería de Agroganadería y Recursos Autóctonos del Principado de Asturias, Oviedo.

Plan de Xestión do lobo en Galicia (2008). Consellería de Medio Ambiente de Desenvolvemento Sostible de la Xunta de Galicia, Santiago de Compostela.

Plan de gestión del lobo en Castilla y León (2008). Consejería de Medio Ambiente de la Junta de Castilla y León, Valladolid.

Plan de gestión del lobo en Castilla y León (2016). Consejería de Fomento y Medio Ambiente de la Junta de Castilla y León.

Sweden

Åtgärdsprogram för bevarande av varg (*Canis lupus*) (2003). Environmental Protection Agency.

Nationell förvaltningsplan för varg Förvaltningsperioden 2014–2019 (2014). Environmental Protection Agency.

Switzerland

Strategie der Volkswirtschaftsdirektion über den Umgang mit dem Wolf im Kanton Bern (2007). Economic Policy Directorate.

Konzept Wolf Managementplan für den Wolf in der Schweiz (2008). Federal Department of Foreign Affairs Environment, Transport, Energy and Communications/Federal Office for the Environment/Department of Species Management.

Strategia Lupo Svizzera: Aiuto all'esecuzione dell'UFAM sulla gestione del lupo in Svizzera (2016). Federal Department of Environment, Transport, Energy and Communications/Federal Office for the Environment.

APPENDIX 2.3.3 (RESULTS). Presence of references, actions or guidelines regarding general habitat or breeding sites in wolf plans and strategies in European countries[1].

Country	Region	BC	HD	Year	References on habitat	Guidelines or Actions on habitat	Guidelines or Actions on breeding sites
Austria	-	II	IV	2012	-	-	-
Croatia	-	II	IV	2005	X	X	X
Denmark	-	II	IV	2013	X	-	-
Estonia	-	II	V	2001	-	-	-
Estonia	-	II	V	2012	X	X	-
Finland	-	-	IV, V	2005	-	-	-
Finland	-	-	IV, V	2015	-	-	-
France	-	II	IV	2004	-	-	-
France	-	II	IV	2008	-	-	-
France	-	II	IV	2013	-	-	-
Germany	B-Württenberg	II	IV	2013	-	-	-
Germany	Bayern	II	IV	2014	X	-	-
Germany	Brandenburg	II	IV	2012	X	-	-
Germany	Hessen	II	IV	2015	X	-	-
Germany	Niedersachsen	II	IV	2010	X	X	-
Germany	MVorpommern	II	IV	2010	X	-	-
Germany	N-Westfalen	II	IV	2016	-	-	-
Germany	R-Pfalz	II	IV	2015	-	-	-
Germany	Saarland	II	IV	2015	X	-	-
Germany	Sachsen	II	IV	2014	X	-	-
Germany	Thüringen	II	IV	2014	X	-	-
Hungary	-	II	IV	2004	X	X	-
Italy	-	II	IV	2002	X	X	X
Latvia[2]	-	-	V	2001	X	X	-
Latvia	-	-	V	2008	X	X	-
Lithuania	-	III	V	2014	X	X	X
The Netherlands	-	II	IV	2013	X	X	X
Portugal	-	II	IV	2015	X	X	X
Slovakia	-	-	V	2016	X	X	X
Slovenia (Strategy)	-	-	IV	2009	X	X	-
Slovenia (Plan)	-	-	IV	2014	X	X	-
Spain	-	III	IV, V	2005	X	X	-
Spain	Álava	III	V	2010	-	-	-

[1]European Union member states where the Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora applies and/or countries of the Council of Europe that ratified the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). The countries for which plans do not exist have been excluded from the table.

[2]Plan issued in frame of the project "Inventories of Species and Habitats, Development of Management Plans and Capacity Building in relation to Approximation of EU Birds and Habitats Directives" financed by the Danish Environmental Protection Agency and discussed in the 21st meeting of the Standing Committee of the Convention on The Conservation Of European Wildlife and Natural Habitats (Bern Convention) in 2001.

Country	Region	BC	HD	Year	References on habitat	Guidelines or Actions on habitat	Guidelines or Actions on breeding sites
Spain	Asturias	III	V	2002	X	X	-
Spain	Asturias	III	V	2015	X	X	-
Spain	Castilla y León	III	IV, V	2008	X	-	-
Spain	Castilla y León	III	IV, V	2016	-	-	-
Spain	Galicia	III	V	2008	X	X	-
Sweden	-	II	IV	2003	-	-	-
Sweden	-	II	IV	2014	-	-	-
Switzerland	-	II	-	2008	-	-	-
Switzerland	-	II	-	2016	-	-	-
Switzerland	Bern	II	-	2007	-	-	-

Chapter 3

Discontinued coexistence with humans as the main driver of the impact of wolves on livestock[1]

ABSTRACT

Depredation on domestic animals lies under the conflict between humans and large carnivores wherever they coexist. Limiting large carnivore populations has been regularly seen as a management strategy aiming to reduce the impact of these species on livestock and thus the potential or actual conflict. This approach necessarily assumes a positive correlation between large carnivore abundance and livestock losses. However, the generality of this assumption has never been explored, and site-specific studies regarding this issue provide disparate outcomes. In order to assess the generality of this effect, we built the most extensive dataset on wolf numbers and livestock depredations from 103 study areas from Europe and North America. We found no general relationship between wolf numbers and livestock depredations using the entire dataset or a subset of areas where wolves have been continuously present from the mid 20th century. Nonetheless, we found a significant positive correlation between the number of wolves and livestock losses in areas recolonized by wolves after its extirpation in the last decades. We argue that certain husbandry practices adopted by humans to minimize the risk of livestock depredation by wolves may be lost when wolves disappear. These practices should be promoted in detriment to other controversial strategies such as lethal control, and the forefronts of expanding populations should be prioritized areas to implement them.

[1] The following persons have contributed to the data compilation for this chapter: Vaidas Balys, Paul Frame, Yorgos Ilipopoulos, Jens Frank, Miha Krofel, Miroslav Kutal, Agnese Marino, Andrea Morehouse, Sabina Nowak, Janis Ozolins, Virginia Pimenta, Ilka Reinhardt, Robin Rigg, Valeria Salvatori, Mathias Vögeli.

Introduction

Although large carnivores are charismatic species for modern societies, with fundamental roles in ecosystem functioning (Kellert *et al.* 1996; Ripple *et al*. 2014), their predatory behaviour often represents the main factor opposing a land-sharing model for human-carnivore coexistence (López-Bao *et al.* 2017). Such predatory behaviour has triggered persecution of these species worldwide, both illegal and legally supported. Competitive persecution of large carnivores dates back to prehistoric times (Reynolds & Tapper 1996; Fritts *et al.* 2003). Since then, it has intensified with human population growth, sophistication of killing techniques and the systematization of their (often sponsored) persecution (Dannenfeldt 1982; Mech 1970). Persecution contributed largely to the general rarefaction and extirpation of large carnivores in recent times (Ripple *et al.* 2014), influencing in their behaviour too (Ordiz *et al.* 2013; Sazatornil *et al.* 2016). For example, in continental Europe, long-standing persecution resulted in population decrease and range contraction, and at the end of the 20th century large carnivores had vanished from most West European countries (Curry-Lindahl 1972; Chapron *et al.* 2014).

Among the management strategies adopted to alleviate actual and potential human-carnivore conflicts grounded on carnivore attacks on livestock, the selective and non-selective removal of predators is still prevalent worldwide. Lethal control of large carnivores is performed as a retaliatory response or as a preventive strategy to reduce potential threat on livestock (Treves & Naughton-Treves 2005). It can be executed by trained agents or integrated in other sectoral policies (e.g. hunting quotas), and the intensity of the intervention can be set upon multiple criteria (social unrest, number of livestock losses or setting population caps), which often lack supportive evidence of their effectiveness (McManus *et al*. 2015; Miller *et al*. 2016, Eklund *et al.* 2017) and data reliability (e.g., Darimont *et al*. 2018). Large carnivore removal can also have a spatial component, in which different intensities of extraction are applied to each management unit according to different population targets (Linnell *et al.* 2005). Worryingly, other strategies, such as the adoption of non-lethal damage prevention measures and low-risk husbandry practices, or proper compensation schemes are not fully integrated and implemented in management strategies yet (Nyhus *et al.* 2005; van Eeden *et al.* 2018). Lethal control is controversial and gives rise to ethical objections from opposing interest groups (Vucetich & Nelson 2017). The lack of a robust, general evidence basis on its effectiveness can further reduce social acceptability of lethal control (Treves *et al.* 2016) and affect trust on managing authorities.

While conservation and the eventual recovery of large carnivores across their former ranges are highly supported by modern societies and the scientific community, these are increasingly aware that some level of conflict is inherent to wherever large carnivores and humans coexist (Lute *et al.* 2018). The reduction of attacks on livestock is usually integrated as a fundamental pillar of carnivore conservation, aiming to keep the conflict at what is called as "sustainable" levels. While reasonable concerns are expressed on the effectiveness of killing large carnivores as a pretext to reduce livestock depredations (Treves *et al.* 2016; Eklund *et al*. 2017; van Eeden *et al*. 2018), it is frequently considered in official management strategies (Treves & Karanth 2003; Treves & Naughton-Treves 2005). The reduction of large carnivore populations through lethal control should rely on a proper policy evaluation because of its ethical dimension, social controversy, and the poor current evidential support. The current global context of range expansion of some large carnivore species in developed countries (Chapron *et al*. 2014), and foreseeable design and enforcement of policies oriented to guarantee food security under global change scenarios worldwide, suggest that the potential for intensification of the conflict in the future should not be underestimated (Baker *et al*. 2008).

Population-based lethal control implicitly assumes a positive relationship between large carnivore population size and the number of attacks on livestock. The prevalence of the lethal approach despite its controversy suggests that this relationship is perceived as necessary by the authorities and policy-makers. In contrast, evidence assessing the effectiveness of lethal control is not abundant and does not provide consistent conclusions, suggesting high context specificity (Harper *et al.* 2008; van Eeden *et al.* 2018). Limiting or reducing predator numbers has been prescribed to prevent further livestock losses (Bjorge & Gunson 1985; Bangs *et al.* 2006, Ausband *et al*. 2015; Poudyal *et al.* 2016) even if the achievement of the intended outcome has been questioned (Fernández-Gil *et al.* 2016; Treves *et al*. 2016). Other studies underline that the effect is dependent on the intensity of the measure (Bradley *et al.* 2015) or forecast negative impacts on the conservation of target species (Treves & Naughton-Treves 2005; Woodroffe & Frank 2005) and ecosystem function (Colman *et al.* 2014).

Comparative studies also point out that non-lethal methods may outcompete lethal control in effectiveness (McManus *et al*. 2015; Eklund *et al.* 2017; Miller *et al.* 2016; Van Eeden *et al* 2018). Correlations between large carnivore population size and depredations on livestock have never been explored at a scale large enough to bring some light on its generality and the suitability of lethal control as a fully transferable tool. The wolf (*Canis lupus*) is an ideal model species to understand large carnivore-human conflicts at large spatial scales because of its occurrence over a vast area, widespread depredation on livestock (Newsome *et al*. 2016), and flexibility in habitat selection, that allows this species to persist in multiple human-dominated landscapes (Llaneza *et al*. 2012; Ahmadi *et al.* 2014; Sazatornil *et al.* 2016).

Limiting predator populations is often considered as a suitable, objectively oriented policy, when reducing attacks on livestock is pursued. From a management point of view, the reduction of wolf numbers (or setting wolf population caps) is frequently considered in wolf management strategies. For example, forty-five out of 71 wolf management and conservation plans from North America and Europe (Appendix 3.1) consider the reduction of wolf numbers as an intervention to mitigate livestock-wolf conflicts and/or explicitly set goals about wolf population size (n=26), assuming a positive correlation between wolf numbers and attacks on livestock. Herein, we report a worldwide assessment of the relationship between wolf abundance and the number of livestock attacks. In order to bring generality and transferability to our results, we decontextualized the relationship between wolf numbers and the number of livestock attacks by pooling together multiple study areas (n=103; Fig. 3.1; Appendix 3.2) encompassing diverse social and ecological contexts.

The effect of wolf abundance on livestock depredations

We compiled the most extensive dataset to date containing official wolf population estimates and livestock depredations from Europe (10 European countries, or 78 European regions) and North America (10 states of the US, and 5 Canadian provinces), where reliable data on both parameters is most accessible, spanning from 2005 to 2015 (Fig. 3.1; Appendix 3.2).

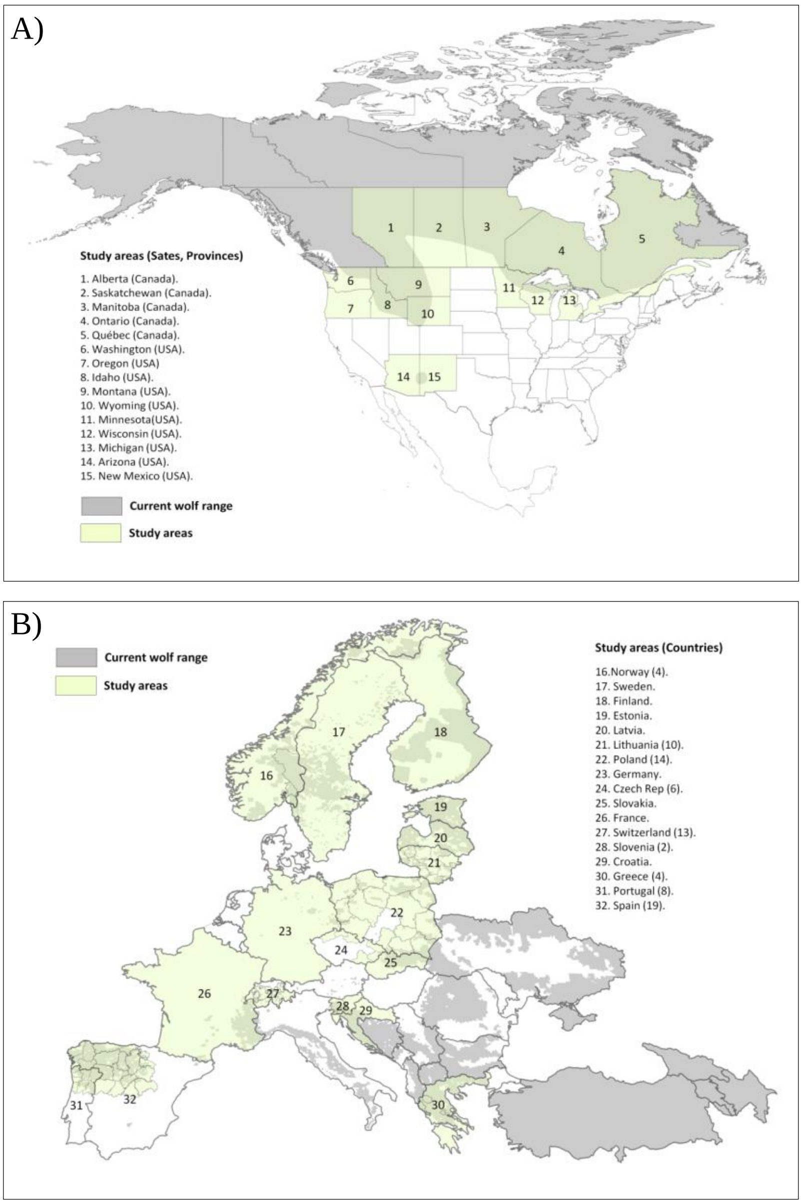


Figure 3.1: Distribution of the A) North American States (USA) and Provinces (Canada), and B) European countries from which data on wolf population and livestock losses was obtained (for map simplicity study areas corresponding to European regions below national level were represented but not listed. Numbers in brackets indicate the number of study areas within a country).

We considered the total number of livestock heads officially killed by wolves each year in each nation/region and estimates of wolf numbers (mean, minimum and maximum number of individuals in the same areas according to official sources; Appendix 3.2; 3.3). The final dataset contains information on wolf estimates and livestock losses from 393 combinations area-year including 106,520 estimated wolves and 146,573 livestock heads reported as killed by wolves for the entire time series (see Appendix 3.3).The mean number of livestock losses per area and year was 372.95 (S.E.= 53.5) (Fig. 3.2; Appendix 3.4).

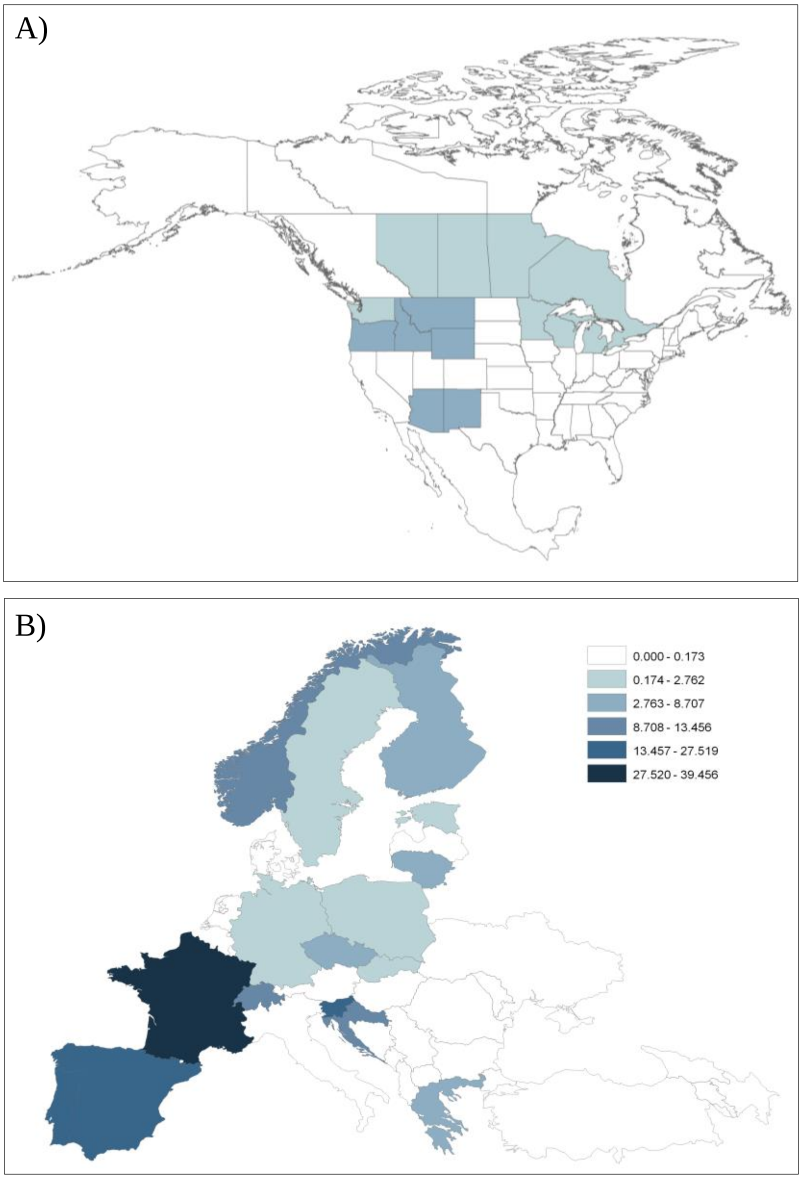


Figure 3.2. Mean livestock depredations per wolf in A) North America (States/Provinces) and B) Europe (countries).

In order to explore the relationship between wolf abundance and livestock losses, we built Bayesian latent Gaussian models using an Integrated Nested Laplace approximation (INLA) with the entire dataset to define the posterior marginal distribution of the total number of livestock heads lost to wolves as a function of wolf abundance (Appendix 3.5). In order to account for spatial and temporal autocorrelation we integrated spatiotemporal terms in the equation by setting the study area as an independent random noise variable and the year as a first order autoregressive model (Appendix 3.5). We also built partial models using separately the study areas where wolves have always been present in recent times and areas where wolf presence has been interrupted at some point in the last decades (from the mid 20th century onwards). Additionally, we built Bayesian generalized linear multilevel models in order to assess the effect of the abundance of livestock on the number of wolf depredations (Appendix 3.6).

Contrarily to the preconceived idea, overall, we found no correlation between the number of wolves and livestock losses (Fig 3.3. Appendix 3.5). Worth mentioning, the lack of such relationship is consistent across different wolf population size estimates (Appendix 3.3; Appendix 3.5).

Interestingly, we found a strong effect of the coexistence history on the relationship between wolf abundance and livestock depredations. While this relationship was not significant in areas where wolves have continuously occurred at least from the mid 20th century (n=124 area-years), we found a positive significant correlation between wolf abundance and the number of livestock depredations in areas recolonized by wolves or where they have been reintroduced after complete extirpation (n=269 area-years; Fig. 3.3; Appendix 3.5). Again, these results were not sensitive to the use of different criteria to estimate wolf numbers.

As expected, we also found a positive correlation between the number of livestock heads in an area and the number of depredations of the same species (Appendix 3.6).

Discussion

The strong correlation between wolf abundance and livestock depredations found in the recolonized areas indicates that the number of livestock losses can be influenced by wolf abundance under certain circumstances (Musiani *et al.* 2003) but such relationship cannot be generalized. Our results indicate that wherever wolves have persisted, livestock vulnerability to predators may have been kept at low levels by the continuous use of traditional husbandry practices, such as the use of fences or livestock guarding dogs (Chapron *et al.* 2014; Eklund *et al.* 2017). Thus, the persistence of carnivores might prompt farmers to keep traditional antipredator methods that explain the observed disengagement between wolf numbers and livestock losses. The observed effect is in line with other studies suggesting that certain non-lethal techniques to minimize livestock losses are an effective way to reduce accessibility to livestock by wolves (Treves *et al.* 2016; Miller *et al*. 2016; Eklund *et al.* 2017; van Eeden *et al.* 2018).

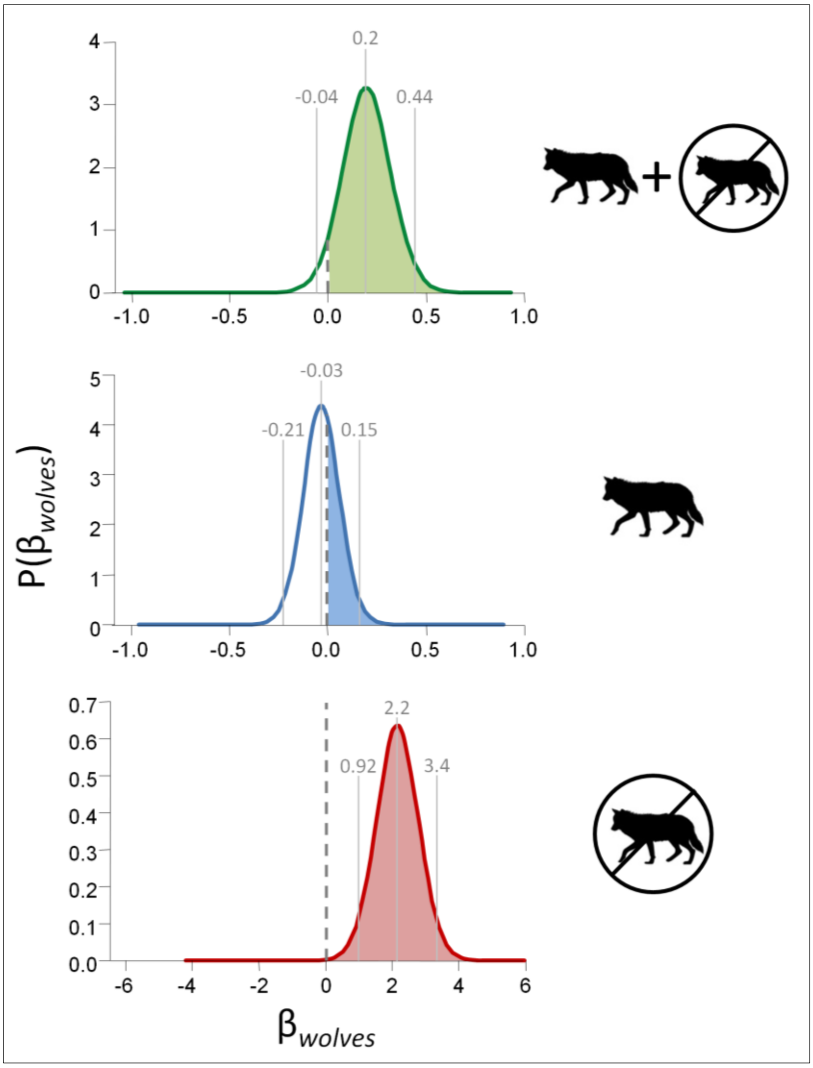


Figure 3.3: Probability distributions of the β coefficients for the number of wolves in the structured additive regression models testing the relation between wolf abundance and livestock losses. The lower graphs represent different scenarios of coexistence history: areas with permanent wolf presence in the last decades (blue) and areas recolonized by wolves after extirpation (red). The green graph is from the full model using all the data. The dashed line is set at 0 and grey numbers represent the most probable coefficient, and the lower and upper limits of the 0.025 - 0.975 interquantile interval (when 0 is within the interval the effect is considered not significant). (wolf silhouette:www.getdrawings.com).

On the contrary, in those areas where wolves were extirpated, the risk of depredation vanishes (López-Bao *et al.* 2017). Consequently, husbandry practices oriented to reduce livestock depredations lose their *raison d'être* and are often abandoned. Non-lethal strategies to deter livestock depredations are costly and could affect the economies of farmers, especially in areas of marginal productivity. Thus, despite wolves may have recolonized parts of their former distribution range (Chapron *et al.* 2014), the (re)adoption of such techniques after wolf recovery can show a strong resistance (Breitenmoser *et al.* 2005). Inexperience related with loss of skills transmission, especially where wolves have been absent for two or more generations of farmers, could also be an issue to implement effectively preventive antipredator measures even when herders show a positive attitude (Reinhardt *et al.* 2012). Finally, the loss of predatory pressure in areas were wolves were extirpated could have induced behavioural changes in stocks or favoured breeds with higher productive potential rather than attributes associated with lower vulnerability to depredation (Hansen 2001), but these factors deserve further exploration.

According to our results, as soon as newly settled wolf populations grow, increasing livestock losses are expected to occur. Strong opposition to wolves is expected in these areas (Naughton-Treves *et al.* 2003; Skogen *et al.* 2008). Although re-colonization forefronts are strategic areas for large-scale wolf recovery, they also become fertilized ground for intense wolf-human conflict which, in addition, may hinder further wolf expansion towards areas with lower potential for conflict and eventually the large-scale restitution of the functional role of wolves in ecosystems. Restoring husbandry techniques oriented to reduce attacks on livestock is expected to result in lower levels of wolf-human conflict, and may help achieve committed conservation goals at lower social costs.

Since the conflict associated to livestock depredations is one of the main drawbacks to large carnivore conservation and recovery, the generalized use of non-lethal prevention techniques is expected to improve the prospects for coexistence and increase the available space for large carnivores in human-dominated landscapes (Ogada *et al.* 2003; López-Bao *et al.* 2017). Limited resources available to reduce carnivore-livestock conflict should be diverted from lethal-control to facilitate the widespread adoption of non-lethal techniques by livestock owners (Dickman *et al.* 2011). Additional efforts should be oriented to expanding wolf populations in recently recolonized areas. In addition, prioritising damage prevention instead of lethal control requires a shift in a long-standing paradigm in areas where lethal control to reduce the wolf population is still regarded as a pivotal management approach.

The broad-scale representativeness of our data underlines the international dimension of human-carnivore (wolf) conflicts and the fact that the convenience to improve the management of this conflict is generalized and common to a large number of territories. Our study provides an example of how even consolidated and generalized practices in wildlife management can be based on inconsistent assumptions. Leading wildlife conservation and management to the sphere of science-based decision-making is necessary to get rid of flawed strategies that can be costly in terms of resources, and opportunities lost due to a lack of proper evaluation performed upon objective and representative data.

References

Ahmadi M., López-Bao, J.V., Kaboli, M. (2014). Spatial Heterogeneity in Human Activities Favors the Persistence of Wolves in Agroecosystems. *PLoS ONE* 9: e108080.

Ausband, D.E., Stansbury, C.R., Stenglein, J.L., Struthers, J.L., Waits, L.P. (2015) Recruitment in a social carnivore before and after harvest. *Animal Conservation* 18: 415–423.

Bangs, E.M. Jimenez, C. Niemeyer, J. Fontaine, M. Collinge, R. Krischke, L. Handegard, J. Shivik, C. Sime, S. Nadeau, C. Mack, D. Smith, V. Asher, & Stone, S. (2006). Non-lethal and lethal tools to manage wolf-livestock conflict in the northwestern United States. *Proceedings of Vertebrate Pest Conference* 22:7–16.

Baker, P.J., Boitani, L., Harris, S., Saunders, G., & White, P.C. (2008). Terrestrial carnivores and human food production: impact and management. *Mammal Review* 38: 123-166.

Bjorge, R.R & Gunson, J. (1985). Evaluation of Wolf Control to Reduce Cattle Predation in Alberta. *Journal of Range Management* 38: 483-487.

Bradley, E.H., Robinson, H.S., Bangs, E.E., Kunkel, K., Jimenez, M.D., Gude, J.A. & Grimm, T. (2015). Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. *Journal of Wildlife Management* 79: 1337-1346.

Breitenmoser, U., Angst, C., Landry, J.M., Breitenmoser-Wursten, C., Linnell, J.D.C. & Weber, J.M. (2005). Non-lethal techniques for reducing depredation. In: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds). People and wildlife: conflict or coexistence? 49–61. Cambridge: Cambridge University Press.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López- Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517-1519.

Colman, N.J., Gordon, C.E., Crowther, M.S., & Letnic, M. (2014). Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceeding of the Royal Society B* 281: 20133094.

Curry-Lindahl, K. (1972). Bears: Their Biology and Management. Pp: 74-80 *In:* A Selection of Papers from the Second International Conference on Bear Research and Management, Calgary, Alberta, Canada, 6-9 November 1970 (Vol.2). IUCN Publications New Series no. 23.

Darimont, C.T., Paquet, P.C., Treves, A., Artelle, K.A., & Chapron, G. (2018). Political populations of large carnivores. *Conservation Biology* 32: 747-749.

Dickman, A.J., MacDonald, E.A. & MacDonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *PNAS* 108: 13937-13944.

Eklund, A., López-Bao, J.V., Tourani, M., Chapron, G., & Frank, J. (2017). Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7: 2097.

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M. (2016). Conflict Misleads Large Carnivore Management and Conservation: Brown Bears and Wolves in Spain. *PLoS ONE* 11: e0151541.

Hansen, I., Christiansen, F., Hansen, H.S., Braastad, B., & Bakken, M. (2001). Variation in behavioural responses of ewes towards predator-related stimuli. *Applied Animal Behaviour Science* 70: 227-237.

Harper, W.J., Mech, L.D. & Weisberg, S. (2008). Effectiveness of Lethal, Directed Wolf-Depredation Control in Minnesota. *Journal of Wildlife Management* 72: 778–784.

Kellert, S.R., Black, M., Rush, C.R. & Bath, A.J. (1996). Human Culture and Large Carnivore Conservation in North America. *Conservation Biology* 10: 977-990.

Linnell, J.D., Nilsen, E.B., Lande, U.S., Herfindal, I., Odden, J., Skogen, K., Andersen, R., & Breitenmoser, U. (2005). Zoning as a means of mitigating conflicts with large carnivores: principles and reality. Pp: 162-175 *In*: Woodroffe, R., Thirgood, S., Rabinowitz, A., (Eds.) People and Wildlife: Conflict or Co-Existence? Cambridge Univeristy Press. Cambridge, UK.

Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions* 18: 459-469.

López-Bao, J.V., Bruskotter, J., & Chapron, G. (2017). Finding space for large carnivores. *Nature Ecology & Evolution* 1 n0140.

Lute, M.L., Carter, N.H., López-Bao, J.V., Linnell, J.D.C. (2018). Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biological Conservation* 218: 223-232.

McManus, J., Dickman, A., Gaynor, D., Smuts, B., & Macdonald, D. (2015). Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. *Oryx* 49: 687-695.

Mech, L.D. (1970). The wolf, the ecology and behaviour of an endangered species. Natural History Press, Doubleday Publishing Co., New York.

Miller, J.R., Stoner, K.J., Cejtin, M.R., Meyer, T.K., Middleton, A.D. & Schmitz, O.J. (2016). Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin* 40: 806-815.

Musiani, M., Mamo, C., Boitani, L., Callaghan, C., Gates, C.C., Mattei, L., Visalberghi, E., Btreck, S., & Volpi, G. (2003). Wolf Depredation Trends and the Use of Barriers to Protect Livestock in Western North America. *Conservation Biology* 17: 1-10.

Naughton-Treves, L., Grossberg, R., & Treves, A. (2003). Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. *Conservation Biology* 17: 1500-1511.

Nyhus, P.J., Osofsky, S.A., Ferraro, P., Fischer, H., & Madden, F. (2005). Bearing the costs of human-wildlife conflict: the challenges of compensation schemes. Pp: 107-121 *In:* Woodroffe, R., Thirgood, S.J., & Rabinowitz, A. (Eds.). People and Wildlife: Conflict or Coexistence? Cambridge University Press. Cambridge, UK.

Ogada, M.O., Woodroffe, R., Oguge, N.O., & Frank, L. G. (2003). Limiting Depredation by African Carnivores: The Role of Livestock Husbandry. *Conservation Biology* 17: 1521-1530.

Ordiz, A., Støen, O., Sæbø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., Swenson, J.E. & Rhodes, J. (2013). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology* 50: 306-314.

Poudyal, N., Baral, N., Asah, S.T. (2016). Wolf Lethal Control and Livestock Depredations: Counter-Evidence from Respecified Models. *PLOS ONE* 11: e0148743.

Reinhardt, I., Rauer, G., Kluth, G., Kaczensky, P., Knauer, F., & Wotschikowsky, U. (2012). Livestock protection methods applicable for Germany - a country newly recolonized by wolves. *Hystrix Italian Journal of Mammalogy* 23: 62-72.

Reynolds, J.C. & Tapper, S.C. (1996). Control of mammalian predators in game management and conservation. *Mammal Review* 26: 127-155.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., and Wirsing, A.J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science* 343(6167).

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand H., Unger, D., Wabakken, P., & López-Bao, J.V. (2016). The role of human-related risk in breeding site selection by wolves. *Biological Conservation* 201: 103-110.

Skogen, K., Mauz, I., & Krange, O. (2008). Cry Wolf! Narratives of Wolf Recovery in France and Norway. *Rural Sociology* 73: 105-133.

Treves, A. & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* 17: 1491-1499.

Treves, A. & Naughton-Treves, L. (2005). Evaluating lethal control in the management of human–wildlife conflict. People and Wildlife, Conflict or Coexistence? (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 86–106. Cambridge University Press, Cambridge, UK.

Treves, A., Krofel, M., & McManus J. (2016). Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment* 14:380-388.

van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G. & Newsome, T.M. (2018). Managing conflict between large carnivores and livestock. *Conservation Biology* 32: 26-34.

Vucetich, J., & Nelson, M.P. (2017). Wolf Hunting and the Ethics of Predator Control. Pp: 411-432 *In*: Kalof, L. (Ed.) The Oxford Handbook of Animal Studies. Oxford University Press, New York.

Woodroffe, R., & Frank, L. (2005). Lethal control of African lions (*Panthera leo*): Local and regional population impacts. *Animal Conservation* 8: 91-98.

APPENDIX CHAPTER 3

(Discontinued coexistence with humans as the main driver of the impact of wolves on livestock)

APPENDIX 3.1: Review of wolf management/action plans assuming wolf population reduction or limitation as a way to mitigate conflict (not necessarily within the objectives of the plan).

Wolf Plan Range	Continent	Year issued	Population goal	Limit wolf population
Álava	Europe	2010	-	X
Alberta	North America	1991	4,000	X
Asturias	Europe	2002	-	X
Asturias	Europe	2015	-	X
Austria	Europe	2012	-	-
Baden-Württenberg	Europe	2013	-	-
Bayern	Europe	2014	-	-
Bern	Europe	2007	-	-
Blackfeet IR	North America	2008	-	X
Brandenburg	Europe	2012	-	-
British Columbia	North America	2014	-	X
Castilla y León	Europe	2016	-	X
Castilla y León	Europe	2008	149 packs	X
Croatia	Europe	2005	-	X
Denmark	Europe	2013	-	-
Eastern Wolf Range	North America	2017	2,500-4,545	-
Estonia	Europe	2001	100-200	X
Estonia	Europe	2012	150-350	X
Finland	Europe	2015	-	X
Finland	Europe	2005	Yes, but undefined	X
Flathead IR	North America	2009	-	X
France	Europe	2004	-	X
France	Europe	2008	-	X
France	Europe	2013	-	X
France	Europe	2018	500	X
Galicia	Europe	2008	similar to current population (420-625)	X
Hessen	Europe	2015	-	-
Hungary	Europe	2004	-	-
Idaho	North America	2002	15 packs	X
Idaho	Europe	2008	15packs	X
Italy	Europe	2002	-	-
Latvia	Europe	2008	300-500	X
Latvia	Europe	2001	300-400	X

Lithuania	Europe	2014	250	X
Mecklenburg-Vorpommern	Europe	2010	-	-
Mexican Wolf	North America	82	-	-
Mexican Wolf	North America	98	100	-
Mexican Wolf	North America	17 (review)	320 (USA); 170 (Mex)	-
Michigan	North America	2008	-	X
Michigan	North America	2015	-	X
Michigan	North America	1997	200	-
Minnesota	North America	2001	1,600	X
Montana	North America	2004	14-17 packs	X
Niedersachsen	Europe	2010	-	-
Nordrhein-Westfalen (NRW)	Europe	2016	-	-
Northern Rockies WRA	North America	1987	30	-
Ontario	North America	2005	-	-
Oregon	North America	2005(2010)	7 packs	X
Oregon	North America	2017	7 packs	X
Portugal	Europe	2017	-	-
Rheinland-Pfalz	Europe	2015	-	-
Saarland	Europe	2015	-	-
Sachsen	Europe	2014	-	-
Sachsen	Europe	2009	-	-
Sachsen Anhalt	Europe	2008	-	-
Slovakia	Europe	2016	-	X
Slovenia	Europe	2009	-	-
Slovenia	Europe	2013	-	X
Spain	Europe	2005	-	X
Sweden	Europe	2003	200	-
Sweden	Europe	2014	270	-
Switzerland	Europe	2008	-	-
Switzerland	Europe	2016	-	X
The Netherlands	Europe	2013	-	-
Thüringen	Europe	2014	-	-
Utah	North America	2004	-	-
Washington	North America	2011	15 pairs	-
Wind River IR	North America	2007	-	X
Wisconsin	North America	1999	350	X
Wyoming	North America	2011	100 (outside YNP and Wind River I.R.)	X
Yukon	North America	2012	-	-

APPENDIX 3.2: Preparation of the wolf/livestock damage dataset: Study areas, data sources and criteria for estimation of wolf population data and livestock losses data.

STUDY AREAS

List of study areas included in the dataset.

Study area	Country
Alberta	Canada
Manitoba	Canada
Ontario	Canada
Quèbec	Canada
Saskatchewan	Canada
Croatia	Croatia
Hradec kralove	Czech Republic
Liberec	Czech Republic
Moravian Silesian	Czech Republic
S. Moravian	Czech Republic
Usti nad Labem	Czech Republic
Zlin	Czech Republic
Estonia	Estonia
Finland	Finland
France	France
Germany	Germany
Domokos	Greece
Greece	Greece
Northern Pindos N.P.	Greece
Thesprotia	Greece
Latvia	Latvia
Alytaus	Lithuania
Kauno	Lithuania
Klaipèdos	Lithuania
Marijampolės	Lithuania
Panevėžio	Lithuania
Šiaulių	Lithuania
Tauragės	Lithuania
Telšių	Lithuania
Utenos	Lithuania
Vilniaus	Lithuania
Akershus	Norway
Hedmark	Norway
Norway (other)	Norway
Østfold	Norway

Study area	Country
Dolnośląskie	Poland
Kujawsko-Pomorskie	Poland
Lubelskie	Poland
Lubuskie	Poland
Małopolskie	Poland
Mazowieckie	Poland
Podkarpackie	Poland
Podlaskie	Poland
Pomorskie	Poland
Śląskie	Poland
Świętokrzyskie	Poland
Warmińsko-Mazurskie	Poland
Wielkopolska	Poland
Zachodniopomorskie	Poland
Aveiro	Portugal
Braga	Portugal
Bragança	Portugal
Guarda	Portugal
Porto	Portugal
Viana do Castelo	Portugal
Vila Real	Portugal
Viseu	Portugal
Slovakia	Slovakia
E. Slovenia	Slovenia
W. Slovenia	Slovenia
Asturias	Spain
Ávila	Spain
Burgos	Spain
Cantabria	Spain
Coruña	Spain
Guadalajara	Spain
León	Spain
Lugo	Spain
Madrid	Spain
Ourense	Spain
Palencia	Spain
Pontevedra	Spain
Rioja, La	Spain
Salamanca	Spain
Segovia	Spain
Soria	Spain
Valladolid	Spain
Basque Country	Spain
Zamora	Spain

Study area	Country
Sweden	Sweden
Bern	Switzerland
Fribourg	Switzerland
Glarus	Switzerland
Grisons	Switzerland
Lucerne	Switzerland
Nidwalden	Switzerland
Obwalden	Switzerland
Saint Gallen	Switzerland
Schwiz	Switzerland
Ticino	Switzerland
Uri	Switzerland
Valais	Switzerland
Vaud	Switzerland
Arizona	USA
Idaho	USA
Michigan	USA
Minnesota	USA
Montana	USA
New Mexico	USA
Oregon	USA
Washington	USA
Wisconsin	USA
Wyoming	USA

DATA SOURCES

Data sources for wolf population estimates and livestock depredations to wolves (study areas sorted in alphabetical order).

ALBERTA (CANADA)

Wolf population estimates:
Cluff, D. Status of wolves in Canada: 2013 provincial/territorial survey. International Wolf Symposium. Duluth, Minnesota, October 10-13, 2013 (Data provided by the author).

Livestock depredationss:
Data provided by the Alberta Environment and Parks and The Alberta Conservation Association.

ARIZONA/N MEXICO (USA)

Wolf population estimates:
https://www.fws.gov/southwest/es/mexicanwolf/pdf/MW_popcount_web.pdf

Livestock depredations:
Data retrieved from the following reports
(https://www.fws.gov/southwest/es/mexicanwolf/):

2006: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program. Progress Report #9, Reporting Period: January 1 – December 31, 2006. 55pp.

2007: Arizona Game and Fish Department, New Mexico Department of Game and Fish, U.S. Department of Agriculture - Animal and Plant Health Inspection Service - Wildlife Services, U.S. Fish and Wildlife Service, & White Mountain Apache Tribe. Mexican Wolf Blue Range Reintroduction Project Interagency Field Team Annual Report Reporting Period: January 1 – December 31, 2007. 44pp.

2008: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #11Reporting Period: January 1 – December 31, 2008. 55pp.

2009: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #12 Reporting Period: January 1 – December 31, 2009. 54pp..

2010: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #13. Reporting Period: January 1 – December 31, 2010. 55pp.

2011: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #14 Reporting Period: January 1 – December 31, 2011. 63pp.

2012: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #15 Reporting Period: January 1 – December 31, 2012. 66pp.

2013: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #16 Reporting Period: January 1 – December 31, 2013. 70pp.

2014: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #17 Reporting Period: January 1 – December 31, 2014. 74pp.

2015: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #18 Reporting Period: January 1 – December 31, 2015. 57pp.

2016: U.S. Fish and Wildlife Service, Arizona Game and Fish Department, New Mexico Department of Game and Fish, USDA-APHIS Wildlife Services, US Forest Service, & White Mountain Apache Tribe. Mexican Wolf Recovery Program: Progress Report #19 Reporting Period: January 1 – December 31, 2016. 58pp.

ASTURIAS (SPAIN)

Wolf population estimates and livestock depredations:
Data provided by the Regional Government of Asturias.

BASQUE COUNTRY (SPAIN)

Wolf population estimates
Sáenz de Buruaga, M.; Campos, M.A., Canales, F., Hidalgo, S. y Calvete, G. Censo de lobo (Canis lupus) en la Comunidad Autónoma del País Vasco 2014. Government of the Vasque Country, Provincial Delegation of Álava and Provincial Delegation of Bizkaia. 105pp.

Livestock losses:
Data provided by the Regional Government of the Basque Country.

CANTABRIA (SPAIN)

Wolf population estimates:
Censo 2012-2014 de Lobo Ibérico (*Canis lupus*, Linnaeus, 1758) en España. Ministry of Agriculture, Food, and Environment, Government of Spain.

Livestock depredations:
Data provided by the Government of the Autonomous Region of Cantabria.

CASTILLA-LA MANCHA (SPAIN)

Wolf population estimates:
Blanco, J.C. (TRAGSATEC). (2015). Apoyo para la cooordinación técnico-científica del censo de lobo ibérico en la comunidad autónoma de Castilla-La Mancha. 48pp.

Livestock depredations:
Data provided by the Government of the Autonomous Region of Castilla-La Mancha.

CASTILLA Y LEÓN (SPAIN)

Wolf population estimates and livestock depredations:
Data provided by the Regional Government of Castilla y León.

CROATIA

Wolf population estimates and livestock depredations:
State Institute For Nature Protection, Zagreb, Croatia.

Izvješće o stanju populacije vuka u Hrvatskoj u 2014. Godini. Zagreb, Croatia.

CZECH REPUBLIC (ALL REGIONS)

Wolf population estimates and livestock depredations
Data provided by Miroslav Kutal

DOMOKOS (GREECE)

Wolf population estimates:
Iliopoulos Y, Petridou M., Lazarou Y., Selinides M. (2012). Wolf (*Canis lupus* L.) activity patterns in Central and Northern Greece studied with satellite telemetry. International Congress on the Zoogeography, Ecology and Evolution of Southeastern Europe and the Eastern Mediterranean. June 18 -22, Athens, Greece.

Livestock depredations:
Data provided by the Hellenic Farmers Insurance Organization (ELGA).

ESTONIA

Wolf population estimates and livestock depredations:
Action plan for conservation and management of large carnivores (wolf *Canis lupus*, lynx *Lynx lynx*, brown bear *Ursus arctos*) in Estonia in 2012–2021 (2012). Estonian Ministry of the Environment, Tartu.

FINLAND

Wolf population estimates:
Natural Resources Institute of Finland. Helsinki, Finland.
(http://riistahavainnot.fi/suurpedot/kannanarviointi/lausunnot)

Livestock depredations:
Data provided by the Ministry of Agriculture and Forestry (Game animal damages register).

FRANCE

Wolf population estimates:
Duchamp, C., Chapron, G., Gimenez, O., Robert, A., Sarrazin, F., Beudels-Jamar, R., Le Maho, Y., (2017). Expertise collective scientifique sur la viabilité et le devenir de la population de loups en France à long terme. Coordinated by ONCFS-MNHN: Guinot-Ghestem, M., Haffner, P., Marboutin, E., Rousset, G., Savoure-Soubelet, A., Siblet, J.P., Trudelle, L. Technical Report, 92 pp.

Livestock losses:
Data retrieved from http://www.auvergne-rhone-alpes.developpement-durable.gouv.fr/protocole dommages-a3854.html

GALICIA (SPAIN)

Wolf population estimates:
Censo 2012-2014 de Lobo Ibérico (*Canis lupus*, Linnaeus, 1758) en España. Ministry of Agriculture, Food, and Environment, Government of Spain.

Livestock depredations:
Data provided by the Government of the Autonomous Region of Galicia.

GERMANY

Wolf population estimates and livestock depredations
Data provided by Ilka Rheinhardt

GREECE

Wolf population estimates:
Iliopoulos, Y., Astaras, C., Petridou, M., Pylidis, Ch., Sideri, E., Giannakopoulos, A., Lazarou, Y. (2016)Estimates of population size and distribution area of wolves (*Canis lupus*) in Greece based on multimethod presence detection. 8th Congress of Hellenic Ecological Society. 20-23 October 2016, Thessaloniki, Greece (oral presentation).

Livestock depredations:
Data provided by the Hellenic Farmers Insurance Organization (ELGA).

IDAHO (USA)

Wolf Population estimates and Livestock depredations:
Data retreived from the following reports:

2005: Nadeau, M.S., Mack, C., Holyan, J., Husseman, J., Lucid, M., & Thomas, B. 2006. Wolf conservation and management in Idaho; progress report 2005. Idaho Department of Fish and Game. Lapwai, ID. 61 pp.

2006: Nadeau, M.S., Mack, C., Holyan, J., Husseman, J., Lucid, M., Frame, P., & Thomas, B. 2007. Wolf conservation and management in Idaho; progress report 2006. Idaho Department of Fish and Game. Lapwai, ID. 73 pp.
U.S. Fish and Wildlife Service, Nez Perce Tribe, National Park Service, Montana Fish, Wildlife & Parks, Idaho Fish and Game, and USDA Wildlife Services. 2007. Rocky Mountain Wolf Recovery 2006 Annual Report. In: Sime C.A., & Bangs, E.E. (Eds.). USFWS, Ecological Services, Helena, MT. 235pp.

2007: Nadeau, M.S., Mack, C., Holyan, J., Husseman, J., Lucid, M., Thomas, B., & Spicer, D. 2008. Wolf conservation and management in Idaho; progress report 2007. Idaho Department of Fish and Game. Boise, Idaho; Nez Perce Tribe, Lapwai, ID. 73 pp.

2008: Nadeau, M.S., Mack, C., Holyan, J., Husseman, J., Lucid, M., Spicer, D., & Thomas, B. 2009. Wolf conservation and management in Idaho; progress report 2008. Idaho Department of Fish and Game. Boise, Idaho; Nez Perce Tribe, Lapwai, ID. 106 pp.
2009: Mack, C., Rachael, J., Holyan, J., Husseman, J., Lucid, M., & Thomas, B. 2010. Wolf Conservation and management in Idaho; progress report 2009. Nez Perce Tribe Wolf Recovery Project, P.O. Box 365, Lapwai, Idaho; Idaho Department of Fish and Game, 600 South Walnut, Boise, ID. 67pp.
2010: Holyan, J., Holder, K., Cronce, J., & Mack, C. 2011. Wolf conservation and management in Idaho; progress report 2010. Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 90 pp.
2011: Idaho Department of Fish and Game and Nez Perce Tribe. 2012. 2011 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho; Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 94 pp.
2012: Idaho Department of Fish and Game and Nez Perce Tribe. 2013. 2012 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho; Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 72 pp.
2013: Idaho Department of Fish and Game and Nez Perce Tribe. 2014. 2013 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho; Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 74 pp.
2014: Idaho Department of Fish and Game and Nez Perce Tribe. 2015. 2014 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho; Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 70 pp.
2015: Idaho Department of Fish and Game and Nez Perce Tribe. 2016. 2015 Idaho wolf monitoring progress report. Idaho Department of Fish and Game, Boise, Idaho; Nez Perce Tribe Wolf Recovery Project, Lapwai, ID. 71 pp.

LATVIA

Wolf population estimates and livestock depredations
Data provided by Janis Ozolins

LITHUANIA (ALL REGIONS)

Wolf Population estimates:
http://www.am.lt/VI/

Livestock depredations:
Data from Official livestock registry (http://www.vic.lt/), provided by Vaidas Balys.

MADRID (SPAIN)

Wolf population estimates and livestock depredations:
Data provided by the Government of the Autonomous Region of Madrid.

MANITOBA (CANADA)

Wolf population estimates:
Cluff, D. (2013). Status of wolves in Canada: 2013 provincial/territorial survey. International Wolf Symposium. Duluth, Minnesota, October 10-13, 2013 (Data provided by the author).

Data provided by the Big Game Unit, Wildlife and Fisheries Branch, Manitoba Sutainable Development, Government of Manitoba.

Livestock depredations:
Data provided by the Wildlife and Fisheries Branch, Manitoba Sutainable Development, Government of Manitoba.

MICHIGAN (USA)

Wolf population estimates:
Data retrieved from https://www.fws.gov/midwest/wolf/aboutwolves/mi_wi_nos.htm

Livestock depredations:
Data provided by the Michigan Department of Natural Resources.

MINNESOTA (USA)

Wolf population estimates:
Data retrieved from https://www.fws.gov/midwest/wolf/aboutwolves/mi_wi_nos.htm

Livestock depredations:
Data provided by Minnesota Department of Agriculture

MONTANA (USA)

Livestock depredations and Wolf Population estimates:
Data retrieved from the following reports:

2005: Sime, C. A., Asher, V., Bradley, L., Laudon, K., Ross, M., Trapp, J., & Handegard, L. 2006. Montana gray wolf conservation and management 2005 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 95pp.
2006: Sime, C. A., Asher, V., Bradley, L., Laudon, K., Ross, M., Trapp, J., Atkinson, M., Handegard, L & Steuber, J. 2007. Montana gray wolf conservation and management 2006 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 119 pp.
2007: Sime, C. A., Asher, V., Bradley, L., Laudon, K., Ross, M., Trapp, J., Atkinson, M., & Steuber, J. 2008. Montana gray wolf conservation and management 2007 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 137 pp.
2008: Sime, C. A., Asher, V., Bradley, L., Laudon, K., Lance, N., Ross, M., & Steuber, J. 2009. Montana gray wolf conservation and management 2008 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 154 pp.

2009: Sime, C. A., Asher, V., Bradley, L., Laudon, K., Lance, N., Ross, M., & Steuber, J. 2010. Montana gray wolf conservation and management 2009 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 173 pp.
2010: Sime, C. A., Asher, V., Bradley, L., Lance, N., Laudon, K., Ross, M., Nelson, A., & Steuber., J. 2011. Montana gray wolf conservation and management 2010 annual report. Montana Fish, Wildlife & Parks. Helena, MT. 168 pp.
2011: Hanauska-Brown, L., Bradley, L., Gude, J., Lance, N., Laudon, K., Messer, A., Nelson, A., Ross, M., & Steuber, J. 2012. Montana Gray Wolf Conservation and Management 2011 Annual Report. Montana Fish, Wildlife & Parks. Helena, MT. 54 pp.
2012: Bradley, L., Gude, J., Lance, N., Laudon, K., Messer, A., Nelson, A., Pauley, G., Ross, M., Smucker, T. & Steuber, J. 2013. Montana Gray Wolf Conservation and Management 2012 Annual Report. Montana Fish, Wildlife & Parks. Helena, MT. 55 pp.
2013: Bradley, L., Gude, J., Lance, N., Laudon, K., Messer, A., Nelson, A., Pauley, G., Podruzny, K., Ross, M., Smucker, T. & Steuber, J. 2014. Montana Gray Wolf Conservation and Management. 2013 Annual Report. Montana Fish, Wildlife & Parks. Helena, MT. 54 pp.
2014: Bradley, L., Gude, J., Lance, N., Laudon, K., Messer, A., Nelson, A., Pauley, G., Ross, M., Smucker, T., Steuber, J. & Vore, J. 2015. Montana Gray Wolf Conservation and Management. 2014 Annual Report. Montana Fish, Wildlife & Parks. Helena, MT. 60 pp.
2015: Coltrane, J., Gude, J., Inman, B., Lance, N., Laudon, K., Messer, A., Nelson, A., Parks, T., Ross, M., Smucker, T., Steuber, J. & Vore, J. 2015. Montana Gray Wolf Conservation and Management 2015 Annual Report. Montana Fish, Wildlife & Parks. Helena, MT. 74pp.

NORWAY (ALL REGIONS)

Wolf population estimates:
Data retrieved from the following reports:

2005: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., & Kojola, I. 2006. Ulv i Skandinavia: Statusrapport for vinteren 2005-2006. Høgskolen i Hedmark Oppdragsrapport nr. 2-2006. 43pp.
2006: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., Svensson, L., & Kojola, I. 2007. Ulv i Skandinavia: Statusrapport for vinteren 2006-2007. Høgskolen i Hedmark Oppdragsrapport nr. 6-2007. 50pp.
2007: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., Svensson, L., & Kojola, I. 2008. Ulv i Skandinavia: Statusrapport for vinteren 2007-2008. Høgskolen i Hedmark Oppdragsrapport nr. 6-2008. 54pp.
2008: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., Maartmann, E., Svensson, L., & Kojola, I. 2009. Ulv i Skandinavia: Statusrapport for vinteren 2008-2009. Høgskolen i Hedmark Oppdragsrapport nr. 6-2009. 51pp.
2009: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., Maartmann, E., Svensson, L., Flagstad, Ø., Hedmark, E., Liberg, O. & Kojola, I. 2010. Ulv i Skandinavia: Statusrapport for vinteren 2009-2010. Høgskolen i Hedmark Oppdragsrapport nr. 4-2010. 58pp.
2010: Wabakken, P., Aronson, Å., Strømseth, T., Sand H., Maartmann, E., Svensson, L., Åkesson, M., Flagstad, Ø., Liberg, O. & Kojola, I. 2011. Ulv i Skandinavia: Statusrapport for vinteren 2010-2011. Høgskolen i Hedmark Oppdragsrapport nr. 1-2011. 62pp.
2011: Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T., Flagstad, Ø., Åkesson, M., & Zetterberg, A. 2012. Ulv i Skandinavia og Finland: Sluttrapport for

bestandsovervåking av ulv vinteren 2011-2012. Høgskolen i Hedmark Oppdragsrapport nr. 5-2012. 46pp.
2012: Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T., Flagstad, Ø., Åkesson, M., & Zetterberg, A. 2013. Ulv i Skandinavia og Finland: Sluttrapport for bestandsovervåking av ulv vinteren 2012-2013. Høgskolen i Hedmark Oppdragsrapport nr. 5-2013. 34pp.
2013: Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T., Flagstad, Ø., & Åkesson, M. 2014. Ulv i Skandinavia og Finland: Sluttrapport for bestandsovervåking av ulv vinteren 2013-2014. Høgskolen i Hedmark Oppdragsrapport nr. 11-2014. 40pp.
2014: Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., & Flagstad, Ø., 2015. Inventering av varg vintern 2014-2015. Inventeringsresultat för stora rovdjur i Skandinavien 1-2015. Grimsö, Sweden. 52pp.
2015: Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M., & Flagstad, Ø. 2016. Bestandsovervåking av ulv vinteren 2015-2016. Bestandsstatus for store rovdyr i Skandinavia 1-2016. Grimsö, Sweden. 49 pp.

Livestock depredations:
Data provided by the Wildife Section, Norwegian Environment Agency.

ONTARIO

Wolf population estimates:
Cluff, D. (2013). Status of wolves in Canada: 2013 provincial/territorial survey. International Wolf Symposium. Duluth, Minnesota, October 10-13, 2013 (Data provided by the author).

Livestock depredations:
Data provided by the Rural Program Branch, Ontario Ministry of Agriculture, Food and Rural Affairs.

OREGON (USA)

Livestock depredations and wolf population estimates:
(https://www.dfw.state.or.us/wolves/docs/oregon_wolf_program/2011_Wolf_Conservation_Management_Plan_Annual_Report.pdf).

2011: Oregon Department of Fish and Wildlife. Oregon Wolf Conservation and Management 2011 Annual Report.
2012: Oregon Department of Fish and Wildlife. 2013. Oregon Wolf Conservation and Management 2012 Annual Report. Oregon Department of Fish and Wildlife, Salem, OR.
2013: Oregon Department of Fish and Wildlife. 2014. Oregon Wolf Conservation and Management 2013 Annual Report. Oregon Department of Fish and Wildlife, Salem, OR.
2014: Oregon Department of Fish and Wildlife. 2015. Oregon Wolf Conservation and Management 2014 Annual Report. Oregon Department of Fish and Wildlife, Salem, OR.
2015: Oregon Department of Fish and Wildlife. 2016. Oregon Wolf Conservation and Management 2015 Annual Report. Oregon Department of Fish and Wildlife, Salem, OR.
2016: Oregon Department of Fish and Wildlife. 2017. Oregon Wolf Conservation and Management 2016 Annual Report. Oregon Department of Fish and Wildlife, Salem, OR.

PINDUS N.P. (GREECE).

Wolf population estimates:
"Pindus National Park". Pp. 100 *In*: Special Environmental study (monitoring) of the Northern Pindus National Park. Callisto NGO, Management authority of Northern Pindus National Park.

Livestock depredations:
Data provided by the Hellenic Farmers Insurance Organization (ELGA).

POLAND (ALL REGIONS)

Wolf population estimates and livestock depredations
Data provided by Sabina Nowak.

PORTUGAL (ALL REGIONS)

Wolf population estimates and livestock depredations:
Data provided by Instituto da Conservação da Natureza e das Florestas, I.P.

QUÉBEC (CANADA)

Wolf population estimates:
Cluff, D. (2013). Status of wolves in Canada: 2013 provincial/territorial survey. International Wolf Symposium. Duluth, Minnesota, October 10-13, 2013 (Data provided by the author).

Livestock depredations:
Data provided by the Ministère des Forêts, de la Faune et des Parcs.

RIOJA, LA (SPAIN)

Wolf population estimates and livestock depredations:
Data provided by the Regional Government of La Rioja.

SASKATCHEWAN (CANADA)

Wolf population estimates:
Cluff, D. (2013). Status of wolves in Canada: 2013 provincial/territorial survey. International Wolf Symposium. Duluth, Minnesota, October 10-13, 2013 (Data provided by the author).

Livestock depredations:
Data provided by the Saskatchewan Crop Insurance Corporation

SLOVAKIA

Wolf population estimates:

Data provided by the Slovak Wildlife Society.

Livestock depredations:
Data provided by the National Forestry Centre.

SLOVENIA (ALL REGIONS)

Wolf population estimates:
Data provided by Slovenia Forest Service, Ljubljana, Slovenia.

Livestock *depredations*:
Data provided by Agencija Republike Slovenije za Okolje, Ljubljana, Slovenia
https://sirena.arso.gov.si/

SWEDEN

Wolf population estimates:
Data provided by Jens Frank

Livestock depredations:
Frank, J., Månsson J., & Zetterberg, A. (2016). Viltskadestatistik 2015: Skador av fredat vilt på tamdjur, hundar och gröda. Viltskadecenter, Institutionen för ekologi, SLU. Grimsö, Sweden. 23pp.

SWITZERLAND (ALL REGIONS)

Wolf population estimates:
Data retrieved from https://chwolf.org/woelfe-in-der-schweiz/wolfspraesenz/fruehere-daten.

Livestock depredations:
Data provided by Mathias Vögeli

TZOUMERKA (GREECE)

Wolf population estimates:
Iliopoulos, Y. (2014). Population assessment of wolf population and status in Aheron-Kalamas National Park. Management authority of Kalamas-Aheron NP, OIKOS S.A, Callisto wildlife society (in Greek).

Livestock depredations:
Data provided by the Hellenic Farmers Insurance Organization (ELGA).

VASQUE COUNTRY (SPAIN)

Wolf population estimates:
Sáenz de Buruaga, M.; Campos, M.A., Canales, F., Hidalgo, S. & Calvete, G. (2015). Censo de lobo (*Canis lupus*) en la Comunidad Autónoma del País Vasco 2014. Government of the Vasque Country, Provincial Delegation of Álava and Provincial Delegation of Bizkaia. 105pp.

Livestock depredations:
Data provided by the Regional Government of the Vasque Country.

WASHINGTON (USA)

Livestock depredations and wolf population estimates:
Data retrieved from the following reports:

2011: Frame, P.F. & Allen, H.L. 2012. Washington Gray Wolf Conservation and Management Annual Report 2011. Pages WA-1 to WA-11 *In:* U.S. Fish and Wildlife Service Rocky Mountain Wolf Recovery 2011 Annual Report. USFWS, Ecological Services, Helena, MT.
2012: Becker, S.A., Frame, P.F., Martorello, D., & Krausz, E. 2013. Washington Gray Wolf Conservation and Management 2012 Annual Report. Pages WA-1 to WA-16 *In:* U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2012 Annual Report. USFWS, Ecological Services, Helena, MT.
2013: Becker, S.A., Roussin, T., Spence, G., Krausz, E., Martorello, D., Simek, S., & Eaton, K. 2014. Washington Gray Wolf Conservation and Management 2013 Annual Report. Pages WA-1 to WA-20 *In:* U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2013 Annual Report. USFWS, Ecological Services, Helena, MT.
2014: Becker, S.A., Roussin, T., Krausz, E., Martorello, D., Simek, S., & Kieffer, B. 2015. Washington Gray Wolf Conservation and Management 2014 Annual Report. Pages WA-1 to WA-24 *In:* U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2014 Annual Report. USFWS, Ecological Services, Helena, MT.
2015: Becker, S.A., Roussin, T., W. Jones, W., Krausz, E., Walker, S., Simek, S., Martorello, D., & Aoude, A. 2016. Washington Gray Wolf Conservation and Management 2015 Annual Report. Pages WA-1 to WA-24 *In:* U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2015 Annual Report. USFWS, Ecological Services, Helena, MT.

WISCONSIN (USA)

Wolf population estimates:
Data retrieved from https://www.fws.gov/midwest/wolf/aboutwolves/mi_wi_nos.htm

Livestock depredations:
Data retrieved from
https://dnr.wi.gov/topic/wildlifehabitat/wolf/documents/WolfDamagePayments.pdf

WYOMING (USA)

Livestock losses and wolf population estimates:
Data retrieved from the following reports:

2005: Jimenez, M.D., Smith, D.W., R. Stahler, D.R., D.S. Guernsey, D.S. & Krischke, R.F. 2006. Wyoming Wolf Recovery 2005 Annual Report. Pages 81-101 *In:* Sime C.A. & Bangs E.E. (eds.). U.S. Fish and Wildlife Service. 2006. Rocky Mountain Wolf Recovery 2005 Annual Report. USFWS, Ecological Services, Helena, MT.130pp.

2006: Jimenez, M.D., Smith, D.W., Guernsey, D.S. & Krischke, R.F. 2007. Wyoming Wolf Recovery 2006 Annual Report. Pages 174- 201 In: Sime C.A. & Bangs E.E. (eds.). U.S. Fish and Wildlife Service Rocky Mountain Wolf Recovery 2006 Annual report. USFWS, Ecological Services, Helena, MT. 235 pp.

2007: Jimenez, M.D., Smith, D.W., Stahler, D.R., Guernsey, D.S Woodruff, S.P, & Krischke, R.F. 2008. Wyoming Wolf Recovery 2007 Annual Report. Pages 204-236 201 In: Sime C.A. & Bangs E.E. (eds.). Rocky Mountain Wolf Recovery 2007 Interagency Annual Report. USFWS, Ecological Services, Helena, MT. 275pp.

2008: Jimenez, M.D., Smith, D.W., Woodruff, S.P, Stahler, D.R., Albers, E. & Krischke, R.F. 2009. Wyoming Wolf Recovery 2008 Annual Report. Pages WY-1 to WY-46 In: Sime C.A. & Bangs E.E. (eds.). Rocky Mountain Wolf Recovery 2008 Interagency Annual Report. USFWS, Ecological Services, Helena, MT.

2009 Jimenez, M.D., Smith, D.W., Stahler, D.R., Albers, E. & Krischke, R.F. 2010. Wyoming Wolf Recovery 2009 Annual Report. Pages WY-1 to WY-28 In: U.S. Fish and Wildlife Service Rocky Mountain Wolf Recovery 2009 Annual Report. USFWS, Ecological Services, Helena, MT.

2010: Jimenez, M.D., Smith, D.W., Stahler, D.R., Becker, S.A., Albers, E., Krischke, R.F., Woodruff, S., McIntyre, R., Metz, M., Irving, J., Raymond, R.,. Anton, C., Cassidy-Quimby K., & Bowersock, N. 2011. Wyoming Wolf Recovery 2010 Annual Report. Pages WY-1 to WY-30 In: U.S. Fish and Wildlife Service Rocky Mountain Wolf Recovery 2010 Annual Report. USFWS, Ecological Services, Helena, MT.

2011 Jimenez, M.D., Smith, D.W., Becker, S.A., Stahler, D.R., Stahler, E., Metz, M., McIntyre, R., Irving, J., Raymond, R., Anton, C., Kindermann, R., Bowersock, N., & Krischke, R.F. 2012. Wyoming Wolf Recovery 2011 Annual Report. Pages WY-1 to WY-25 In: U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2011 Annual Report. USFWS, Ecological Services, Helena, MT.

2012: Wyoming Game and Fish Department, U.S. Fish and Wildlife Service, National Park Service, USDA-APHIS-Wildlife Services, and Eastern Shoshone & Northern Arapahoe Tribal Fish and Game Department. 2013. 2012 Wyoming Gray Wolf Population Monitoring and Management Annual Report. Mills, K.J., & Trebelcock, R.F. (eds.). Wyoming Game and Fish Department, Cheyenne, WY.

2013: Wyoming Game and Fish Department, U.S. Fish and Wildlife Service, National Park Service, USDA-APHIS-Wildlife Services, & Eastern Shoshone and Northern Arapahoe Tribal Fish and Game Department. 2014. 2013 Wyoming Gray Wolf Population Monitoring and Management Annual Report Mills, K.J., & Trebelcock, R.F. (eds.). Wyoming Game and Fish Department, Cheyenne, WY.

2014: Wyoming Game and Fish Department, National Park Service, USDA-APHIS-Wildlife Services, & U.S. Fish and Wildlife Service. 2015. 2014 Wyoming Gray Wolf Population Monitoring and Management Interim Report: January 1, 2014 through September 23, 2014. Wyoming Game and Fish Department, Cheyenne, WY.

2015: Jimenez, M.D. and Johnson, A. 2016. Wyoming Wolf Recovery 2015 Annual Report. Pages WY-1 to WY-30 In: U.S. Fish and Wildlife Service Rocky Mountain Wolf Program 2015 Annual Report. USFWS, Ecological Services, Helena, MT.

APPENDIX 3.3. Criteria used for data selection and extraction into the final dataset.

A) WOLF POPULATION ESTIMATES

We extracted three values of wolf population estimates from the available data: mean estimate, lower estimate and upper estimate. Lower and upper estimates were used to build alternative models in order to stress the results obtained with the mean estimate. Data were collected in different formats and were incorporated in the database according to the following criteria:

Fixed estimates: When data were available as a fixed estimate of wolf individuals, we kept the same value for the mean, lower and upper estimates.

Population intervals: When data were available as a population interval, we incorporated the mean value of the interval as the mean estimate, and the lower and upper values of the interval as lower and upper estimates, respectively.

Packs and pairs: When data was provided as an estimated number of packs and pairs, we transformed the data considering six wolves per pack and two wolves per pair as the mean estimate. The lower estimate was obtained considering three wolves per pack, and the upper estimate considering nine wolves per pack. The average number (mean estimate) was considered a suitable estimate according to the mean pack size in winter derived from Fuller *et al*. (2003).[1]

Sporadic occurence: When wolf were reported to have an sporadic occurence in a study area (only in Czech Republic), we considered 1 wolf as the mean and lower estimates, and 3 wolves as the upper estimate. We only included sporadic occurence if at least one livestock loss to wolves was reported the same year. Otherwise we did not consider the data suitable for our database.

[1] Fuller, T.K., Mech, L.D., & Cochrane, J.F. (2003). Wolf Population Dynamics. *In*:Mech, L.D. & Boitani, L. Wolves: Behavior, Ecology and Conservation. The University of Chicago Press.

B) LIVESTOCK LOSSES

We included in the database all reported livestock deaths to wolves available for every study area and year. When livestock losses were reported as a total, we kept this value, classifying them as sheep, goat, cattle, horse, other (i.e., pigs, llamas, reindeer, donkeys, other domesticated ungulates and dogs) if possible and also keeping the total number of heads regardless the species.

We excluded data reported as injured animals unless it was specified that the animal died after inspection. Also, we kept only data reported as confirmed, probable, or with an estimated certainty over 50% to be wolf depredation. We excluded data considered as possible or "wolf not discarded".

APPENDIX 3.4: Estimated mean livestock depredations per wolf. Mean livestock depredations per wolf have been calculated as the average wolf/depredations per year in every study area, at country (Europe), State (USA) and Province (Canada) levels. The mean wolf estimate was used as wolf estimate and the total heads depredated as the livestock depredations estimate.

Continent	Country/State/Province	Depredations/wolf
Europe	Croatia	13.402
Europe	Czech Republic	7.031
Europe	Estonia	2.762
Europe	Finland	4.920
Europe	France	39.456
Europe	Germany	1.877
Europe	Greece	8.454
Europe	Latvia	0.173
Europe	Lithuania	8.707
Europe	Norway	11.454
Europe	Poland	1.310
Europe	Portugal	20.166
Europe	Slovakia	1.332
Europe	Slovenia	27.519
Europe	Spain	17.596
Europe	Sweden	1.538
Europe	Switzerland	13.456
North America	Alberta	0.032
North America	Arizona	0.311
North America	Idaho	0.437
North America	Manitoba	0.081
North America	Michigan	0.047
North America	Minnesota	0.054
North America	Montana	0.261
North America	New Mexico	0.627
North America	Ontario	0.049
North America	Oregon	0.551
North America	Quèbec	0.001
North America	Saskatchewan	0.104
North America	Washington	0.168
North America	Wisconsin	0.105
North America	Wyoming	0.575

APPENDIX 3.5: Hierarchical bayesian models with temporal autocorrelation using integrated nested Laplace approximations (INLA).

LATENT GAUSSIAN MODELS

We built separate hierarchical Bayesian models with temporal autocorrelation using INLA with the entire dataset to define the posterior marginal distribution of the total number of livestock heads lost to wolves as a function of the mean, minimum and maximum wolf estimates. Our basic model structure included livestock losses as response variable and a single covariate (wolf estimates), but in order to account for spatial and temporal autocorrelation we integrated spatiotemporal terms in the equation by setting the study area as an independent random noise variable and the year as a first order autoregressive model. In addition, we also built partial models using separately the study areas where wolves have always been present in recent times and areas with interrupted wolf presence in the last decades. We infered the models using integrated nested Laplace approximations with negative binomial likelihood distribution. We calculated the 0.025 and 0.975 quantiles of the density distribution of the posterior β coefficients of the covariates in order to assess significance of the models (we considered that interquantile intervals including 0 indicated independence of the response variable). Models were built using the INLA package in R (http://www.r-inla.org).

Our basic model structure in R, repeated for each wolf estimate covariate and data subset was:

theads~wolfx.std + f(area, model="iid") + f(year, model = "ar1", replicate=area1)

where,

"*theads"* represents the total number of livestock losses.

"wolfx.std" are the standardized estimates of wolf abundance (mean, maximum, minimum). The regression coefficient β is given a prior Gaussian distribution with mean=0.

f(area, model="iid") is an independent random noise model to account for the study area as a Gaussian distributed random term..

f(year, model = "ar1", replicate=area1) is a first order autoregressive model of Gaussian distribution used to account for temporal (year) autocorrelation as a random effect.

We also calculated the 0.025 and 0.975 quantiles to assess the credibility of the posterior marginal distributions of the covariates.

RESULTS

Posterior summary statistics for the models using the entire dataset (a), areas of continued wolf presence (b), and areas of interrupted wolf presence (c). For each subset, models using mean wolf estimate (*Wolfmean*), minimum wolf estimate (*Wolfmin*) and maximum wolf estimate (*Wolfmax*) as fixed covariates are presented. The 0.025 and 0.975 quantiles (quant) determine the 95% credible intervals.

a) **Models for the entire Dataset**

	Posterior mean	**s.d.**	**0.025quant**	**0.5quant**	**0.975quant**
Intercept	4.295	0.209	3.882	4.296	4.705
Wolfmean	0.197	0.123	-0.043	0.197	0.441

	Posterior mean	**s.d.**	**0.025quant**	**0.5quant**	**0.975quant**
Intercept	4.298	0.211	3.881	4.298	4.711
Wolfmin	0.174	0.124	-0.068	0.174	0.419

	Posterior mean	**s.d.**	**0.025quant**	**0.5quant**	**0.975quant**
Intercept	4.289	0.210	3.874	4.289	4.701
Wolfmax	0.221	0.124	-0.020	0.220	0.466

b) Models for areas with continuous wolf presence

	Posterior mean	s.d.	0.025quant	0.5quant	0.975quant
Intercept	5.397	0.226	4.949	5.397	5.838
Wolfmean	-0.031	0.092	-0.212	-0.031	0.153

	Posterior mean	s.d.	0.025quant	0.5quant	0.975quant
Intercept	5.398	0.225	4.951	5.399	5.840
Wolfmin	-0.0355	0.092	-0.217	-0.036	0.147

	Posterior mean	s.d.	0.025quant	0.5quant	0.975quant
Intercept	5.394	0.226	4.946	5.395	5.836
Wolfmax	-0.026	0.093	-0.208	-0.027	0.157

c) Models for interrupted wolf presence

	Posterior mean	sd	0.025quant	0.5quant	0.975quant
Intercept	3.873	0.302	3.273	3.875	4.462
Wolfmean	2.16	0.633	0.920	2.159	3.407

	Posterior mean	sd	0.025quant	0.5quant	0.975quant
Intercept	3.805	0.3192	3.807	4.406	3.810
Wolfmin	1.910	0.697	0.541	1.910	3.278

	Posterior mean	sd	0.025quant	0.5quant	0.975quant
Intercept	3.886	0.296	3.298	3.888	3.891
Wolfmax	2.160	0.570	1.050	2.156	3.288

APPENDIX 3.6: Relationship between livestock abundance and livestock depredations.(Data colection, depredations in relation to livestock abundance, Bayesian generalized linear multilevel models to estimate the effect of livestock abundance on livestock losses).

A) DATA ON LIVESTOCK ABUNDANCE

To estimate livestock abundance we used the number of sheep, goat and cattle within the wolf distribution range in each study area from the Gridded Livestock of the World v2.0 (Robinson *et al.* 2014). Since annual updates of wolf distribution or livestock abundance were not available for the whole time series, we extracted livestock data for the year closest in time to the date of the wolf distribution map for each area (n=87). As livestock depredations, we extracted data on losses of the same three species pooled together from our database.

B) DEPREDATIONS IN RELATION TO LIVESTOCK ABUNDANCE

Wolf impact on livestock as number of losses of sheep, goat and cattle (pooled together) every 100 heads of the same species within the wolf distribution range, at county (Europe), State(USA) and Province (Canada) levels.

Continent	Country	Year	Losses/100heads
North America	Alberta	2013	0.013
North America	Arizona	2011	0.040
Europe	Croatia	2011	0.693
Europe	Czech Rep	2011	0.432
Europe	Finland	2011	0.006
Europe	France	2013	0.623
Europe	Germany	2011	0.107
Europe	Greece	2013	0.111
North America	Idaho	2011	0.058
Europe	Latvia	2011	0.050
Europe	Lithuania	2015	0.502
North America	Manitoba	2013	0.173
North America	Michigan	2013	0.012
North America	Minnesota	2013	0.032

North America	Montana	2011	0.013
North America	New Mexico	2011	0.065
Europe	Norway	2011	0.066
North America	Ontario	2013	0.970
North America	Oregon	2011	0.012
Europe	Poland	2011	0.151
Europe	Portugal	2005	0.604
North America	Quèbec	2013	0.003
North America	Saskatchewan	2013	0.129
Europe	Slovakia	2011	0.100
Europe	Slovenia	2011	0.929
Europe	Spain	2011	0.307
Europe	Sweden	2011	0.125
Europe	Switzerland	2011	0.150
North America	Washington	2012	0.074
North America	Wisconsin	2011	0.007
North America	Wyoming	2011	0.071

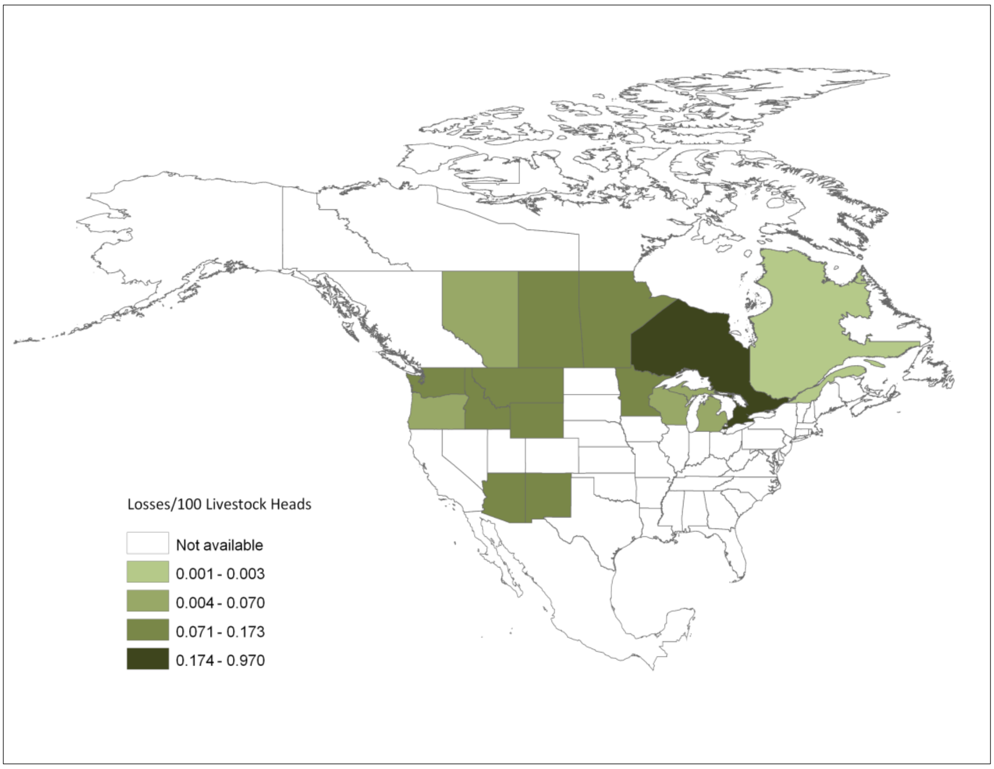


Figure A3.1: Livestock depredations in relation to livestock abundance in North America (US States/ Canadian Provinces.

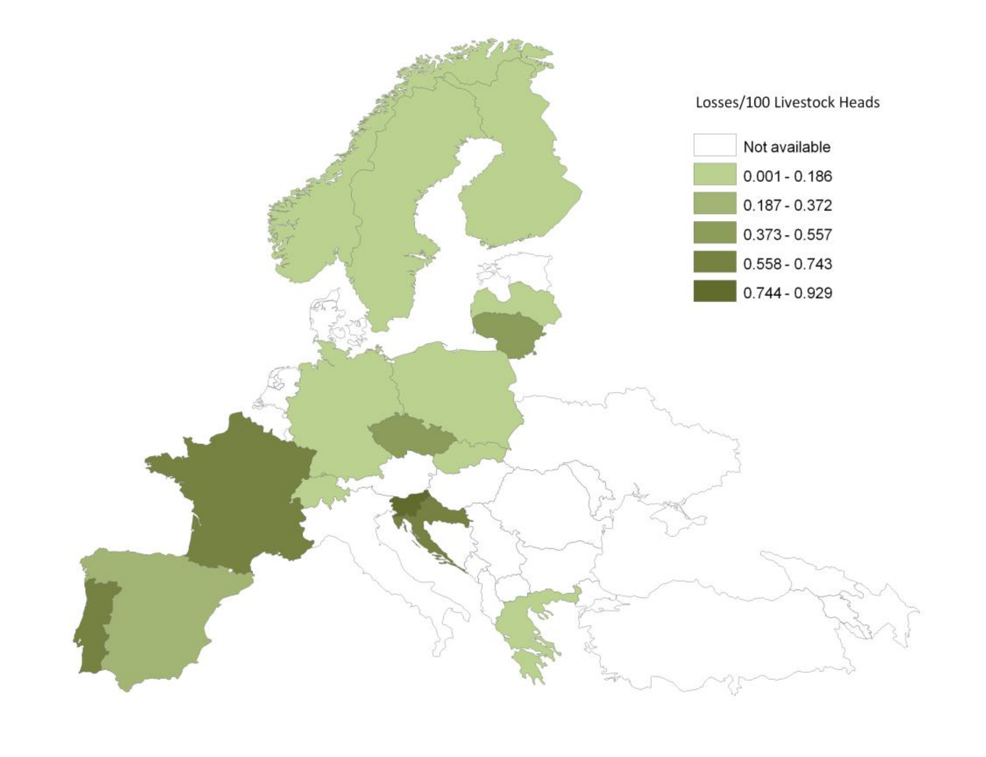


Figure A3.1: Livestock depredations in relation to livestock abundance in Europe (Countries).

C) BAYESIAN GENERALIZED LINEAR MULTILEVEL MODELS

In order to assess the effect of livestock abundance on the corresponding losses to wolves, we used the "brms" package in R (Bürkner, P.K. (2018). *Bayesian Regression Models using 'Stan'*, v.2.2.) to fit negative binomial generalized linear mixed models using Bayesian methods. Models were sampled with 4 Markov chains, each with 5000 iterations (including 1000 warmup iterations). We adjusted the sampling behaviour by setting the adapt_delta argument in *Stan* at 0.95 in order to control the number of divergent transitions. The model sampling was repeated for the whole dataset, the areas with continuous wolf presence and the areas with interrupted wolf presence. The model structure can be summarized as:

theads ~ wolfmean.std + livestockab+ (1|Country) + (1|year)

where,

"*theads"* represents the total number of livestock losses to wolves including only sheep, goat and cattle because the availability of abundance data at a global scale.

"wolfmean.std" is the standardized mean wolf estimate

"*livestockab*" is livestock abundance within the estimated wolf range in each study area.

"Country" and "*Year"* were included as random terms in the equation.

Wolf abundance and livestock losses were derived from the year closest to the date when wolf distribution was estimated in each area .

RESULTS

Summary statistics (mean and 95% conficdence interval) describing the posterior density of the covariates (fixed effects) and random terms for the 3 models. Models included are the total model (all the data), model usiong areas of continuous wolf occurence and model with interrupted wolf presence.

Covariates	Total model	Continuous occurence	Interrupted occurence
Intercept	4.69 (3.15-6.21)	5.56 (3.79-7.16)	4.14 (2.01-6.22)
Mean wolf estimate	0.16 (-0.35-0.70)	0.12 (-0.41-0.70)	-2.27 (-9.75-5.20)
Livestock abundance	0.62(0.16-1.12)	0.51 (0.13-0.96)	2.53(0.20-4.88)

Random effects	Total model	Continuous occurence	Interrupted occurence
Country (sd intercept)	1.63 (1.09-2.34)	0.96 (0.09-2.20)	1.52 (0.78-2.55)
Year (sd intercept)	1.30 (0.39-3.45)	1.37 (0.22-4.05)	0.62 (0.02-2.38)

Chapter 4

Recovering wild prey to mitigate human-wolf conflicts? Insights from academia, management and field observations.

ABSTRACT

Depredation on livestock by large carnivores makes their conservation remarkably complex, especially in human-dominated landscapes. Promoting shifts to less conflictive food items is a recurrent target in their management. An increase in the abundance of wild prey has been suggested to be a potential measure to reduce livestock depredation by wolves (*Canis lupus*). In order to assess the evidence supporting this assumption we reviewed 46 scientific papers potentially addressing this issue and 16 more assessing the preference of wolves towards wild or domestic prey. Ten studies out of 14 tested and supported a positive correlation between wild prey abundance and its frequency in the diet of wolves, and 10 out of 15 concluded a preference for wild prey. Overall, we found a lack of generality and power in the resulting inference. In order to assess to what extent scientific literature inform wolf management we reviewed 71 wolf management and action plans from Europe and North America and found that only the 12.5% (n= 7) of actions were designed to reduce damage on livestock. Finally, we test the generality of the purported effects of increasing wild prey on wolf food habits with a field study in an area of NW Spain where wild prey abundance has been increasing while the staple prey of wolves (free-ranging horses) has declined during the last decades. We examined wolf diet and quantified horse abundance in 6 wolf pack areas between 2006 and 2017. We assessed the effect of the period and the relative abundance of horses on the frequency of occurrence (FO) of three major prey classes: *horse*, *other livestock* and *wild prey*. We found a negative relationship between period and the frequency of horse in the diet, and the opposite effect regarding other livestock species. The consumption of wild prey was not affected by the period or the relative abundance of horses, suggesting that caution should prevail when a shift in consumption of domestic and wild prey is expected after changes in their relative abundances. We suggest a context-dependent effect of increasing the abundance of wild prey, which should be regarded as a mean to reduce the conflict caused by high rates livestock predation when other measures (in our case consolidating horse numbers and protecting other livestock) have already been adopted and after thorough assessment.

Introduction

Large carnivore conservation is often dependent of land-sharing conservation approaches grounded in the persistence of these species outside protected areas (Chapron *et al.* 2014; Johansson *et al.* 2016; López-Bao *et al.* 2017). However, the goal of maintaining viable populations of large carnivores and humans sharing the same landscapes is not exempt from challenges (Chapron & López-Bao 2016; López-Bao *et al.* 2017). The predatory behaviour of large carnivores may represent the main factor interfering with this conservation approach (López-Bao *et al.* 2017). Landscape sharing approaches imply tolerating some levels of conflict, for instance, associated with attacks on livestock. Conflict can also lead to persecution, one of the main drivers together with habitat loss, of large carnivore population declines worldwide (Estes *et al.* 2011; Ripple *et al.* 2016). Consequently, the reduction of carnivore attacks on livestock is usually integrated as a fundamental pillar of conservation and management of these species, such as in the case of gray wolves (*Canis lupus*) (Sillero-Zubiri *et al.* 2007; Muhly & Musiani 2009).

Wolves are opportunistic predators capable to thrive in a wide variety of habitats, including highly human-dominated landscapes (Llaneza *et al.* 2012; Chapron *et al.* 2014; Newsome *et al.* 2016). The grey wolf is also the most widely distributed species of all large carnivores in the world (Mech & Boitani 2003). These attributes translate into a wide range of management regimes and conservation goals across the species range, making the wolf an appropriate model species to shed light into the multiple nature of human-large carnivore conflicts, and to understand how different management strategies and their outcomes impact on wolf conservation and carnivore coexistence.

Understanding wolf feeding ecology has been deemed essential to characterize the issue of human-wolf coexistence (Newsome *et al.* 2016). Much attention has been drawn to the impact of wolves on domestic livestock or game, and the drivers of different predation patterns on these species, particularly in human-dominated landscapes or areas recolonized by the species. For example, predation rates on livestock have been correlated with the abundance and diversity of wild ungulates (Meriggi & Lovari 1996; Sidorovich *et al.* 2003; Imbert *et al.* 2016). Moreover, in multi-prey systems, different species-specific predation rates have been linked to availability in terms of relative abundance (Capitani *et al.* 2004; Garrott *et al.* 2007; Nowak *et al.* 2011), vulnerability (Oakleaf *et al.* 2003; Mattioli *et al.* 2011), or the social behaviour of prey (Meriggi *et al.* 1996; Jedrezejewska & Jedrzejewski 1998). Besides prey accessibility, preference for certain prey species has also been reported as a factor explaining differential predation rates (Barja 2009; Milanesi *et al*. 2012). Predation patterns are also complicated by contrasting prey selection and feeding strategies in different scenarios (Ståhlberg *et al.* 2017). For example, both preference (Gazzola *et al*. 2005) and avoidance (Meriggi *et al*. 1996; Mattioli *et al.* 2011) of red deer *(Cervus elaphus)* has been observed in different areas of Italy.

The ability of wolves to cope with long-term changes in prey availability is well-known (Potvin *et al.* 1988; Sidorovich *et al*. 2003; Zlatanova *et al*. 2014), as exemplified by the increment in the use of wild ungulates in large areas of Europe after a general increase in their populations in the last decades (Capitani *et al.* 2004; Meriggi *et al*. 2011). Such adaptability has also been observed at shorter time scales (Meriggi *et al*. 2014), even on a seasonal basis (Morehouse & Boyce 2011).

Characterizing wolf feeding patterns is relevant for the mitigation of wolf attacks on livestock. Many studies have mentioned a positive selection of wolves towards wild ungulates (Meriggi & Lovari 1996; Poulle *et al*. 1997; Rigg & Gormann 2004; Schenone *et al*. 2004; Chavez & Gese 2005; Barja 2009; Lagos & Bárcena 2018; Ciucci *et al.* 2018). From this evidence it is inferred that increasing the availability of wild prey would have a positive impact on conflict mitigation through a reduction in the number of attacks on livestock (Wagner *et al.* 2012; Ciucci *et al.* 2018). The management of wild prey has been therefore suggested as a plausible strategy to reduce the impact of wolves on livestock (Meriggi & Lovari 1996; Poulle *et al.* 1997), including the re-introduction of wild prey in areas where wolves mainly feed on anthropogenic food sources (Vos 2000; Cruz *et al*. 2014; Ciucci *et al*. 2018). However, the mechanisms underlying the observed preference towards wild prey, and the drivers of the expected positive impacts of an increment of wild prey in human-dominated landscapes, remain poorly debated.

The assumed benefits of boosting populations of wild prey species have been incorporated into wolf management plans and regulations. In 1975, the Wolf Specialist

Group of the International Union for Conservation of Nature released the *Manifesto and Guidelines on Wolf Conservation* (Pimlott 1975 - reviewed for the last time in 2000), aimed to guide decision-makers in relation to key aspects for wolf conservation. Among the recommended guidelines, the need to restore "…*sound ecological conditions for wolves in such areas* (i.e., suitable areas for the existence of wolves) *through the rebuilding of suitable habitats and the re-introduction of large herbivores*" was noted. The areas mentioned in such statement, included areas where "*wolf populations would be regulated according to ecological principles to minimize conflicts with other forms of land use*". General guidelines are often implemented through management and conservation plans, where sovereign territories articulate not only the tenets contained in international (e.g., the European Habitats Directive 92/43/EEC) and national (i.e., national conservation or hunting regulations) legal systems, but also provide an operational and regulatory framework to reach specific management or conservation goals.

In Europe, in 1989, the Standing Committee of the Bern Convention made a recommendation to contracting parties that set specific guidelines regarding wolves, including drawing up wolf management plans (Rec. No. 17/1989). Such guidelines were in accordance with the principles and suggestions included in the *Manifesto and Guidelines on Wolf Conservation*. The convenience of developing and implementing wolf management plans was subsequently endorsed by the *Action Plan for the conservation of wolves in Europe* (Boitani 2000), and a new recommendation from the BC Standing Committee (Rec. No. 74/1999). Moreover, species-specific plans are a suitable, or even required, means of implementing the obligations of EU member states under EU Habitats Directive. The *Action Plan* for wolves in Europe considers the reintroduction of wild ungulates, wherever their populations have been depleted, as a required action to be implemented in order to improve the prey base for the species and divert them from anthropogenic food sources. Therefore, this recommendation assumes that an increase in wild prey populations would translate into a decrease in livestock depredation by wolves.

The suggested preference for wild prey (Barja 2009; Milanesi *et al*. 2012) would be expected to catalyse prey shifting in wolves, decreasing the impact of the species on livestock. Nonetheless, the generality of available evidence is not conclusive. Here, we first analyse the consistency of such assumption in the literature. Then we evaluate how management and conservation instruments (plans) fit it in the operational strategy of improving human-wolf coexistence by promoting wild prey. Finally, we present a case study of long-term monitoring of wolf diet to shed light on the expected impacts of recovering wild prey populations on the use of anthropogenic sources of food by wolves.

Increasing wild ungulates as a tool to reduce livestock attacks by wolves: What does evidence say?

In order to assess the strength of the relationship between wild prey abundance and livestock depredation, we first conducted a literature review searching for references suggesting a negative relationship between the size of wild ungulate populations and the importance of livestock in the diet of wolves, or the number of livestock attacks. We assumed such relationships would indicate that promoting or restoring wild prey populations would decrease wolf pressure on livestock (Appendix 4.1, Fig. 4.1). Forty-one out of 46 studies examining this topic (89%, see Appendix 4.1 for details) suggested the abovementioned negative correlation. Therefore, available evidence may a priori strengthen the idea of decreasing livestock damages through enhancing wild prey abundance (Fig. 4.1). It is worth mentioning, however, that only 14 of these studies (30%) explicitly tested this relationship, of which 3 studies did not find any correlation, and one reported a significant opposite effect (Appendix 4.1). Overall, these results suggest a lack of generality in the relationship between wild ungulate populations and wolf impact on livestock.

Evidence other than the ratio between prey frequencies in the diet of wolves have been used to suggest a negative effect of wild prey abundance on livestock predation. Prey vulnerability and the adoption of certain livestock husbandry practices may increase the consumption of livestock disproportionally to its abundance (Meriggi *et al*. 1996; Mattioli *et al*. 2011; Wagner *et al*. 2012). Furthermore, resistance to prey shifting despite changes in prey availability, when a long-term specialization process has taken place (i.e. a specific food item comprised a significant portion of wolf diet for a long time; Potvin *et al.* 1988; Spaulding *et al*. 1998), or when a specific item is highly predictable and efficient in terms of energetic cost (such as leftovers from farms; Tourani *et al*. 2014), may also influence the consumption ratios beyond relative abundance. Prey switching has also been suggested as a functional response to changes in food availability resulting in disproportionate predation of main and alternative prey when their abundance is extremely disparate (Garrott *et al*. 2007).

Accordingly, we also reviewed the available evidence for the preference of wild prey by wolves over livestock, which would catalyse prey shifting, and could justify predation management through increasing wild prey availability. In the reviewed selected literature (Appendix 4.1), 10 out of 15 studies (67%) considering wolf preference for wild prey or livestock suggested a positive selection of wild prey, 3 of them (30%) being reviews. Interestingly, 2 studies (13%) suggested preference or specialisation on domestic prey (Tourani *et al.* 2014; Torres *et al.* 2015) and one found disparate effects depending on the social status of wolves (Imbert *et al*. 2016). Two studies (13%) did not find any selection pattern. Overall, only 5 original studies (33%) estimated the relative abundance of each prey type. Only 2 studies (13%) measured the abundance of both livestock and wild prey using the same techniques and sources of monitoring data (Barja 2009; Chetri *et al*. 2017), which may limit the strength of the inference about prey type preference in this set of 15 papers. Using different sources of data and spatial scales to assess availability of the different prey types may lead to inaccurate prey selection estimates. Moreover, important attributes determining livestock availability, such as vulnerability to wolf attacks, associated with livestock husbandry practices, can easily be overseen.

Prey shifting as a consequence of changes in the relative availability of prey types is still not fully understood when it comes to multi-prey systems involving wild and domestic prey, neither is the suggested preference for wild ungulates a consistent pattern across wolf populations.

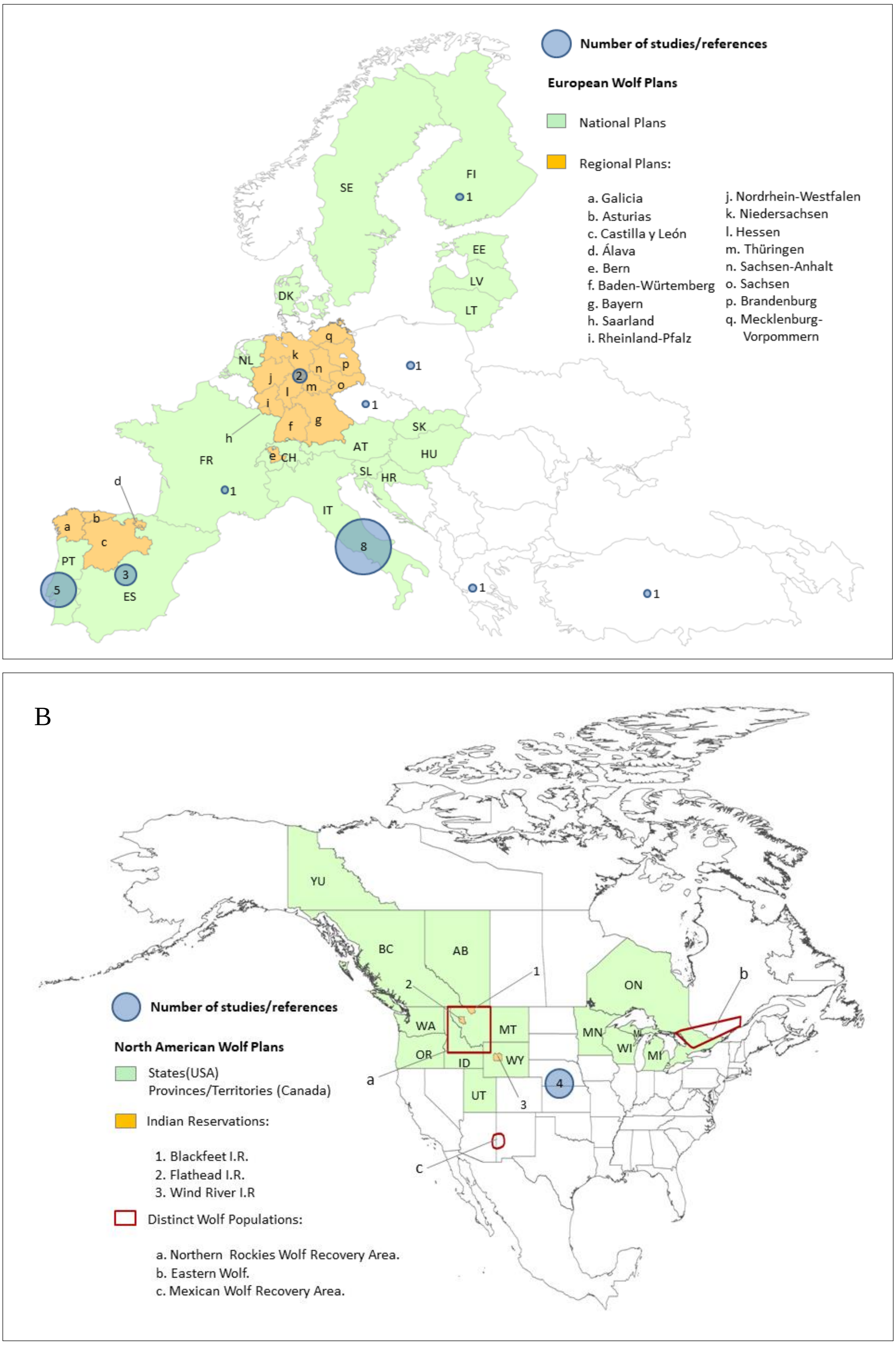


Figure 4.1. Maps showing the territories (national and subnational levels) where wolf plans (drafted or implemented) in Europe (A) and North America (B) were analysed. The distribution of studies testing or assuming a relationship between wild prey abundance and damages to livestock (number of studies, proportional blue circles) are also shown.

Increasing wild ungulates as a tool to reduce livestock attacks by wolves: Does wolf management integrate available evidence?

We assessed the concomitance between evidence and policy-making in relation to the impact of increasing wild ungulate populations on human-wolf conflict. To do that, we reviewed 71 wolf management and action plans from Europe and North America (Fig. 4.1; Appendix 4.2). In Europe, 25 plans were issued at the national level (belonging to 17 countries), and 21 at the subnational level (16 regions). In North America, 4 plans belonged to Canadian Provinces or Territories, and 12 plans were from 9 USA States. In addition, 8 plans were circumscribed to other geographical boundaries, such as Indian Reservations or the range of distinct wolf populations.

Within plans, we searched and classified all references regarding wild prey according to their nature and objectives (Appendix 4.2). We discriminated between references of descriptive nature and references that entailed specific actions or management guidelines affecting wild prey. In this case, we separated between those measures aimed to monitor wild prey populations or improve knowledge, and those directly delineated to enhance wild prey populations. Furthermore, actions on wild prey were classified according to the level/intensity of the intervention suggested: i) monitoring and diagnosis actions, ii) regulatory (preventive) actions, and iii) direct intervention on wild prey populations.

Overall, we found 198 references. Ninety-two references (46%) were descriptive of the wolf prey base or wolf-prey interactions (i.e., description of wolf diet); whereas 106 references entailed specific action related to wild prey. However, from these references, 50 actions (47%) did not imply an expected direct impact on wild prey populations (monitoring prey populations or assessing the impact of wolf predation on prey populations). Among the 56 actions with expected impact on wild prey populations, 39 (70%) were mainly of regulatory nature (i.e., avoiding game fencing in protected areas, regulating harvest to increase their populations) or were stated in vague terms (i.e., to provide large areas with adequate prey or to reduce illegal killing of game species in wolf occupied areas). The remaining 17 actions (30%) foresee direct intervention on wild prey populations, being most of them (n=9; 53%) oriented to reduce wolf impact on prey populations. Most actions lacked a proper description of the concrete actions needed to reach the specific goal of improving or securing wild prey availability.

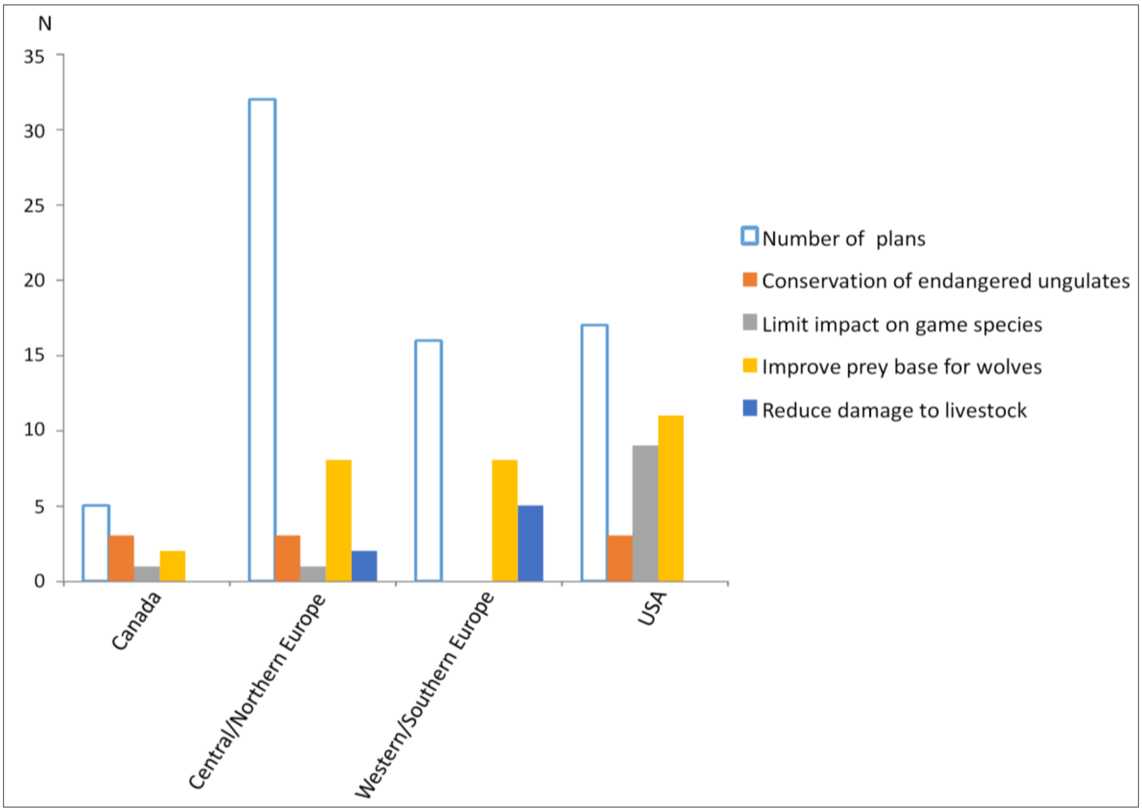


Figure 4.2. Number of actions potentially impacting wild prey populations and/or wild prey/wolf interactions, classified according to the main objective they were delineated for. Actions are roughly grouped in four geographical areas to better illustrate contextual differences according to coexistence frameworks and wolf ecological patterns (Meriggi & Lovari 1996; Newsome *et al.* 2016).

Overall, the 56 actions with expected direct impact on wild prey populations were included in 30 plans from 10 countries and 2 regions from Europe, 10 States/Provinces and 3 distinct wolf population units from North America (Appendix 4.2). Among them, only 7 actions related with wild prey (12.5%) were aimed to reduce predation on livestock, assuming that livestock depredation by wolves is partially mediated by wild prey abundance. These actions were from 3 plans at regional (2 in Asturias, Spain and 1 in Bern, Switzerland) and 2 plans at national (Italy and Slovenia) levels, all of them from Europe. Nine actions (16.1%) from 7 plans were focused on the conservation of wild ungulate species and 11 actions (19.6%) to preserve game stocks (mainly from North America; Fig. 4.2). The 29 remaining actions (51.8%) were aimed to improve prey base for wolves, but did not explicitly establish a link with livestock depredation. We only found 2 actions (3.6%) that eventually foresee the (re)introduction of wild prey to improve prey base for wolves or reduce the level of damages to livestock (in Croatia and Italy).

Despite the promotion of wild prey is found regularly in management and conservation instruments, the idea of enhancing wild prey populations as a tool to mitigate the impact of wolves on livestock is rarely found in wolf plans. Thus, this link, more frequently suggested in the scientific literature is rarely explicitly considered in wolf plans. Direct actions in this regard were only found in 5 out of the 71 plans reviewed, mainly from human-dominated landscapes in Central and Southern Europe, matching some of the regions where the effects of wild prey abundance on livestock depredations has attracted more attention from a scientific point of view (Fig. 4.1; Appendix 4.1).

Contrary to academia, policy-makers seem to be more cautious with the idea of improving wild prey populations as a mean to reduce the impact of wolves on livestock (as suggested by the Wolf Manifesto). Nevertheless, in many areas of the wolf range in Central and Northern Europe and North America, wild prey, especially ungulates, make the bulk of wolf's diet (Newsome *et al.* 2016). High abundance of wild prey in these areas may discourage the delineation of specific actions aiming to increase wild prey availability for wolves but, at the same time, livestock damages are still an issue of social concern. Moreover, increasing wild ungulate populations should consider multiple socio-ecological factors. In certain contexts, the level of damages caused by wild ungulates to agriculture or forestry may be a source of discontent (Geisser & Reyer 2004; Ward *et al*. 2004). Therefore, potential side-effects of increasing wild prey populations suggest that caution should prevail when artificially promoting prey populations in multi-use landscapes.

Does a growing abundance of wild ungulates necessarily reduce the frequency of wolf predation on livestock? A case study

In order to shed light on the expected impacts of recovering wild prey on wolf feeding patterns, we explored temporal shifts in the diet of wolves in NW Spain (Costa da Morte; Figs. 4.3; 4.4; 4.5; Appendix 4.6) over a 12-yr period, where substantial variations in the availability of wild and domestic prey have occurred over time. Wolf diet was assessed by scat analysis (Appendix 4.3).

Between 2006 and 2017 we studied the variation in the diet of wolves from 6 wolf packs occurring over an area of approximately 100,000 ha (Pacheco *et al* 2017, López-Bao *et al.* 2018; Appendix 4.4). We divided the study into three periods (Period 1: 2006 to 2008; Period 2: 2011 to 2013; Period 3: 2015 to 2017). Wolf diet in this area has been largely dominated by livestock, specifically free-ranging horses (*Equus caballus*) at least for the last four decades (Guitián *et al.* 1979; Lagos 2013; López-Bao *et al.* 2013). Wolf packs were detected and breeding events were frequently observed during the study period (Appendix 4.4).

Extensive husbandry of horses (López-Bao *et al.* 2013) and land tenure (traditional minifundios with disperse population) make the study area highly heterogeneous in horse abundance. Horses have been traditionally concentrated in commons at high elevations dominated by scrublands (López-Bao *et al.* 2013). However, the current marginality of this husbandry practice, the lack of generational relief and the impact of new sanitary regulations for horses (López-Bao *et al*. 2013) has resulted in an overall decrease in horse numbers in many regions of Galicia (Lagos 2013), including our study area. A steep generalized decline in horse numbers has occurred in the study area between 2006 and 2017 (Table 4.1; Fig. 4.3; Appendix 4.5).

Table 4.1. Estimates of the relative abundance of horses within areas occupied by six wolf packs in Costa da Morte (NW Spain). Relative abundance was expressed as the mean number of dung piles per km across transects surveyed in each area. During Period 1 data were not collected in three areas. N= number of transects.

	Period 1 (2006-2008)			**Period 2 (2011-2013)**			**Period 3 (2015-2017)**			**Mean inter-period change rate (%)**
Area	**N**	**Dungs/Km**	**S.E.**	**N**	**Dungs/km**	**S.E.**	**N**	**Dungs/km**	**S.E.**	
Baiñas	10	3.25	1.77	13	0.98	0.41	10	0.21	0.17	-74.22
Ruña	8	13.06	4	11	9.73	3.55	7	1.95	1.25	-52.73
Vimianzo	10	7.26	1.73	17	3.37	1.2	11	2.91	1.66	-33.62
Buxantes	-	-	-	7	14.61	5.5	6	14.6	6.6	-0.03
Carnota	-	-	-	7	23.86	4.8	8	8.06	3.07	-66.23
Muxía	-	-	-	4	0	0	12	0.12	0.1	-
Total	28	7.85	2.84	59	8.75	3.78	54	5.67	2.32	-45.37

Rural depopulation has been intense in Costa da Morte area, losing a 23.5% of its human population between 1981 and 2017 (Instituto Galego de Estatística 2018). Accordingly, extensive livestock husbandry has also decreased and the numbers of cattle, sheep, and goats grazing outdoors have declined by 16.7%, 48.9%, and 26.0%, respectively, from 1999 to 2009 in the whole province (A Coruña province; Instituto Galego de Estatística 2018).

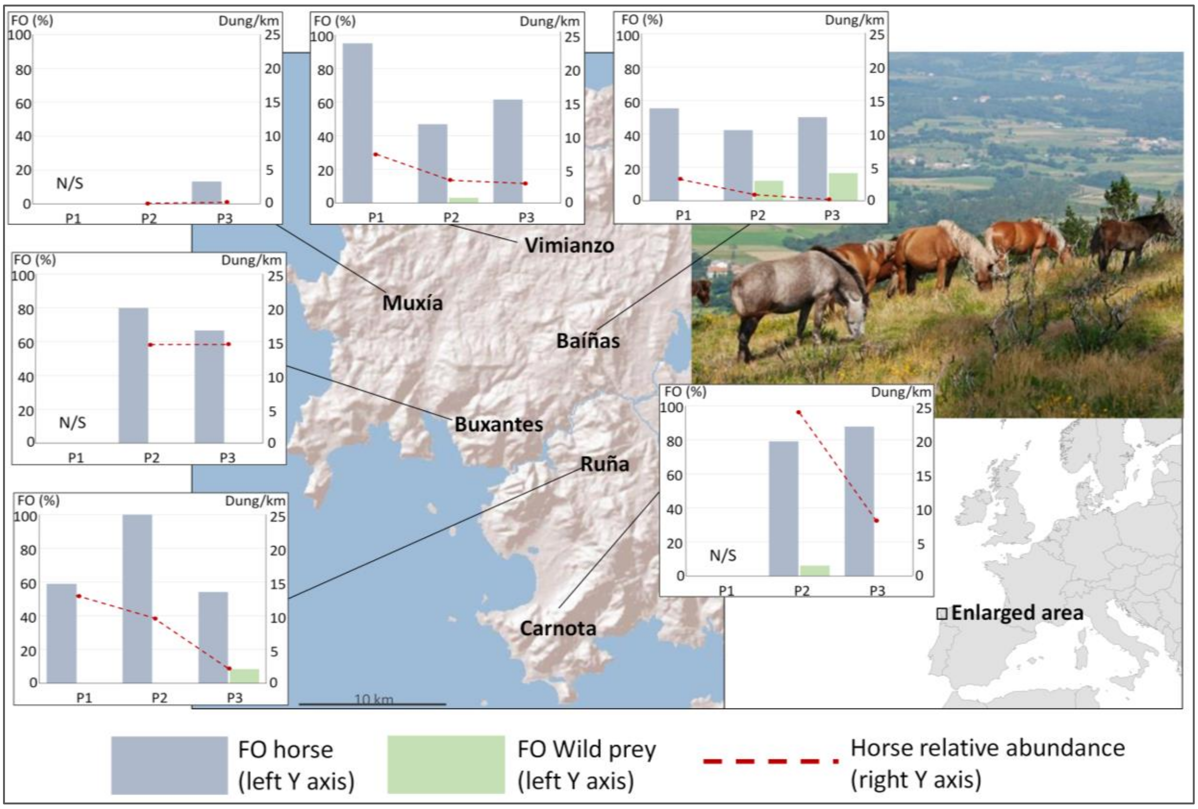


Figure 4.3. Map of the study area (Costa da Morte, Galicia, Spain) and the approximate location of the wolf pack-areas surveyed (see López-Bao *et al.* 2018). Frequency of Occurrence (FO) of horses and wild prey in the diet of wolves, and the relative abundance of horses (mean number of dung piles/km, Appendix 4.5) for every wolf area and period are shown (P1: 2006-2008, P2: 2011-2013, P3: 2015-2017; N/S= Not Surveyed). Our results are in accordance with a different prey composition basis among neighbouring packs, denoting large variation in wolf feeding patterns at fine spatial scales (Ciucci *et al*. 2018). Only in one area ("*Muxía*"), where horses were very rare, they increased slightly between periods 2 and 3 (Fig. Table 4.1). Map Copyright© 2014 Esri.

Wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) are the only species of wild ungulates occurring in the area. After decades of absence or extreme low densities (SGHN, 1995; López-Bao *et al.* 2013; Llaneza & López-Bao 2015), these two species have experienced a remarkable comeback, increasing their range and abundance (Figs. 4.4 and 4.5, Appendix 4.6). While roe deer hunting is still closed in Costa da Morte, wild boar captures per hunt (a surrogate for abundance; Imperio *et al*. 2010) have increased at a rate of 1.93% annually. Multiple factors associated with rural abandonment seem to lie behind the increase of these species in Spain and elsewhere in Europe (Sáez-Royuela & Tellería 1986; Aragón *et al*. 1995; Massei *et al*. 2015).

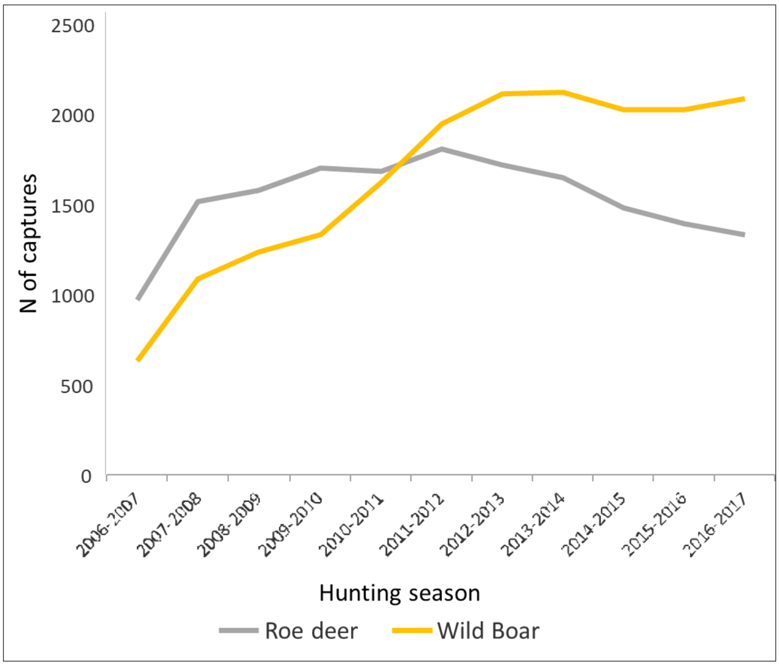


Figure 4.4. Total captures of roe deer and wild boar in the A Coruña province (Galicia, Spain) between 2006 and 2017 (data provided by the Ministry of Environment and Landscape Planning of the Regional Government of Galicia).

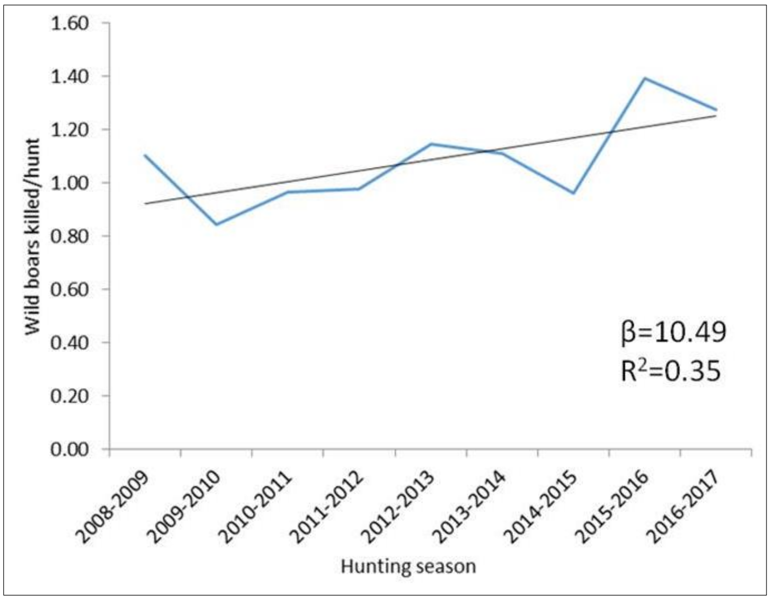


Figure 4.5. Mean number of wild boars killed per hunt in Costa da Morte Hunting Areas between 2008 and 2017 (data provided by the Ministry of Environment and Landscape Planning of the Regional Government of Galicia).

The described changes in the relative abundance of prey types, including a process of marked decrease of horses, the long-standing staple prey of wolves, make this system suitable to test the hypothesis of prey shifting between livestock and wild prey. If the recovery of wild prey populations as a tool for conflict mitigation and the preference of wild prey over livestock were to be a general expected outcome of ungulate management, the hypothesis predicts a shift in diet of wolves towards an increasing consumption of wild prey, in parallel with a decreasing frequency of horse, and other livestock species, in the diet of wolves.

Overall, wild prey remains were found only in 3.1% of the wolf scats analysed in the entire study period (Table 4.2; average frequency by periods: Period 1=0%, Period 2=3.6%, Period 3=4.2%). The species of wild ungulates present in our study area have been described previously as preferred prey for wolves in other contexts (Mattioli *et al.* 2004, Stahlberg *et al.* 2016, Mori *et al.* 2017), suggesting that a potential unsuitability of these species could explain such low frequency of occurrence.

When assessing the effect of horse abundance and period on the frequency of occurrence (FO) of prey classes (*Horse*, *Other livestock* and *Wild prey*) in the diet of wolves, we found only a significant negative effect of period on FO of horses, and a significant positive effect of period on other livestock, but not on wild prey (Table 4.3; Appendix 4.8). Horse abundance did not contribute to any of the best models ranked using the AICc criterion (Appendix 4.8). These results show that wolves increased their consumption of domestic prey instead of wild prey as a response to horse decline. Predation on wild prey did not significantly increase during the study period despite the positive population trends of wild ungulates and the gradual decrease of horse abundance. Considering the general negative trend in the abundance of free-ranging livestock, a significant increase in availability cannot be a plausible explanation for the increasing consumption rates of other livestock species. These have been always available and consumed by wolves with low frequency. A higher vulnerability of livestock compared to wild prey could contribute to explain the observed increment in livestock consumption by wolves and the lack of a prey shifting towards wild prey.

Table 4.2. Composition of wolf diet during summer in Costa da Morte from 6 wolf packs between 2006 and 2017, expressed as percentage of occurrence. n= number of scats.

Period	1 (2006-2008)			2 (2011-2013)						3 (2015-2017)					
Wolf pack	**Baiñas**	**Ruña**	**Vimianzo**	**Baiñas**	**Ruña**	**Vimianzo**	**Buxantes**	**Carnota**	**Muxía**	**Baiñas**	**Ruña**	**Vimianzo**	**Buxantes**	**Carnota**	**Muxía**
	n=47	n=22	n=81	n=33	n=6	n=32	n=10	n=48	n=4	n=6	n=29	n=13	n=25	n=25	n=18
Domestic prey	**100**	**100**	**100**	**87.9**	**100**	**96.9**	**100**	**93.8**	**100**	**83.3**	**100**	**100.0**	**100**	**100**	**100**
Horse (*Equus caballus*)	55.3	59.1	95.1	42.4	100.0	46.9	80.0	79.2	0.0	50.0	54.2	61.5	66.7	88.0	13.3
Sheep (*Ovis aries*)	31.9	9.1	2.5	21.2	0.0	21.9	20.0	8.3	75.0	33.3	12.5	23.1	16.7	0.0	33.3
Cattle (*Bos taurus*)	2.1	22.7	2.5	15.2	0.0	18.8	0.0	6.3	0.0	0.0	37.5	7.7	0.0	4.0	20.0
Rabbit (*Oryctolagus cuniculus*)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	46.7
Goat (*Capra aegagrus hircus*)	2.1	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	4.2	7.7	16.7	8.0	6.7
Pig (*Sus scrofa domestica*)	2.1	4.5	0.0	9.1	0.0	3.1	0.0	0.0	0.0	0.0	4.2	0.0	4.2	0.0	0.0
Dog (*Canis lupus familiaris*)	4.3	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Poultry (*Gallus gallus domesticus*)	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wild prey	**0.0**	**0.0**	**0.0**	**12.1**	**0.0**	**3.1**	**0.0**	**6.3**	**0.0**	**16.7**	**8.3**	**0.0**	**0.0**	**0.0**	**0.0**
Roe deer (*Capreolus capreolus*)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.7	8.3	0.0	0.0	0.0	0.0
Wild Boar (*Sus scrofa castilianus*)	0.0	0.0	0.0	12.1	0.0	3.1	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Only an annual average of 13 (s.e.=3.4) heads of livestock other than horse have been officially registered as lost to wolves in the study area during summer (Appendix 4.9), not reflecting the observed increase of livestock consumption by wolves revealed by scat analysis. This fact raises concern about the reliability of livestock claims as a surrogate for wolf depredation in our area. However, the proportion of domestic ungulates that were consumed in the form of carrion or predated remained unknown. Current regulations at the European level (CE 1774/2002 Regulation) obligate livestock owners to remove carcasses from the field, so livestock carcasses available to wolves are not expected to be abundant (Llaneza & López-Bao 2015). Carcasses need to be found and examined by official rangers in order to account as wolf depredations in the official database. The proportion of livestock killed that is not claimed or is not found remains unknown.

Table 4.3. Parameter estimates in the best candidate Generalized Linear Mixed Models testing the influence of horse relative abundance and period (three levels) in the consumption rates of Horses, Wild prey and Other livestock by wolves in Costa da Morte (Galicia, NW Spain).

FO of horse

Parameter	Estimate (β)	S.E.	Z-value	P-value
Intercept	1.684	0.577	2.920	0.004
Period	-0.612	0.168	-3.636	0.000

FO of wild prey

Parameter	Estimate (β)	S.E	Z-value	P-value
Intercept	-5.185	1.249	-4.151	0.000
Period	0.680	0.458	1.485	0.138

FO of other livestock

Parameter	Estimate (β)	S.E	Z-value	P-value
Intercept	-1.560	0.595	-2.622	0.009
Period	0.498	0.170	2.936	0.003

Shifting prey patterns in wolves

The assumption of an expected negative relationship between wild prey abundance and consumption on livestock by wolves has been frequently mentioned in the literature (Meriggi & Lovari 1996; Barja 2009; Meriggi *et al.* 2014). Similarly, wolf preference for wild prey over livestock has been stated recurrently in scientific literature (Appendix 4.1). However, strong evidence of the potential benefits of an increment in wild prey populations to mitigate human-wolf conflicts has seldom been provided (Sidorovich *et al.* 2003, Gula 2008), while opposed or inconclusive results have regularly been reported (Patalano & Lovari 1993; Suryawanshi *et al*. 2013). Some have pointed out contextual particularities as the main factor unbalancing the relationship between availability and consumption of prey choice by wolves.

Here we showed a resistance by wolves to shift from livestock to wild prey in the mid-term, despite a substantial decrease in the availability of their staple prey and an increase of wild prey over time. The reliance on a particular prey for a long period has been pointed out as a potential mechanism responsible for wolf reluctance to shift prey despite marked changes in prey availability (Potvin *et al*. 1988; Mattioli *et al*. 1995; Spaulding *et al.* 1998, Jedrzejewski *et al*. 2000). This mechanism could partially explain the high proportion of horses in the diet of wolves in our study area over time, where the traditional system of free ranging horse husbandry has not changed substantially for centuries (Iglesias 1973), and may have played a key role in wolf persistence and conflict mitigation (López-Bao *et al.* 2013). The inverse direction of resistance to diet shifting (to livestock, after a strong decrease in the availability of wild prey, has also been observed (Chavez & Gese 2005).

Our results also suggest the convenience of maintaining horse numbers as a measure to alleviate the conflict. In addition, horses in this area provide important regulation ecosystem services, reducing fuel biomass in an area prone to forest fires, and maintaining biodiverse heathland ecosystems of important conservation value (López-Bao *et al.* 2013; Fagúndez 2016). Establishing innovative mechanisms that incentivize free-ranging horse husbandry in the area should deserve further attention since it could help reduce depredation on more valuable stocks, keeping the conflict at sustainable levels, while entailing positive side-effects.

Wolf management and conservation plans pay much attention to reducing the impact of wolves on livestock, especially in human-dominated landscapes. Nonetheless, despite interventions aiming to improve or maintain wild prey populations appear frequently in these legal instruments (Appendix 4.2), the motivation behind this action is rarely specified as a way to mitigate the conflict with livestock. Instead, preservation of game stocks and conservation of prey species are frequent justifications. We acknowledge that management plans in northern Europe and North America seldom aim to enhance wild prey populations because these are already healthy (Newsome *et al*. 2016). In southern and central Europe, improving wild prey populations to reduce livestock damages has received more attention (Appendix 4.2). This is one of the regions within the wolf range where wolves feed more frequently on anthropogenic sources of food (Newsome *et al.* 2016; Ståhlberg *et al.* 2017).

With our illustrative example we aimed to highlight potential pitfalls of integrating blindly the promotion of wild prey populations to mitigate livestock-wolf conflicts. We argue that in-deep knowledge of every particular context is required before recommending wild prey enhancement, since the expected outcome from this action in the mid-term may be interfered by multiple factors, including the interaction between wolf behaviour and livestock husbandry practices. In particular, the higher vulnerability of livestock as compared to that of wild prey may hamper an effective reduction of attacks on livestock (Eklund *et al.* 2017). We do not state that increasing wild prey should not be considered, but it should be planned carefully under site-specific assessments before considering this action as a general rule. A delayed response in prey shifting can limit the expected outcomes of this intervention, which can last for several wolf generations in areas where wolves have relied in a particular prey for a long time.

While promoting wild prey alone will not necessarily trigger the expected response in decreasing the number of wolf attacks on livestock in the mid-term, we argue that when needed (e.g., areas with very low wild prey abundance) this intervention should be better fit as complementary to extensively reducing livestock vulnerability to wolf attacks, by promoting husbandry practices and adopting interventions aimed to reduce the access of wolves to livestock (Eklund *et al.* 2017). Without a proper protection of livestock, prey shifting may not be possible in multiple scenarios where wolves have relied on livestock for generations, and where livestock is easier to capture than wild prey. Livestock protection may be enough in many situations. Otherwise the joint enhancement of wild prey populations and livestock protection may be suitable for mitigating the human-wolf conflict. Other issue associated with the promotion of wild ungulate populations, namely its potential impact on forestry, agriculture and road safety, should also be considered.

References

Andersone, Ž., & Ozoliņš, J. (2004). Food habits of wolves *Canis lupus* in Latvia. *Acta Theriologica* 49: 357.

Ansorge, H., Kluth, G., & Hahne, S. (2006). Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriologica* 51: 99–106.

Aragón, S., Braza, F., San Jose, C. (1995). Socioeconomic, physiognomic, and climatic factors determining the distribution pattern of roe deer Capreolus capreolus in Spain. *Acta Theriologica* 40: 37-43**.**

Barja, I. (2009). Prey and Prey-Age Preference by the Iberian Wolf *Canis Lupus Signatus* in a Multiple-Prey Ecosystem. *Wildlife Biology* 15: 147-154.

Boitani, L. (2000). Action plan for the conservation of Wolves in Europe (Canis lupus) Strasbourg Cedex, Council of Europe (85pp).

Breitenmoser, U., Angst, C., Landry, J.M., Breitenmoser-Wursten, C., Linnell, J.D.C. & Weber, J.M. (2005). Non-lethal techniques for reducing depredation. Pp: 49.61 *In*: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds). People and wildlife: conflict or coexistence? Cambridge. Cambridge University Press.

Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., & Apollonio, M. (2004). A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mammalian Biology* 69:1–10.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López- Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517-1519.

Chavez, A.S, & Gese E.M. (2005). Food Habits of Wolves in Relation to Livestock Depredations in Northwestern Minnesota. *The American Midland Naturalist* 154:253-263.

Chetri, M., Odden, M., & Wegge, P. (2017). Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal. *PLoS ONE* 12: e0170549.

Ciucci, P., Artoni, L., Crispino, F., Tosoni, E., & Boitani, L. (2018). Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. *European Journal of Wildlife Research* 64: 5.

Cruz, T., Fonseca, C., Carvalho, J., Oliveira, B., Torres, R.T. (2014). Roe deer reintroduction in central Portugal: a tool for Iberian wolf conservation. *Galemys* 26: 31-40.

Cuesta L., F. Barcena, F., Palacios, F., & Reig, S. (1991). The trophic ecology of the Iberian Wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia* 55: 239-254.

Dale, B., Adams, L., & Bowyer, R. (1994). Functional Response of Wolves Preying on Barren-Ground Caribou in a Multiple-Prey Ecosystem. *Journal of Animal Ecology* 63: 644-652.

Dickman, A., MacDonald, E.A. & MacDonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *PNAS* 108: 13937-13944.

Eklund, A., López-Bao, J.V., Tourani, M., Chapron, G., & Frank, J. (2017). Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific Reports* 7: 2097.

Fagúndez, J. (2016). Grazing effects on plant diversity in the endemic *Erica mackayana* heathland community of north-west Spain. *Plant Ecology & Diversity* 9: 207-217.

Garrott, R.A., Bruggeman, J.E., Becker, M.S., Kalinowski, S.T., & White, P.J. (2007). Evaluating prey switching in wolf–ungulate systems. *Ecological Applications*, 17: 1588–1597.

Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P., & Apollonio, M. (2005). Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology* 266:205–213.

Gazzola, A., Capitani, C., Mattioli, L. and Apollonio, M. (2008). Livestock damage and wolf presence. *Journal of Zoology*, 274: 261-269.

Geisser, H., and Reyer, H-U. (2004). Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. *The Journal of Wildlife Management*, 68 :939-946.

Gittleman, J.L., Funk, S.M., Macdonald, D. & Wayne, R.K. (2001). Carnivore Conservation. Cambridge University Press, Cambridge, UK.

Guitián, J., De Castro, A., Bas, S. & Sánchez, J.L. (1979). Nota sobre la dieta del lobo (*Canis lupus* L.) en Galicia. *Trabajos Compostelanos de Biología* 8: 95–104.

Gula, R. (2008). Wolf Depredation on domestic animals in the polish Carpathian Mountains. *The Journal of Wildlife Management* 72: 283-289.

Iglesias, P.J. (1973). Los caballos gallegos explotados en régimen de libertad o caballos salvajes en Galicia. Tesis doctoral inédita. Facultad de Veterinaria de la Universidad Complutense de Madrid.

Imbert, C., Caniglia, R., Fabbri, E., Milanesi, P., Randi, E., Serafini, M., Torretta, E., & Meriggi, A. (2016). Why do wolves eat livestock? Factors influencing wolf diet in northern Italy. *Biological Conservation* 195: 156–168.

Imperio, S., Ferrante, M., Grignetti, A., Santini, G., and Focardi, S. (2010). Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? *Wildlife Biology* 16: 205-214.

Instituto Galego de Estatística (2018). Xunta de Galicia (Regional Government of Galicia). Livestock census series. https://www.ige.eu.

Jędrzejewska, B., & Jędrzejewski, W. (1998). Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a case study. Ecological Studies (Analysis and Synthesis), 135. Springer, Berlin, Heidelberg.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., & Musiani, M. (2000). Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *Journal of Mammalogy* 81: 197–212.

Karlsson, J., & M. Sjöström. (2011). Subsidized fencing of livestock as a means of increasing tolerance for wolves. *Ecology and Society* 16: 16.

Kellert, S.R., Black, M., Rush, C.R. and Bath, A.J. (1996). Human Culture and Large Carnivore Conservation in North America. *Conservation Biology* 10: 977-990.

Lagos, L. (2013). Ecología del lobo (*Canis lupus*), del poni salvaje *(Equus ferus atlanticus*) y del ganado vacuno semiextensivo (*Bos taurus*) en Galicia: interacciones depredador-presa. *Ph.D Thesis*, Santiago de Compostela University, Spain.

Lagos, L., & Bárcena, F. (2018). Spatial variability in wolf diet and prey selection in Galicia (NW Spain). *Mammal Research* 63: 125.

Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions* 18: 459–469.

Llaneza, L., & López-Bao, J.V. (2015). Indirect effects of changes in environmental and agricultural policies on the diet of wolves. *European Journal of Wildlife Research* 61: 895.

Löe, J. & Röskaft, E. (2004). Large Carnivores and Human Safety: A Review. *AMBIO* 33: 283-288.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013). Indirect Effects on Heathland Conservation and Wolf Persistence of Contradictory Policies that Threaten Traditional Free-Ranging Horse Husbandry. *Conservation Letters* 6: 448-455.

López-Bao, J.V., Blanco, J.C., Rodríguez, A., Godinho, R., Sazatornil, V., Álvares, F., García, E.J., Llaneza, L., Rico, M., Cortés, Y., Palacios, V., & Chapron, G. (2015). Toothless Wildlife Protection Laws. *Biodiversity and Conservation* 24: 2105-2108.

López-Bao J.V., Godinho, R., Pacheco, C., Lema, F.J., García, E.J., Llaneza, L., Palacios, V., & Jiménez, J. (2018). Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. *Scientific Reports* 8: 2177.

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., Ozoliņš, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C., & Náhlik, A. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. *Pest Management Science* 71: 492-500.

Mattioli, L., Apollonio, M., Mazzarone, V., & Centofani, E. (1995). Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta Theriologica* 40: 387-402.

Mattioli, L., Capitani, C., Avanzinelli, E., Bertelli, I., Gazzola, A., & Apollonio, M. (2004). Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in North-Eastern Apennine, Italy. *Journal of Zoology* 264: 249-258.

Mattioli, L., Capitani, C., Gazzola, A., Scandura M., & Apollonio, M. (2011). Prey selection and dietary response by wolves in a high-density multi-species ungulate community. *European Journal of Wildlife Research* 57:909–922.

Mech; L.D. & Karns, P. D. (1977). Role of the wolf in a deer decline in the Superior National Forest. U.S. Department of Agriculture Forest Service. Saint Paul (MN). 23pp.

Meriggi, A., Brangi, A., Matteucci, C., & Sacchi, O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* 19:287-295.

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33: 1561-1571.

Meriggi A., Brangi A., Schenone L., Signorelli D., Milanesi P. (2011). Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution* 23: 195–210.

Meriggi, A., Dagradi, V., Dondina, O., Perversi, M., Milanesi, P. Lombardini, M., Raviglione S., & Repossi, A. (2014). Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy. *Ethology Ecology & Evolution* 27: 389-411.

Milanesi, P., Meriggi A., & Merli, E. (2012). Selection of wild ungulates by wolves *Canis lupus* (L. 1758) in an area of the Northern Apennines (North Italy). *Ethology Ecology & Evolution* 24: 81-96.

Morehouse, A.T., & Boyce, M.S. (2011). From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. *Frontiers in Ecology and the Environment* 9: 440-445.

Mori, E., Benatti L., Lovari, S., & Ferretti, F. (2017). What does the wild boar mean to the wolf? *European Journal of Wildlife Research* 63: 9.

Muhly, T.B., & Musiani, M. (2009). Livestock depredation by wolves and the ranching economy in the Northwestern U.S. *Ecological Economics* 68: 2439-2450.

Naughton-Treves, L., Grossberg, R., & Treves, A. (2003). Paying for Tolerance: Rural Citizens' Attitudes toward Wolf Depredation and Compensation. *Conservation Biology* 17: 1500-1511.

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., López-Bao J.V., Peterson R.O., Shores, C.R., Wirsing, A.J., & Ripple, W.J. (2016). Food habits of the world's grey wolves. *Mammal Review* 46: 255–269.

Nowak, S., Mysłajek, R.W., Kłosińska, A., & Gabryś, G. (2011). Diet and prey selection of wolves (*Canis lupus*) recolonising Western and Central Poland. *Mammalian Biology* 76: 709-715.

Oakleaf, J., Mack, C., & Murray, D. (2003). Effects of Wolves on Livestock Calf Survival and Movements in Central Idaho. *The Journal of Wildlife Management* 67: 299-306.

Pacheco, C., López-Bao, J.V., García, E.J., Lema, F.J., Llaneza, L., Palacios, V., & Godinho, R. (2017). Spatial assessment of wolf-dog hybridization in a single breeding period. *Scientific Reports* 7: 42475.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., Maclennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O. and Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters* 16: 635–641.

Patalano, M., & Lovari, S. (1993). Food habits and trophic niche overlap of the wolf *Canis lupus*, (L. 1758) and the red Fox *Vulpes vulpes* (L. 1758) in a Mediterranean mountain area. *Revue d'écologie* 48: 279-294.

Pimlott, D.H. (Ed.). (1975). Wolves: Proceedings of the First Working Meeting of Wolf Specialists and of the First International Conference on the Conservation of the Wolf. Stockholm, Sweden, 5-6 September, 1973. IUCN Publications: Supplementary paper 43; International Union for Conservation of Nature and Natural Resources.

Potvin, F., Jolicoeur, H., & Huot, J. (1988). Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. *Canadian Journal of Zoology*, 66: 1274-1279.

Poulle, M.L., Carles, L., & Lequette, B. (1997). Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (Southeastern France). *Revue d'écologie* 52: 357-368.

Rigg, R., & Gorman, M. (2004). Spring-autumn diet of wolves (*Canis lupus*) in Slovakia and a review of wolf prey selection. *Oecologia Montana* 13: 30-41.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., & Wirsing, A.J. (2014). Status and Ecological Effects of the World's Largest Carnivores. Science 343: 1241484.

Sáez-Royuela, C. & Tellería, J.L. (1986). The increased population of the wild boar (*Sus scrofa*) in Europe. *Mammal Review* 16: 97-101.

Schenone, L., Aristarchi, C., & Meriggi, A. (2004). Ecologia del lupo (*Canis lupus*) in provincia di Genova: distribuzione, consistenza, alimentazione e impatto sulla zootecnia. *Hystrix Italian Journal of Mamalogy* 15:13-30.

Sidorovich, V.E., Tikhomirova, L.L, & Jędrzejewska, B. (2003). Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. *Wildlife Biology* 9: 103-111.

Sillero-Zubiri, C., Sukumar, R. & Treves, A. (2007). Living with Wildlife: the roots of conflict and the solutions. *In*: Macdonald, D.W. & Service, K. (Eds.) Key Topics in Conservation Biology. Blackwell Publishing Ltd, UK.

SGHN (Sociedade Galega de Historia Natural). (1995). Atlas de Vertebrados de Galicia, volume I. Consello da Cultura Gallega, Santiago de Compostela.

Spaulding, R.L., Krausman,P.R., & Ballard, W.B. (1998). Summer diet of Grey Wolves, *Canis lupus*, in north-western Alaska. *Canadian Field Naturalist* 112: 262-266.

Ståhlberg, S., Bassi, E., Viviani, V., & Apollonio, M. (2017). Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*). *Mammalian Biology* 83: 34-43.

Suryawanshi, K.R., Bhatnagar, Y.V., Redpath, S., Mishra, C. & Pettorelli, N. (2013) People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology* 50: 550-560.

Torres, R.T., Silva, N., Brotas, G., & Fonseca, C. (2015). To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (*Canis lupus signatus*) in a Human-Dominated Landscape in Central Portugal. *PLoS ONE* 10: 129379.

Tourani, M., Moqanaki, E.M., Boitani, L., & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78: 117–121.

Treves, A., & Karanth, K.U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* 17: 1491-1499.

Treves, A., Naughton-Treves, L., Harper, E. K., Mladenoff, D. J., Rose, R. A., Sickley, T. A., & Wydeven, A. P. (2004). Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock. *Conservation Biology* 18: 114-125.

Valdmann H., Koppa O., & Looga L. (1998). Diet and prey selectivity of wolf Canis lupus in rniddle- and south-eastern Estonia. *Baltic Forestry* 1: 42-46.

Vittersø, J., Kaltenborn, B.P. & Bjerke, T. (2015). Attachment to Livestock and Attitudes Toward Large Carnivores Among Sheep Farmers in Norway. *Anthrozoös* 11: 210-217.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. *Journal of Zoology* 251: 457-462.

Vucetich, J., & Nelson, M.P. (2017). Wolf Hunting and the Ethics of Predator Control. Pp: 411-432 *In*: Kalof, L. (Ed.) The Oxford Handbook of Animal Studies. Oxford University Press, New York.

Wagner, C., Holzapfel, M., Kluth, G., Reinhardt, I., & Ansorge, H. (2012). Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. *Mammalian* 77: 196–203.

Ward, A.I., White, P.C.L., Smith, A., & Critchley, C.H. (2004). Modelling the cost of roe deer browsing damage to forestry. *Forest Ecology and Management* 191: 301-310.

Weaver, J.L. (1993). Refining the equation for interpreting prey occurrence in gray wolf scats. *Journal of Wildlife Management* 57: 534–538.

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165-173.

APPENDIX CHAPTER 4

(*Recovering wild prey to mitigate human-wolf conflicts? Insights from academia, management and field observations*).

APPENDIX 4.1: Available evidence regarding A) the relationship between livestock losses and wild prey abundance and B) wolf preference for wild or domestic prey

A) RELATIONSHIP BETWEEN LIVESTOCK LOSSES AND WILD PREY ABUNDANCE

We searched for references dealing with the numerical effect of wild prey on the number of wolf attacks on livestock, in order to assess the feasibility of increasing wild prey populations as a mitigation intervention to reduce livestock losses, and the supporting evidence for this.

We used the Google Scholar database and searched for references from the last 30 years using the keywords (“*wolf” OR “wolves”*) *AND "wild prey" AND ("livestock" OR "domestic"*) *AND "depredation" AND "conflict"*. The search returned 850 studies from which we selected those assuming an effect of wild prey abundance on livestock depredation (including assumptions bibliographically supported), and those testing such effect. Overall, we kept 46 studies, of which 31 assumed a negative correlation between wild prey abundance and livestock losses and 10 provided statistical evidence for this relationship; 3 did not find any effect, and 1 showed a positive correlation (more wild prey, more damages to livestock).

- List of references <u>assuming a negative correlation</u> between wild prey availability and wolf damages to livestock.

Ansorge, H., Kluth, G., & Hahne, S. (2006). Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriologica* 51: 99–106.

Breitenmoser. U., Angst, C., Landry, J.M., Breitenmoser-Wursten, C., Linnell, J.D.C., & Wever, J.M. (2005) Non-lethal techniques for reducing depredation. *In*: Woodroffe, R., Thirgood, S., & Rabinowitz, A. (Eds.) People and Wildlife. Conflict or Co-existence? New York: Cambridge University Press. 49–71.

Capitani, C., Chynoweth, M., Kusak, J., Çoban, E., & Şekercioğlu, Ç. H. (2015). Wolf diet in an agricultural landscape of north-eastern Turkey. *Mammalia* 80:329-334.

Ciucci, P., Artoni, L., Crispino, F., Tosoni, E., & Boitani, L. (2018). Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. *European Journal of Wildlife Research* 64: 5.

Cruz, T., Fonseca, C., Carvalho, J., Oliveira, B., Torres, R.T. (2014). Roe deer reintroduction in central Portugal: a tool for Iberian wolf conservation. *Galemys* 26: 31-40.

Davie, H.S., Murdoch, J.D., Lhagvasuren, A., & Reading, R.P. (2014) Measuring and mapping the influence of landscape factors on livestock predation by wolves in Mongolia. *Journal of Arid Environments* 103: 85-91.

Davis, M.L., Stephens, P.A., Willis, S.G., Bassi, E., Marcon, A., Donaggio, E., Capitani, C., & Apollonio, M. (2012). Prey Selection by an Apex Predator: The Importance of Sampling Uncertainty. *PLoS ONE* 7: e47894.

Ekernas, L. S., Sarmento, W. M., Davie, H. S., Reading, R. P., Murdoch, J., Wingard, G. J., Amgalanbaatar, S. & Berger, J. (2017). Desert pastoralists' negative and positive effects on rare wildlife in the Gobi. *Conservation Biology* 31: 269-277.

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E. & Delibes, M. (2016). Conflict Misleads Large Carnivore Management and Conservation: Brown Bears and Wolves in Spain. *PLoS ONE* 11: e0151541.

Grilo, C., Moço, G., Cândido, A. T., Alexandre, A. S. & Petrucci-Fonseca, F. (2002). Challenges for the recovery of the Iberian wolf in the Douro river south region. *Revista de Biologia* 20:121-133.

Haney, J.C., Kroeger, T., Casey, F., Quarforth, A., Schrader, G., & Stone, S.A. (2007). Wilderness discount on livestock compensation costs for imperiled gray wolf *Canis lupus*. *In*: USDA Forest Service Proceedings. RMRS-P-49, Fort Collins, CO.

Iliopoulos, Y., Sgardelis, S., Koutis, V., & Savaris, D. (2009). Wolf depredation on livestock in central Greece. *Acta Theriologica* 54: 11-22.

Kaartinen, S., Luoto, M. & Kojola, I. (2009). Carnivore-livestock conflicts: determinants of wolf (*Canis lupus*) depredation on sheep farms in Finland. *Biodiversity and Conservation* 18: 3503.

Graham, K., Beckerman, A.P., & Thirgood, S. (2005). Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. *Biological Conservation* 122: 159-171.

Lagos, L., & Bárcena, F. (2018). Spatial variability in wolf diet and prey selection in Galicia (NW Spain). *Mammal Research* 63: 125.

Linnell, J.D.C., Oden, J., & Mertens, A. (2012). Mitigation mehtods for conflicts associated with carnivore depredation on livestock. *In*: Boitani, L. & Powell, R.A. (Eds.). Carnivore Ecology and Conservation: A handbook of techniques. Techniqes in Ecology & Conservation Series. Oxford University Press. New York.

Linnell, J.D.C., Promberger, C., Boitani, L., Swenson, J.E., Breitenmoser, U., & Andersen, R. (2013). The Linkage between Conservation Strategies for Large Carnivores and Biodiversity: The View from the "Half-Full" Forests of Europe. Pp 381-399 *In*: Ray, J.C., Redford, K.H., Steneck, R.S., & Berger, J. Large Carnivores and the Conservation of Biodiversity. Island Press. Washington D.C.

Li, C., Jiang, Z., Li, C., Tang, S., Li, F., Luo, Z., Ping, X., Liu, Z., Chen, J., & Fang, H. (2015). Livestock depredations and attitudes of local pastoralists toward carnivores in the Qinghai Lake Region, China. *Wildlife Biology* 21: 204-212.

Meriggi, A., Dagradi, V., Dondina, O., Perversi, M., Milanesi, P., Lombardini, M., Raviglione, S. & Repossi A. (2014). Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy. *Ethology Ecology & Evolution* 27: 389-411.

Mishra, C. (1997). Livestock depredation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. *Environmental Conservation* 24: 338–343.

Newsome TM, Boitani L, Chapron G, Ciucci P, Dickman CR, Dellinger JA, López-Bao JV, Peterson R.O, Shores CR,WirsingAJ, RippleWJ (2016) Food habits of the world's grey wolves. *Mammal Review* 46: 255–269.

Poulle, M.L., Carles, L., & Lequette, B. (1997) Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (southeastern France). *Revue d'écologie* 52: 357-368.

Rajaratnam, R., Vernes, K., & Sangay, T. (2016). A Review of Livestock Predation by Large Carnivores in the Himalayan Kingdom of Bhutan. *In*: Angelici, F. (Ed.) Problematic Wildlife. Springer, Switzerland.

Rigg, R., & Gorman, M. (2004). Spring-autumn diet of wolves (*Canis lupus*) in Slovakia and a review of wolf prey selection. *Oecologia Montana* 13: 30 - 41.

Rigg, R., Findo, S., Wechselberger, M., Gorman, M.L., Sillero-Zubiri, C., & Macdonald, D.W. (2011). Mitigating carnivore–livestock conflict in Europe: lessons from Slovakia. *Oryx* 45: 272-280.

Schenone, L., Aristarchi, C., & Meriggi, A. (2004). Ecologia del lupo (canis lupus) in provincia di Genova: distribuzione, consistenza, alimentazione e impatto sulla zootecnia. *Hystrix Italian Journal of Mammalogy* 15:13-30.

Torres, R.T., Silva, N., Brotas, G., & Fonseca, C. (2015). To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (*Canis lupus signatus*) in a Human-Dominated Landscape in Central Portugal. *PLoS ONE* 10: 129379.

Torres, R.T., & Fonseca, C. (2016). Perspectives on the Iberian wolf in Portugal: population trends and conservation threats. *Biodiversity and Conservation* 25: 411-425.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. *Journal of Zoology* 251: 457-462.

Wagner, C., Holzapfel, M., Kluth, G., Reinhardt, I., & Ansorge, H. (2012) Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. *Mammalian* 77: 196–203.

Wydeven, A.P., Wiedenhoeft, J.E., Schultz, R.N., Thiel, R.P., Jurewicz, R.L., Kohn, B.E., & Van Deelen, T.R. (2009). History, Population Growth, and Management of Wolves in Wisconsin. *In*:Wydeven, A.P., Van Deelen, T.R., & Heske, E.J. (Eds.). Recovery of gray wolves in the Great Lakes Region of the United States. Springer Science & Business Media,New York.

- List of references reporting a statistically significant <u>negative correlation</u> between wild prey abundance and damages to livestock (or proportion of livestock in diet).

Barja, I. (2009). Prey and Prey-Age Preference by the Iberian Wolf *Canis Lupus Signatus* in a Multiple-Prey Ecosystem. *Wildlife Biology* 15: 147-154.

Gula, R. (2008). Wolf Depredation on domestic animals in the polish Carpathian Mountains. *The Journal of Wildlife Management* 72: 283-289.

Hovens, P.M., Tungalaktuja, K. (2005). Seasonal fluctuations of the wolf diet in the Hustai National Park (Mongolia). *Mammalian Biology* 70: 210-217.

Imbert C., Caniglia, R., Fabbri, E., Milanesi, P., Randi, E., Serafini, M., Torretta, E., & Meriggi, A. (2016) Why do wolves eat livestock? Factors influencing wolf diet in northern Italy. *Biological Conservation* 195: 156–168.

Mech, L., Fritts, S., & Paul, W. (1988). Relationship between Winter Severity and Wolf Depredations on Domestic Animals in Minnesota *Wildlife Society Bulletin* 16: 269-272.

Meinecke, L., Soofi, M., Riechers, M., Khorozyan, I., Hosseini, H., Schwarze, S., Waltert, M. (2018). Crop variety and prey richness affect spatial patterns of human-wildlife conflicts in Iran's Hyrcanian forests. *Journal for Nature Conservation* 43: 165-172.

Meriggi,A., & Lovari, S. (1996). A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33: 1561-1571.

Meriggi, A., Brangi, A., Matteucci, C., & Sacchi, O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* 19:287-295.

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., & Milanesi, P. (2011). Changes ofwolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution* 23: 195-210.

Sidorovich, V.E., Tikhomirova, L.L, & Jędrzejewska, B. (2003). Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. *Wildlife Biology* 9: 103-111.

- List of references testing the effect of wild prey abundance on damages to livestock and founding <u>no correlation</u>.

Chetri, M., Odden, M., & Wegge, P. (2017) Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal. *PLoS ONE* 12: e0170549.

Patalano, M., & Lovari, S. (1993). Food habits and trophic niche overlap of the wolf *Canis lupus* (L. 1758) and the red Fox *Vulpes vulpes* (L. 1758) in a Mediterranean mountain área. *Revue d'écologie* 48: 279-294.

Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., Mishra, C. & Pettorelli, N. (2013) People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology* 50: 550-560.

- References reporting a statistically significant positive correlation between wild prey abundance and damages to livestock.

Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff,D.J., Rose, R.A., Sickley, T.A. & Wydeven, A.P. (2004). Predicting carnivore-human conflict: A spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* 18: 114-125.

B) WOLF PREFERENCE FOR WILD OR DOMESTIC PREY

We assessed whether available evidence supports a preference of wolves for wild prey rather than livestock.

We searched Google Scholar for references published since 1990 using the terms (*"wolf" OR "wolves"*) *AND* (*"diet" OR "food habits"*) *AND "wild" AND "domestic" AND* (*"preference" OR "selection"*). The search returned 651 references of which we selected 56 for further scrutiny after removing those not really addressing the topic of interest. As we wanted to analyse the interaction between wild prey and livestock on the feeding ecology of wolves, we also excluded studies in which the frequency of domestic prey in the wolf diet was <5%. We also included four references that explored prey preference through data reviews. Within the filtered database we searched for papers actually examining prey preference by wolves (pooling together wild and domestic prey). Overall, we found 10 studies assuming a preference for wild prey, of which only five confirmed such assumption conducting a specific comparison between the frequencies of domestic and wild prey in the diet of wolves. Two studies suggested a preference or specialisation on domestic prey but only one tested and quantified such an effect. One study (Imbert *et al*. 2016) concluded that selection of domestic or wild prey is dependent on the social status of individual wolves. One correlational analyses and one review concluded that the frequency of each prey class in wolf diet was proportional to the abundance/availability of each prey type.

- Studies suggesting preference of wolves towards wild prey over livestock. References marked with * assess prey selection through correlations between the frequency of wild and domestic prey in the diet of wolves:

*Barja, I. (2009). Prey and Prey-Age Preference by the Iberian Wolf *Canis Lupus Signatus* in a Multiple-Prey Ecosystem. *Wildlife Biology* 15: 147-154.

*Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., & Apollonio, M. (2004) A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mammalian Biology* 69:1–10. (review)

*Chetri, M., Odden, M., & Wegge, P. (2017) Snow Leopard and Himalayan Wolf: Food Habits and Prey Selection in the Central Himalayas, Nepal. *PLoS ONE* 12: e0170549.

*Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P., & Apollonio, M. (2005) Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. *Journal of Zoology* 266:205–213.

*Meriggi,A., & Lovari, S. (1996). A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33: 1561-1571. (review).

Meriggi A., Brangi A., Matteucci C. and Sacchi O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* 19: 287-295.

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., & Milanesi, P. (2011). Changes ofwolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution* 23: 195-210.

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., López-Bao, J.V., Peterson, R.O., Shores, C.R., Wirsing, A.J., & Ripple,W.J. (2016) Food habits of the world's grey wolves. *Mammal Review* 46: 255–269. (review)

Poulle, M.L., Carles, L., & Lequette, B. (1997) Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (southeastern France). *Revue d'écologie* 52: 357-368.

Torretta, E., Serafini,M., Imbert, C., Milanesi, P., & Meriggi, A. (2017). Wolves and wild ungulates in the Ligurian Alps (Western Italy): prey selection and spatial-temporal interactions. *Mammalia* 81: 537-551.

- Studies suggesting preference of wolves for domestic prey over wild prey.

Torres, R.T., Silva, N., Brotas, G., & Fonseca, C. (2015). To Eat or Not To Eat? The Diet of the Endangered Iberian Wolf (*Canis lupus signatus*) in a Human-Dominated Landscape in Central Portugal. PLoS ONE 10: 129379.

Tourani, M., Moqanaki, E.M., Boitani, L., & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78: 117–121.

- Studies suggesting preference of wolves both for domestic and wild prey, depending on their social status. References marked with * assess prey selection through correlations between the frequency of wild and domestic prey in the diet of wolves.

*Imbert C., Caniglia, R., Fabbri, E., Milanesi, P., Randi, E., Serafini, M., Torretta, E., & Meriggi, A. (2016) Why do wolves eat livestock? Factors influencing wolf diet in northern Italy. *Biological Conservation* 195: 156–168 (concludes preference for wild prey by wolves established in packs and for domestic prey by disperser wolves).

- Studies suggesting that predation rates on each group (wild/domestic) are proportional to their availability.

Patalano, M., & Lovari, S. (1993) Food habits and trophic niche overlap of the wolf *Canis lupus*, L. 1758 and the red Fox *Vulpes vulpes* (L. 1758) in a Mediterranean mountain área. *Revue d'écologie* 48: 279-294.

Rigg, R., & Gorman, M. (2004). Spring-autumn diet of wolves (*Canis lupus*) in Slovakia and a review of wolf prey selection. *Oecologia Montana* 13: 30 - 41. (review)

APPENDIX 4.2: Review of wolf management and conservation instruments. Methods (Appendix 4.2.1), Sources (Appendix 4.2.2) and Results (Appendix 4.2.3) are presented.

APPENDIX 4.2.1. (METHODS)

We searched for wolf management and conservation instruments available in literature search engines (Google – www.google.com -, Google Scholar - www.scholar.google.com -) in Europe and North America, and also contacted at least one wolf expert from each country of interest, in order to compile the existing wolf conservation, management and/or action plans and strategies.

We classified papers on wild prey for wolves according to the general topic or objective they were written for. Thus, we considered the following categories: "Diet (descriptive)", "Wild prey availability (no relation with livestock)", "Wild prey availability (related with livestock)", "Interaction with game species/populations", "Ecological impact", "Conservation of prey species". We also classified the studies as to whether they entailed some management interventions or were merely descriptive. We also classified action depending on if they require direct intervention on wild prey or correspond to regulatory measures or the necessity of direct intervention is not clear.

APPENDIX 4.2.2. (SOURCES)

European Plans reviewed and used in Chapter 4

Austria

Wolfs management in Österreich. Grundlagen und Empfehlungen (2012). Koordinierungsstelle für den Braunbären, Luchs und Wolf. Forschungsinstitut für Wildtierkunde und Ökologie, Veterinärmedizinische Universität Wien.

Croatia

Wolf Management Plan for Croatia. Towards understanding and addressing key issues in wolf management planning in Croatia (2005). State Institute for Nature Protection, Zagreb.

Denmark

Forvaltningsplan for ulv i Danmark (2013). Miljøministeriet Naturstyrelsen, København.

Estonia

Status of Large Carnivore Conservation in the Baltic States: Large Carnivore Control and Management Plan for Estonia, 2002-2011 (2001). Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg.

Action plan for conservation and management of large carnivores (wolf *Canis lupus*, lynx *Lynx lynx*, brown bear *Ursus arctos*) in Estonia in 2012–2021 (2012). Estonian Ministry of the Environment, Tartu.

Finland

Management plan for the wolf population in Finland. (2005). Ministry of Agriculture and Forestry, Helsinki.

Suomen susikannan hoitosuunnitelma. (2015). Maa-ja metsätalousministeriö, Helsinki.

France

Plan d'Action Sur le Loup 2004-2008. (2004). Ministère de l'Ecologie et du Développement Durable/Ministère de l'Agriculture, de l'Alimentation, de la Pêche et des Affaires Rurales.

Plan d'Action National Sur Le Loup 2008-2012, dans le contexte Français d'une activité importante et traditionnelle d'élevage. (2008). Ministère de l'Ecologie, de l'Energie, du Développement durable et de l'Aménagement du territoire/Ministère de l'Agriculture et de la Pêche.

Plan d'Action National Loup 2013-2017. (2013). Ministère de l'Ecologie et du Développement Durable et de l'Énergie/Ministère de l'Agriculture, de l'Agroalimentaire et de la Forêt.

Plan national d'actions 2018-2023 sur le loup et les activités d'élevage. (2018). Ministère de la Transition écologique et solidaire/Ministère de l'Agriculture et de l'Alimentation.

Action Plan for the preservation of pastoralism and the wolf in the Alpine chain. (2000). Document prepared by the Ministry of Agriculture and Fisheries & the Ministry for Regional Planning and the Environment (France) for the Council of Europe. Strasbourg.

Germany

Die Rückkehr des Wolfs nach Baden-Württemberg. Handlungsleitfaden für das Auftauchen einzelner Wölfe. (2013). Ministerium für Ländlichen Raum und Verbraucherschutz, Baden-Württemberg.

Managementplan Wölfe in Bayern-Stufe 2: Stand April 2014. (2014). Bayerisches Landesamt für Umwelt, Augsburg.

Managementplan für den Wolf in Brandenburg 2013 – 2017 (2012). Ministerium für Umwelt, Gesundheit und Verbraucherschutz, Brandenburg.

Wolfsmanagement für Hessen (2015). Hessisches Ministerium für Umwelt, Klimaschutz, Landwirtschaft und Verbraucherschutz, Wiesbaden.

Managementplan für den Wolf in Mecklenburg-Vorpommern (2010). Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz, Schwerin.

Der Wolf in Niedersachsen. Grundsätze und Maßnahmen im Umgang mit dem Wolf (2010) Niedersächsisches Ministerium für Umwelt, Energie und Klimaschutz. Hannover.

Wolfsmanagementplan für Nordrhein-Westfalen. Handlungsleitfaden für das Auftauchen einzelner Wölfe (2016). Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen, Recklinghausen.

Managementplan für den Umgang mit Wölfen in Rheinland-Pfalz (2015). Ministerium für Umwelt, Landwirtschaft, Ernährung, Weinbau und Forsten, Mainz.

Managementplan für den Umgang mit Wölfen im Saarland (2015) Ministerium für Umwelt und Verbraucherschutz Saarland. 2015.

Managementplan für den Wolf in Sachsen (2009). Staatministerium für umwelt und Landwirtschaft, Dresden.

Managementplan für den Wolf in Sachsen (2014). Staatministerium für umwelt und Landwirtschaft, Dresden.

Leitlinie Wolf -Grundsätze zum Umgang mit Wölfen in Sachsen-Anhalt (2008). Ministerium für Landwirtschaft und Umwelt des Landes Sachsen-Anhalt, Magdeburg.

Managementplan für den Wolf in Thüringen (2014). Thüringer Ministerium für Umwelt, Energie und Naturschutz, Erfurt.

Hungary

Farkas (*Canis lupus*) (2004). Környezetvédelmi és Vízügyi Minisztérium, Természetvédelmi Hivatal.

Italy

Piano d'azione nazionale per la conservazione del lupo (*Canis lupus*) (2002). Ministero dell'Ambiente e della Tutella del Territorio/Istituto Nazionale per la fauna selvatica "Alessandro Ghigi".

Latvia

Status of Large Carnivore Conservation in the Baltic States: Action Plan for the Conservation of Wolf (*Canis lupus*) in Latvia (2001). Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg.

Wolf (*Canis lupus*) conservation plan (2008). Latvian State Forestry Institute-*Silava*.

Lithuania

Wolf (*Canis Lupus*) Protection Plan (2014). Ministry of Environment of the Republic of Lithuania.

Netherlands

Voorstel voor een wolvenplan voorNederland; versie 2.0. (2013). Alterra Wageningen UR (University & Research centre), Wageningen.

Portugal

Plano de Ação para a Conservação do Lobo -Ibérico (*Canis lupus signatus*) em Portugal. (Provision (Provision n.º 9727/2017, Diário da República, 215 — november 8th. 2017). Instituto da Conservação da Natureza e das Florestas. Lisboa, Portugal.

Slovakia

Program starostlivosti o vlka dravého (*Canis lupus*) na Slovensku (2016). State Nature Conservation of the Republic of Slovakia.

Slovenia

Strategija ohranjanja volka (*Canis lupus*) v Sloveniji in trajnostnega upravljanja z njim (2009).

Akcijski načrt za upravljanje Populacije volka (*Canis lupus*) v sloveniji Za obdobje 2013–2017 (2013). Ministry of Agriculture and the Environment.

Spain

Estrategia para la conservación y gestión del lobo (*Canis lupus*) en España (2005). Ministerio de Medio Ambiente, Madrid.

Plan de Gestión del Lobo (*Canis lupus*) para afrontar el conflicto con la ganadería extensiva en el Territorio Histórico de Álava (2010). Departamento de Medio Ambiente de la Diputación Foral de Álava, Vitoria.

Plan de Gestión del Lobo en el Principado de Asturias (2002). Consejería de Medio Ambiente del Principado de Asturias, Oviedo

II Plan de Gestión del Lobo en el Principado de Asturias (2015). Consejería de Agroganadería y Recursos Autóctonos del Principado de Asturias, Oviedo.

Plan de Xestión do lobo en Galicia (2008). Consellería de Medio Ambiente de Desenvolvemento Sostible de la Xunta de Galicia, Santiago de Compostela.

Plan de gestión del lobo en Castilla y León (2008). Consejería de Medio Ambiente de la Junta de Castilla y León, Valladolid.

Plan de gestión del lobo en Castilla y León (2016). Consejería de Fomento y Medio Ambiente de la Junta de Castilla y León.

Sweden

Åtgärdsprogram för bevarande av varg (*Canis lupus*) (2003). Environmental Protection Agency.

Nationell förvaltningsplan för varg Förvaltningsperioden 2014–2019 (2014). Environmental Protection Agency.

Switzerland

Strategie der Volkswirtschaftsdirektion über den Umgang mit dem Wolf im Kanton Bern (2007). Economic Policy Directorate.

Konzept Wolf Managementplan für den Wolf in der Schweiz (2008). Federal Department of Foreign Affairs Environment, Transport, Energy and Communications/Federal Office for the Environment/Department of Species Management.

Strategia Lupo Svizzera: Aiuto all'esecuzione dell'UFAM sulla gestione del lupo in Svizzera (2016). Federal Department of Environment, Transport, Energy and Communications/Federal Office for the Environment.

North American Plans reviewed and used in Chapter 4

Canada

Management Plan for Wolves in Alberta. (1991). Fish and Wildlife Division, Forestry, Lands and Wildlife. Edmonton, AB.

Management Plan for the Grey Wolf (Canis lupus) in British Columbia (2014). B.C. Ministry of Forests, Lands and Natural Resource Operations. Victoria, BC.

Management Plan for the Eastern Wolf (Canis lupus lycaon) in Canada (Proposed, 2017). Species at Risk Act Management Plan Series, Environment and Climate Change Canada, Ottawa.

Strategy for Wolf Conservation in Ontario (2005). Ontario Ministry of Natural Resources. Peterborough, ON.

Yukon Wolf Conservation and Management Plan (2012). Environment Yukon, Government of Yukon, Whitehorse, YT.

United States of America

Blackfeet Tribe Wolf Management Plan (2008). Blackfeet Tribal Business Council.

Northern gray wolf management plan for the Flathead Indian Reservation (2009). Confederated Salish and Kootenai Tribes Tribal Wildlife Management Program. Pablo, MT.

Idaho Wolf conservation and management Plan (2002). Idaho Legislative Wolf Oversight Committee.

Idaho Wolf Population Management Plan, 2008-2012 (2008). Idaho Department of Fish and Game. Boise, ID.

Mexican Wolf Recovery Plan (1982). U.S. Fish and Wildlife Service. Albuquerque, NM.

Mexican Wolf Interagency Management Plan (1998). U.S. Fish and Wildlife Service.

Project of the Mexican Wolf Recovery Plan, 1st review (2017). U.S. Fish and Wildlife Service. Albuquerque, NM.

Michigan gray Wolf Recovery and Management Plan (1997). Michigan Department of Natural Resources. Lansing, MI.

Michigan Wolf Management Plan (2008). Michigan Department of Natural Resources. Lansing, MI.

Michigan Wolf Management Plan Updated (2015). Michigan Department of Natural Resources. Lansing, MI.

Minnesota Wolf Management Plan (2001). Minnesota Department of Natural Resources. St. Paul, MN.

Montana Gray Wolf Conservation and Management Plan (2004). Montana Fish, Wildlife and Parks. MT.

Northern Rocky Mountain Wolf Recovery Plan (1987). U.S. Fish and Wildlife Service. Denver, CO.

Oregon Wolf Conservation and Management Plan (2005, updated 2010). Oregon Department of Fish and Wildlife. Salem, OR.

Oregon Wolf Conservation and Management Plan (draft, 2017). Oregon Department of Fish and Wildlife. Salem, OR.

Utah Wolf Management Plan (2004). Utah Division of Wildlife Resources. Salt Lake City, UT.

Wolf conservation and management Plan for Washington (2011). Washington Department of Fish and Wildlife, Olympia, WA.

Wisconsin Wolf Management Plan (1999). Wisconsin Department of Natural Resources. Hayward, WI.

Wolf Management Plan for the Wind River Reservation (2007). Shoshone and Arapaho Tribal Fish and Game Department. Ethete, WY.

Wyoming Gray Wolf Management Plan (2011, Ammended in 2012). Wyoming Game and Fish Comission. Cheyenne, WY.

APPENDIX 4.2.2. (RESULTS). Presence of interventions or guidelines regarding interventions on wild prey in wolf plans and strategies from Europe and North America.

Continent	Country	Geographical Reference (region)	Year	Intervention on wild prey[1]	(Re) introduction of wild prey	Associates wild prey with attacks on livestock
Europe	Austria	-	2012	-	-	-
Europe	Croatia	-	2005	X	X	-
Europe	Denmark	-	2013	-	-	-
Europe	Estonia	-	2001	-	-	-
Europe	Estonia	-	2012	-	-	-
Europe	Finland	-	2005	-	-	-
Europe	Finland	-	2015	-	-	X
Europe	France	-	2004	-	-	-
Europe	France	-	2008	-	-	-
Europe	France	-	2013	-	-	-
Europe	France	-	2018	-	-	-
Europe	Germany	Baden-Württ.	2013	-	-	-
Europe	Germany	Bayern	2014	-	-	-
Europe	Germany	Brandenburg	2012	-	-	-
Europe	Germany	Hessen	2015	-	-	X
Europe	Germany	Niedersachsen	2010	-	-	-
Europe	Germany	M.-Vorpommern	2010	-	-	-
Europe	Germany	N.-Westfalen	2016	-	-	-
Europe	Germany	Rheinland-Pfalz	2015	-	-	-
Europe	Germany	Saarland	2015	-	-	-
Europe	Germany	Sachsen	2009	-	-	-
Europe	Germany	Sachsen	2014	-	-	-
Europe	Germany	Thüringen	2014	-	-	-
Europe	Germany	Sachsen-Anhalt	2008	-	-	-
Europe	Hungary	-	2004	-	-	-
Europe	Italy	-	2002	X	X	X
Europe	Latvia[2]	-	2001	-	-	-
Europe	Latvia	-	2008	X	-	-
Europe	Lithuania	-	2014	-	-	-
Europe	Netherlands	-	2013	X	-	-
Europe	Portugal	-	2017	X	-	-
Europe	Slovakia	-	2016	X	-	-
Europe	Slovenia	-	2009	X	-	X
Europe	Slovenia	-	2013	X	-	X
Europe	Spain	-	2005	X	-	-
Europe	Spain	Álava	2010	-	-	-
Europe	Spain	Asturias	2002	X	-	X
Europe	Spain	Asturias	2015	X	-	X
Europe	Spain	Castilla y León	2008	-	-	-
Europe	Spain	Castilla y León	2016	-	-	-
Europe	Spain	Galicia	2008	-	-	X
Europe	Sweden	-	2003	-	-	-
Europe	Sweden	-	2014	-	-	-
Europe	Switzerland	-	2008	X	-	-
Europe	Switzerland	-	2016	X	-	-
Europe	Switzerland	Bern	2007	X	-	X
N.America	Canada	Alberta	1991	-	-	-
N.America	Canada	B.Columbia	2014	-	-	-
N.America	Canada	East.Wolf Range	2017	X	-	-
N.America	Canada	Ontario	2005	-	-	-
N.America	Canada	Yukon	2012	X	-	-
N.America	USA	Blackfeet IR	2008	-	-	-
N.America	USA	Flathead IR	2009	-	-	-
N.America	USA	Idaho	2002	-	-	-
N.America	USA	Idaho	2008	X	-	-

[1] Actions on wild prey that had no direct effects on population abundance, such as designing monitoring schemes, were not included in this category.

[2] Plan issued within the framework of the project "Inventories of Species and Habitats, Development of Management Plans and Capacity Building in relation to Approximation of EU Birds and Habitats Directives" financed by the Danish Environmental Protection Agency and discussed in the 21st meeting of the Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) in 2001.

Continent	Country	Geographical Reference (region)	Year	Intervention on wild prey[1]	(Re) introduction of wild prey	Associates wild prey with attacks on livestock
Europe	Austria	-	2012	-	-	-
Europe	Croatia	-	2005	X	X	-
Europe	Denmark	-	2013	-	-	-
Europe	Estonia	-	2001	-	-	-
N.America	USA	Mexican Wolf	1982	-	-	-
N.America	USA	Mexican Wolf	1998	-	-	-
N.America	USA	Mexican Wolf	2017	-	-	-
N.America	USA	Michigan	1997	X	-	-
N.America	USA	Michigan	2008	X	-	-
N.America	USA	Michigan	2015	X	-	-
N.America	USA	Minnesota	2001	X	-	-
N.America	USA	Montana	2004	X	-	-
N.America	USA	N. Rockies	1987	X	-	-
N.America	USA	Oregon	2005(2010)	-	-	-
N.America	USA	Oregon	2017	-	-	-
N.America	USA	Utah	2004	-	-	-
N.America	USA	Washington	2011	X	-	X
N.America	USA	Wisconsin	1999	-	-	-
N.America	USA	Wind River IR	2007	-	-	-
N.America	USA	Wyoming	2011	X	-	-

APPENDIX 4.3: Methods for sample collection and analysis used to determine wolf diet during the period 2006-2017 in Costa da Morte, Galicia, Spain.

We conducted wolf scat surveys during three periods of three years (Period 1: 2006-2008, Period 2: 2011-2013, Period 3: 2015-2017). We collected wolf scats in predefined transects using 4WD vehicles during July-August every year surveyed (n=42 transects; 156 replicates; mean= 7.5 transects/area*period^{-1}) in six areas occupied by different wolf packs (Pacheco *et al.* 2017, López-Bao *et al.* 2018). More details on wolf scat identification and collection in this area is given by López-Bao *et al.* (2013). The average transect length was 3.8 km (s.e.=0.26). Not all areas were surveyed in every period: three areas were surveyed during three periods and three areas were surveyed during two periods).

Hair from prey remains and, when possible, bones or other hard parts useful for prey identification were thoroughly extracted from scats, previously labelled and frozen at -20ºC. Hairs were washed in running water on a sieve (Valente *et al.* 2015). We identified prey items from scats by analysing hair cuticular and medullar patterns using reference manuals (Teerink, 1991; Valente *et al.* 2015) and our own collection of hair samples from the main prey of wolves in the study area.

Overall, we collected 447 scats from which we identified 399 prey items. The number of samples per period and wolf pack is given in Appendix S7.

We recorded the frequency of occurrence (FO) of prey items in the diet of wolves during each period and pack area. Many studies on diet analyses suggest the use of consumed biomass rather than FO (e.g. Ciucci *et al.* 1996; Klare *et al.* 2011) but we chose FO because we could not estimate age for all prey species, which might introduce bias in the predicted consumed biomass. In addition, in our study area and during the survey period wolves were known to prey preferably on foals rather than adult horses, and calves also account for an important portion of consumed cattle (Lagos 2013; Planella *et al.* 2016).

In addition, in our study area, livestock other than free ranging horses killed by wolves is susceptible to economic compensation and carcasses have to be removed from the field according to European regulations (CE 1774/2002 Regulation). This means that carcasses are generally found and removed before being fully consumed, which has a potential effect on the biomass consumed per prey item that we could not quantify (see Llaneza & López-Bao, 2018; Ciucci *et al.* 2018). As the aim of our analysis was detecting variations in the consumption of large ungulates during a long period from replicated surveys, we considered FO an informative estimator.

REFERENCES FOR APPENDIX 4.3

Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M., & Guy, I. (1996). A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biology* 2: 37-48.

Ciucci, P., Artoni, L., Crispino, F., Tosoni, E., & Boitani, L. (2018). Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy. *European Journal of Wildlife Research* 64: 5.

Klare, U., Kamler, J.F., & Macdonald, D.W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review* 41: 294-312.

Lagos, L. (2013). Ecología del lobo (*Canis lupus*), del poni salvaje (Equus ferus atlanticus) y del ganado vacuno semiextensivo (*Bos taurus*) en Galicia: interacciones depredador-presa. Ph.D. Thesis, Santiago de Compostela University, Spain.

Llaneza, L., & López-Bao, J.V. (2015). Indirect effects of changes in environmental and agricultural policies on the diet of wolves. *European Journal of Wildlife Research* 61: 895.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013) Indirect Effects on Heathland Conservation and Wolf Persistence of Contradictory Policies that Threaten Traditional Free-Ranging Horse Husbandry. *Conservation Letters*, 6: 448-455.

Planella, A., Palacios, V., García, E.J. Llaneza, L., García-Domínguez, F., Muñoz-Igualada, J., & López-bao, J.V. (2016). Influence of different GPS schedules on the detection rate of wolf feeding sites in human-dominated landscapes. *European Journal of Wildlife Research* 62: 471-478.

Teerink, B.J. (1991). Hair of West European mammals. Cambrige University Press.

Valente, A.M., Rocha, R.G., Lozano, E., Ferreira, J.P., & Fonseca, C. (2015) Atlas dos Pelos dos mamíferos terrestres ibéricos. Edições Afrontamento, Porto.

APPENDIX 4.4: Additional information on use by wolves (relative scat abundance and evidences of reproduction) of the six wolf pack areas in Costa da Morte (NW Spain).

A) Relative abundance index (mean number of wolf scats per kilometre) in transects across six areas occupied by wolf packs (see Appendix 4.3 for details on wolf scat survey). Three areas were not surveyed before 2011.

	Period 1 (2006-2008)		Period 2 (2011-2013)		Period 3 (2015-2017)	
Area	**Wolf scats/km**	**S.E.**	**Wolf scats/km**	**S.E.**	**Wolf scats/km**	**S.E.**
Baíñas	0.20	0.09	0.56	0.40	0.09	0.07
Ruña	0.69	0.36	0.32	0.18	0.73	0.51
Vimianzo	0.61	0.31	0.30	0.16	0.16	0.03
Buxantes	-	-	0.77	0.40	0.21	0.14
Carnota	-	-	0.76	0.31	0.99	0.55
Muxía	-	-	1.38	0.74	0.65	0.31

B) Evidence of wolf pack reproduction in Costa da Morte (Galicia, NW Spain). Wolf reproduction was estimated by howling surveys, direct observation of pups, capture of wolf pups (during wolf collaring), camera trapping and confirmed reports of dead pups.

Wolf pack	Years surveyed	Confirmed reproduction events
Baíñas	9	2
Ruña	9	4
Vimianzo	9	7
Buxantes	6	5
Carnota	6	3
Muxía	6	3

APPENDIX 4.5: Methods for the estimation of the relative abundance of free-ranging horses in the wolf pack areas surveyed.

As no reliable official statistics exist in relation to horse numbers in Galicia due to the particular free-ranging husbandry system (López-Bao *et al.* 2013), we conducted field surveys to assess changes in the relative abundance of free-ranging horses over time. Along the same transects used for collecting wolf scats (Appendix 4.3) we counted horse dung piles within a 2-m band at both sides of the path. We used these counts as an indirect measure of the relative abundance of horses. We calculated the mean count of dung piles/km along transect lines for each period and wolf pack area, as an indirect estimate of relative abundance of free ranging horses (Zabek *et al*. 2016).

REFERENCES FOR APPENDIX 4.5

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013) Indirect Effects on Heathland Conservation and Wolf Persistence of Contradictory Policies that Threaten Traditional Free-Ranging Horse Husbandry. *Conservation Letters*, 6: 448-455.

Zabek, M. A., Berman, D.M., Blomberg, S., & Wright, J. (2016). Estimating distribution and abundance of feral horses (*Equus caballus*) in a coniferous plantation in Australia, using line-transect surveys of dung. *Wildlife Research* 43: 604-614.

APPENDIX 4.6: Wild (ungulate) prey population trends in Costa da Morte (Galicia, NW Spain).

We assessed wild (ungulate) prey population trends in Costa da Morte during the study period using the number of animals killed per hunt and hunting area as a proxy at the local level (mean size (ha) of hunting area ± s.e. =9516 ± 2052, n=9; Figure A4.1), and the total number of captures at the province level (A Coruña province; 7950 km^2; Figure A4.1) as a proxy at regional level (data provided by the Ministry of Environment and Landscape Planning of the Regional Government of Galicia).

According to the available hunting data of big game for the whole province captures of roe deer have increased between 2006 and 2017, despite such trend has been slowed down in recent years. Since the late 2000s an emerging myiasis outbreak caused by *Cephenemyia stimulator* resulted in high prevalence and intensity in roe deer populations from Northwestern Spain (Sol *et al.* 2016; Pajares *et al.* 2017), including populations from Galicia. *Cephenemya* infestations can lead to depressed fitness and poor body conditions in roe deer (Calero-Bernal & Habela 2013), providing a plausible explanation for the recent discontinuation of a positive population trend (Maublanc *et al*. 2009), as it has been reported in Oestridae parasitism on other cervid species (Vicente *et al.* 2004). Total hunting captures of wild boar between 2006 and 2017 have experienced a 332% increase in the whole Coruña province.

Among big game, only wild boar has been hunted continuously in Costa da Morte. Boars killed per hunt have experienced a mean annual growth of 1.93% between 2008 to 2017. We considered this increase a surrogate for population trend (Imperio *et al*. 2010). Roe deer has only recently colonized the area as a result of a natural expansion from neighbouring populations after decades of absence (SGHN, 1995; Llaneza & López-Bao, 2015; San José, 2007). However, the area of occurrence of roe deer has expanded within our study area between 2002 and 2007 (San José, 2002; San José, 2007).

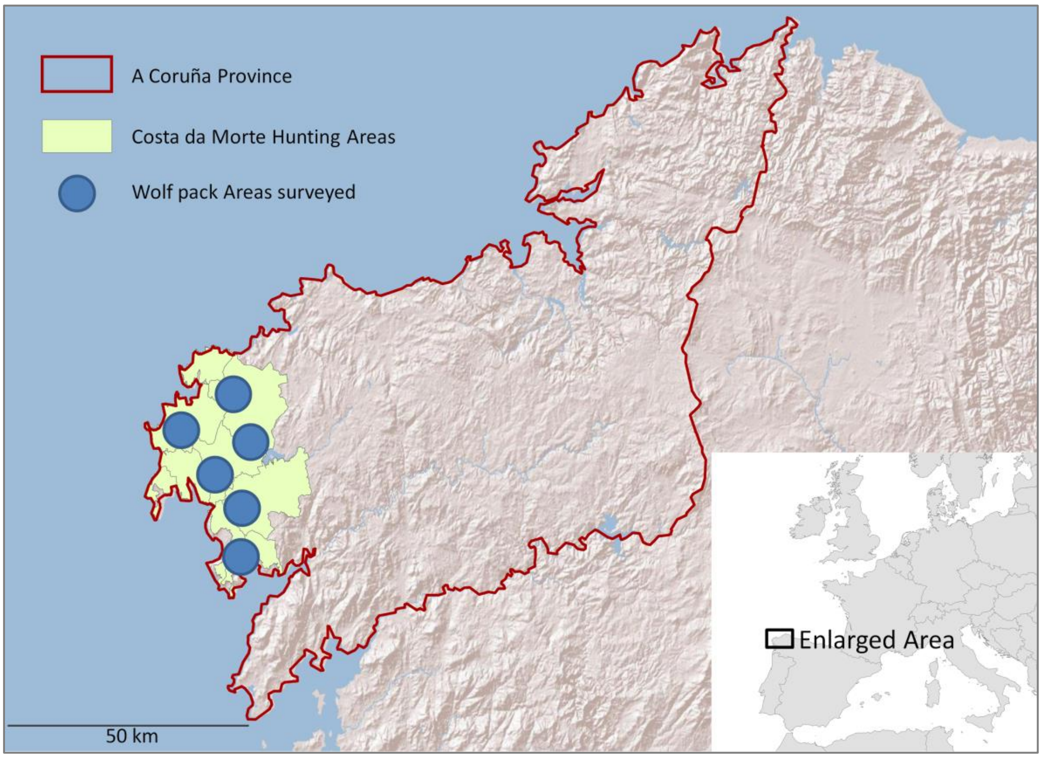


Figure A4.1: Map showing the location of the A Coruña province and the Costa da Morte hunting Areas in relation with the wolf pack areas surveyed in this study.

REFERENCES FOR APPENDIX 4.6

Calero-Bernal, R. & Habela, M. A. (2013). First report of Cephenemyia stimulator (Diptera, Oestridae) parasitizing Roe deer (*Capreolus capreolus*) in Extremadura (Spain). *Galemys* 25: 29-34.

Imperio, S., Ferrante, M., Grignetti, A., Santini, G., and Focardi, S. (2010). Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? *Wildlife Biology* 16: 205-214.

Llaneza, L., & López-Bao, J.V. (2015). Indirect effects of changes in environmental and agricultural policies on the diet of wolves. *European Journal of Wildlife Research* 61: 895.

Maublanc, ML., Bideau, E., Picot, D. Rames, J.L., Dubois, M., Ferté, H., & Gerard, J.F. (2009). Demographic crash associated with high parasite load in an experimental roe deer (*Capreolus capreolus*) population. *European Journal of Wildlife Research* 55: 621-625.

Pajares, G. & Arias, M.S., Pérez-Creo, A., Prieto, A., Callejo, A., Díez-Baños, P., & Morrondo, P. (2017). Epidemiología de la cefenemiosis en corzos del noroeste de España. *Boletín de la Asociación del Corzo Español* 15: 129-134.

Sáez-Royuela, C. & Tellería, J.L. (1986). The increased population of the wild boar (*Sus scrofa*) in Europe. *Mammal Review* 16: 97-101.

San José, C. (2002). *Capreolus capreolus*, Linnaeus, 1758. Pp: 318-321. In: L. J. Palomo and J. Gisbert (eds). Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.

San José, C. (2007). *Capreolus capreolus*, Linnaeus, 1758. Pp: 359-361. In: L. J. Palomo, J. Gisbert y J.C. Blanco (Eds). Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.

SGHN (Sociedade Galega de Historia Natural). (1995). Atlas de Vertebrados de Galicia, volume I. Consello da Cultura Gallega, Santiago de Compostela.

Sol, A.M., Gerardo, P., Natividad, D.B., Pérez-Creo, A., Prieto, A., Díez-Baños, P, & Morrondo, P. (2016). Cephenemyiosis, an emergent myiasis in roe deer (*Capreolus capreolus*) from northwestern Spain. *Parasitology Research* 115: 4605-4610.

Vicente, J., Fierro, Y., Martínez, M., & Gortázar, C. (2004). Long-term epidemiology, effect on body condition and interspecific interactions of concomitant infection by nasopharyngeal bot fly larvae (Cephenemyia auribarbis and Pharyngomyia picta, Oestridae) in a population of Iberian red deer (Cervus elaphus hispanicus). *Parasitology* 129: 349-361.

APPENDIX 4.7: Results of bivariate G tests to assess differences in the frequency of horse, other domestic prey, and wild prey in wolf diet within packs across periods. Tests were conducted regarding the frequency of occurrence (FO) of horses, other livestock and wild prey. Bonferroni-corrected significance levels for horses and other livestock (α=0.004), and for wild prey (α = 0.006).

Horses

	Periods 1-2		Periods 1-3		Periods 2-3	
Area	**G**	**p-value**	**G**	**p-value**	**G**	**p-value**
Baíñas	1.293	0.255	0.061	0.806	0.117	0.732
Vimianzo	32.410	0.000	10.151	0.001	0.801	0.371
Ruña	5.398	0.020	1.023	0.312	8.371	0.004
Muxía	-	-	-	-	0.846	0.358
Carnota	-	-	-	-	0.924	0.337
Buxantes	-	-	-	-	0.895	0.344

Other livestock

	Periods 1-2		Periods 1-3		Periods 2-3	
Area	**G**	**p-value**	**G**	**p-value**	**G**	**p-value**
Baíñas	0.005	0.945	0.285	0.593	0.310	0.578
Vimianzo	29.271	0.000	10.151	0.001	0.498	0.480
Ruña	5.398	0.020	0.275	0.600	6.943	0.008
Muxía	-	-	-	-	0.846	0.358
Carnota	-	-	-	-	0.095	0.759
Buxantes	-	-	-	-	0.895	0.344

Wild prey

	Periods 1-2		Periods 1-3		Periods 2-3	
Area	**G**	**p-value**	**G**	**p-value**	**G**	**p-value**
Baíñas	7.387	0.007	4.515	0.034	0.088	0.767
Vimianzo	2.546	0.111	-	-	0.691	0.406
Ruña	-	-	2.320	0.128	0.777	0.378
Muxía	-	-	-	-	-	-
Carnota	-	-	-	-	2.582	0.108
Buxantes	-	-	-	-	-	-

APPENDIX 4.8: Effect of the relative abundance of horses and the period in the diet of wolves in Costa da Morte (Galicia, Spain).

We assessed the role of the relative abundance of horses (average dung piles/km of transect) and time period (1 to 3 encompassing 2006 to 2017) in the diet composition of wolves at the pack level. We constructed three Generalized Linear Mixed Models (family=binomial, link=logit) with the frequency of occurrence (FO) of horse, wild prey, and livestock as dependent variables, and relative abundance of horses, period and an interaction between both as predictors. We also included the wolf pack as a random term in all models. Models were run using the *lme4* (Bates *et al.* 2009) package in *R* and were ranked using the criteria of the lowest AICc using the *MuMIn* package (Barton 2012).

Table A4.8.1 Selected candidate Generalized Linear Mixed Models evaluating the role of *Horse abundance* and *Period* in the FO of Horses, Wild prey, and Other livestock in the diet of wolves. Models are ranked based on AICc, difference in AICc relative to the highest-ranked model (ΔAICc) and Akaike weights (w_i). For simplicity, only three models are shown for each response variable:

FO of Horses

Variables in the model	AICc	ΔAICc	w_i
Period	466.0	0.00	0.65
Horse abundance + Period	468.1	2.03	0.23
*Horse abundance + Period +Horse abundance*Period*	469.8	3.79	0.10

FO of Wild Prey (wild boar and roe deer pooled)

Variables in the model	AICc	ΔAICc	w_i
Period	103.9	0.00	0.37
Horse abundance + Period	105.8	1.94	0.14
Horse abundance	106.4	2.49	0.11

FO of other livestock

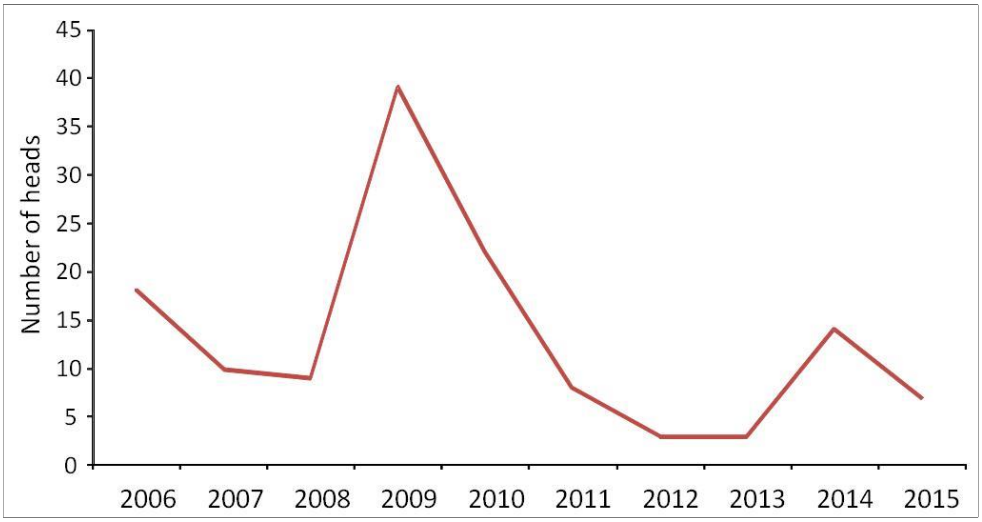
Variables in the model	AICc	ΔAICc	w_i
Period	455.8	0.00	0.49
Horse abundance + Period	457.2	1.35	0.25
Horse abundance	458.0	2.21	0.16

REFERENCES APPENDIX 4.8

Barton, K. 2012. Package '*MuMIn*'. Model selection and model averaging based on information criteria. R package version 1.7.11. R Foundation for Statistical Computing, Vienna, Austria.

Bates, D., Maechler M., & Dai, B. 2009. *lme4:* linear mixed-effects models using S4 classes. *R package version 0.999375-31* 〈http://cran.r-project.org/web/packages/lme4.

APPENDIX 4.9: Livestock losses (number of heads) attributed to wolves in Costa da Morte between 2006 and 2015 during the period of scat collection (June to August). Only cattle, sheep and goat are represented, being the most frequent livestock in wolf diet after horses (Appendix S7). Official data provided by the Regional Government of Galicia.



Discussion

Decision-making regarding biodiversity conservation often impacts over large administrative borders (e.g., nations, states or regions). Policy-makers increasingly demand solid evidence to support and inform policy and decision-making. Nonetheless, a recurrent drawback of using evidence to address environmental dilemmas is that such evidence is generally produced upon context-specific constraints (small spatial scales and short time periods). Consequently, decision making in wildlife management at large spatial scales is often constrained to rely on extrapolation from data collected at smaller scales (Miller *et al*. 2004). To address this scale discrepancy policy-making processes use expert opinion, theory and ecological modelling to predict the dynamics of ecological systems at large scales (Guisan *et al.* 2013).

The gray wolf is a widely distributed and highly adaptable species worldwide. We show that wolves provide a good example of the mismatch between the ecological evidence generated at multiple scales, and the practice of management at specific sites. In addition, we contribute to the knowledge of wolf ecology by describing general, large-scale patterns of breeding behaviour and prey selection. We also present general patterns of livestock attacks that can inform future conservation action, especially in landscapes where humans desire to coexist with wolves. One of these actions would be promoting the protection of known wolf breeding sites.

Wolves are found in very diverse ecological and social contexts (Dawes *et al*. 1986; Shalmon 1986; Blanco & Cortés 2007). Therefore, the species adapts its behaviour to face multiple human and environmental pressures differing in nature and intensity across its range (Fuller 1991; Kusak *et al.* 2005; Llaneza *et al.* 2016). For example, while human disturbance is a frequent driver of den site selection by wolves in human-dominated landscapes (Chapter 1; Theuerkauf *et al.* 2003; Habib & Kumar 2007), wolves may adapt their denning habits to spatial patterns of wild prey abundance in areas with low human presence and high seasonality of prey availability (Walton *et al.* 2001).

As we noted, in the absence of a better alternative, extrapolation of local evidence generated in a different context can be potentially useful to guide the conservation or management of generalist species such as the gray wolf. However, extrapolation as an evidence-based procedure to inform decision-making also has limitations, and the potential pitfalls of this approach need to be assessed carefully. In this thesis we show that identifying large-scale patterns from multi-site data can effectively assist decision-making, while knowing that local particularities can be easily overlooked from the analysis of global patterns and large-scale sources of variation. Decisions should be ideally assisted by site-specific evidence. Nonetheless, producing site-specific knowledge is costly and consumes large amounts of limited resources. It can be unaffordable in many occasions or fall out of the policy-makers priority list in others. We have shown that between building site-specific evidence and managing through preconceived ideas or assuming as general effects context-dependent observations, the use of multi-site data through compilation of primary data and literature review, can provide useful large-scale approaches that capture an important portion of variation and can help predict some of the outcomes and adjust management action.

We also show that the transferability of knowledge on general patterns of wolf ecology can be improved by identifying sources of uncertainty at different scales. Sources of variation are often the consequence of different responses by wolves to environmental gradients, or particular attributes defining distinct or large portions of wolf populations (e.g. continental differences). Finally we show how the combination of multiple sources of data, such as primary data and data extracted from the literature, can be valuable to synthesize evidence and to inform wolf conservation and management actions.

From general patterns to context-dependence: Avoiding spatial mismatches between evidence and decision-making

This thesis illustrates how human activities determine wolf ecology and behaviour by two large-scale studies (Chapters 1 and 3) that allowed uncovering general patterns of breeding site selection and feeding ecology, from multiple site-specific data. Since wolves are persecuted by humans, wolves respond adaptively minimizing the chances of interaction with them, a common behaviour in large carnivores coexisting with humans (Ngoprasert *et al.* 2007; Ordiz *et al.* 2011; Oriol-Cotterill *et al.* 2015a). Exploring the risk component of breeding site selection by wolves (Chapter 1), we found that wolves use areas far from human activity and patches of dense vegetation as refuge against humans at breeding sites, where the pack members are vulnerable (Kaartinen *et al.* 2010; Iliopoulos *et al.* 2014; Llaneza *et al*. 2018). It is worth mentioning that wolves are highly detectable in space and time at breeding sites, which represent a very small fraction of their home ranges. This fact together with the high intrinsic vulnerability of wolf pups determines high wolf sensitivity to human disturbance at homesites. Remarkably, within the general pattern we identified sources of variation in the intensity of breeding site selection across scales. Wolves adjusted the strength of the breeding site selection to the level of human pressure (Capitani *et al.* 2006; Ahmadi et al. 2013; Ciucci *et al.* 2018). Regarding the selection of dense vegetation areas at breeding sites, we observed that the strength of selection is also proportional to human pressure using human density as a surrogate.

Antipredatory strategies, including behavioural adjustments, are trait-mediated interactions that are typically costly in terms of energetic balance (Preisser *et al*. 2005). Nonetheless, human activities can also provide abundant food resources to some large carnivore species (Yirga *et al.* 2015; Athreya *et al*. 2016; Krofel *et al.* 2017). Wolves can also benefit from human activity under certain circumstances, and in some human-dominated areas wolves not only rely on, but are very efficient using food of human origin (Vos 2000; López-Bao *et al*. 2013; Tourani *et al*. 2014; Newsome *et al.* 2016). Adjusting antipredatory behaviour to the strength of human pressure can respond to a trade-off between risk and availability of resources (Basille *et al.* 2009; Valeix *et al.* 2012; Ahmadi *et al.* 2014).

We also found contrasting patterns in breeding site selection across continents (Eurasia vs. North America), that may be related to different histories of coexistence and persecution that had taken place in Eurasia and North America. While tight and long-lasting coexistence has been common in Eurasia, in North America large carnivores have been historically excluded from human-dominated landscapes (Agarwala & Kumar 2009; Ahmadi *et al.* 2014; Chapron *et al.* 2014). Thus, the gradual response of wolves to humans follows a hierarchical spatial pattern which introduces new sources of uncertainty at different levels.

On the other hand, in relation to large-scale patterns in the relationship between wolves and livestock (Chapter 3), we found that whereas in areas where wolves have persisted over time wolf abundance do not correlate with the frequency of livestock depredation, in areas where the species has disappeared and returned later, the number of depredations on livestock is correlated with wolf abundance. This suggests that wolf depredation rates on livestock are to some extent dependent on the persistence of husbandry practices traditionally oriented to reduce livestock vulnerability to wolves, which include the use of traditional damage prevention measures such as livestock guarding dogs or fences (Eklund *et al*. 2017, Breitenmoser *et al.* 2005). In areas where effective damage prevention measures are implemented for a long time, livestock vulnerability and availability for wolves may be segregated from abundance. The positive correlation between wolf abundance and livestock attacks in areas where wolves had been extirpated would have been masked by the lack of a global common pattern had we not explored the potential effect of the history of coexistence as a source of variation. Again, disentangling sources of uncertainty unveiled patterns associated with specific contexts. As for breeding site selection, the history of coexistence brought a plausible explanation for livestock predation patterns and allowed us to discriminate between two different scenarios, namely interrupted vs. continued wolf presence.

The fact that both breeding site selection and livestock depredations patterns are governed by the same mechanism, the history of coexistence, suggests a co-adaptation between wolves and humans (Carter & Linnell 2016). While wolves adjust their behaviour in breeding site selection to avoid negative interactions with humans, it is precisely humans who facilitate coexistence by adopting particular practices to avoid the impact of wolves on their livelihoods (Chapron *et al.* 2014; Pimenta *et al.* 2017; López-Bao *et al.* 2017). These results point out that both wolves and humans may adapt their behaviour to each other, taking into account the associated risks. Whenever this coexistence is interrupted, some of the costly strategies developed to minimize risks, such as husbandry practices, can rapidly get lost (Breitenmoser *et al*. 2005).

Despite general and large-scale patterns can come out if evidence is representative of the niche width of a species, it is nearly unfeasible to capture all site-specific particularities. Along these lines, we exemplified this potential gap through our case study regarding the lack of proportional prey shifting to substantial changes in prey abundance in NW Spain (Chapter 4). Despite prior evidence showed contrasting results, it is recurrent the idea that an increase in wild prey should translate into a decrease in the consumption of livestock and other domestic prey. We tested this hypothesis in a long-term study of a wolf population feeding mainly on domestic prey whose abundance declined markedly throughout the 12-year study period (López-Bao *et al.* 2013). Interestingly, we did not detect the expected prey shift, and some particularities that were specific to our study area could be important factors explaining the observed outcome. First, wild prey (roe deer and wild boar) reappeared after decades of absence or very low densities. Second, wolves fed upon free-ranging domestic horses for decades, leading to feeding specialization. The uniqueness of the long-lasting wolf-horse interaction in this area (López-Bao *et al.* 2013, Lagos 2013) is highly determined by a site-specific social structure and system of land tenure, and was not represented in the reviewed pre-existing literature dealing with the relationship between wild and domestic prey abundance and its relative consumption. This particular case represents a source of uncertainty that was not captured by general patterns derived from multi-site data on the feeding ecology of wolves and its link with different livestock-wolf conflict scenarios. The general assumptions constructed abroad (Meriggi & Lovari 1996; Sidorovich *et al.* 2003; Gula 2008; Meinecke *et al*. 2018) were not suitable to explain wolf-prey relationships in our study area. Our study illustrates that context-dependent factors can substantially modify the response of species with broad niche width and habitat plasticity such as wolves.

We only explored a few sources of variation in environmental constraints associated with wolf interaction with humans. Some of the contextual factors considered, operate at very large-scales below global (e.g., continental differences - Chapter 1- or two levels of wolf persistence - Chapter 3), also allowing generalizations across vast areas. We argue that both generalization at large scales and site-specific research can assist complementarily effective policy decision-making. Local specificity in wolf ecological traits and behaviour should be expected to be much larger and multiple ecological interactions not necessarily related with humans are also expected to increase spatial heterogeneity in wolf ecology and behaviour (Walton *et al.* 2001; Cubaynes *et al*. 2014; Stanek *et al.* 2017). Wolves are known to adapt their spatial and social behaviour to prey densities and prey spatial ecology (Messier 1984; Jędrzejewski *et al.* 2007). In addition, wolves can also adapt to temporal variation within a specific site because of their flexible behaviour. For example, changes in weather patterns may determine shifts in wolf social structure in order to optimize foraging success (Post *et al.* 1999). Also, variation attributable to different wolf subspecies or distinct populations deserves further attention (Muñoz-Fuentes *et al.* 2009; Randi 2011; Stronen *et al.* 2013).

We realized that information on wolf ecology and behaviour was geographically biased, as much of this knowledge has been produced in relatively few areas and ecological contexts. Most scientific studies on wolf ecology and wolf-prey relationships have been conducted in North America during the last six decades (back to Murie 1944), referred mostly to wild ecosystems with little human presence (Mech & Boitani, 2003; Mech *et al.* 2015). In Europe, scientific interest in wolves raised more recently. During the 1980s and 1990s numerous studies on wolf-prey relationships including wild and domestic prey were carried out in Europe (Chapter 4; Newsome *et al*. 2016; Meriggi & Lovari 1996), where wolf-livestock overlap is more frequent than in North America (Chapron *et al.* 2014). Thus, the growth of wolf science grounded in Europe has improved the knowledge of the species in scenarios of tight coexistence with humans (Randi 2011; Llaneza *et al.* 2012; Newsome *et al.* 2016; Hindrikson *et al.* 2017).

The scarcity of wolf studies in Asia is remarkable. This vast continent hosts a large portion of the wolf range (Fritts *et al.* 2003), and is arguably the most overlooked region regarding wolf science (Chapter 1; Newsome *et al.* 2016). From the environmental standpoint Asia is also a very diverse continent where wolves persist both in human-dominated landscapes (Habib & Kumar 2007; Agarwala & Kumar 2009; Ahmadi *et al*. 2014) and wild areas (Harris & Loggers 2003; Jumabay-Uulu *et al*. 2014).

Focusing future efforts on poorly studied contexts would help to further reduce potential bias in wolf science and opinions, and could allow integrating a broader range of environmental constraints. This would help to further reduce uncertainty and improve accuracy in wolf conservation.

From knowledge to effective wildlife management and conservation practice

The case study described in Chapter 4 provided an example of how policy-making under general assumptions can lead to unexpected results or misguided conservation and management action (Larsen & Olsen 2007; Puyravaud *et al.* 2017) even if it is informed by allegedly strong evidence accounting for large amounts of uncertainty. Nonetheless, this is not the only source of weakness for conservation practice.

In Chapter 2 we showed how weakened conservation can occur despite general precepts are in line with available evidence. We exemplified how conservation mandates adopted at the international level by sovereign nations, and intentionally stated in vague terms in order to embrace a wide range of taxa and contexts, can get diluted across a pyramidal system (form international agreements to local level policy-making) if the transfer to lower levels of political decision is not properly assessed. General statements need to be properly translated not only in time and scale (López-Bao & Margalida 2018; Mateo-Tomás *et al.* 2018), but also regarding compliance and enforcement. In the end, the effectiveness of transposed instructions should be assessed through evaluation of their performance in specific contexts, and not being acquiescent with mere legal compliance (Thoman & Sager 2017). We have shown how evidence can assist the transposition process across regulations from international levels to domestic law (which includes wildlife conservation and management plans). In our case, both the commitment (to avoid damage to breeding sites of wolves) and the evidence (see Chapters 1 and 2) existed, but effective protection of breeding sites was not effectively enforced in wolf plans. We argue that the generality and vagueness of the commitments involved, included in the main European conservation agreements, the Bern Convention (BC) on the Conservation of European Wildlife and Natural Habitats (Council of Europe, 1979) and the Habitats Directive (Directive 2009/147/EC) should translate into concrete conservation and management actions when scaling down to species-specific regulations.

There is a wide consensus at the international level regarding the need to preserve wolves. It is a species of conservation concern in Europe and North America (particularly in the lower U.S. States), where important conservation action on wolves has been undertaken in the last decades (Fritts *et al.* 2003). Wolves are also legally protected in some Asian countries (e.g. India, Iran). Providing new data, but also using the existing available data to strengthen evidence can help improve current wolf management practices (Pullin *et al.* 2004; Sutherland *et al.* 2004). Enhancing the share of primary data by building collaborative environments between researchers and managers can provide very valuable information to extract general patterns and assess uncertainty in a useful way to improve conservation action (Chapters 1 and 3; Michener 2015). Combining systematically primary data from collaborators and data from systematic reviews, as we have done in Chapters 1 and 3, can boost the informative ground upon which building strong evidence to inform policy-making. Facilitating data access to scientific community can also be improved through supportive infrastructures (Costello *et al.* 2015).

To date, proper evaluation of conservation action still needs improvement (Schwartz *et al.* 2009; Geist 2015). Wolf conservation and sustainable management have been poorly evaluated (Bradley *et al*. 2015; Browne-Núñez *et al*. 2015; Godinho *et al.* 2015). This thesis provided insights into wolf ecology from a holistic view, but also assessed the suitability of current action on the species from a broad empirical basis. Applying the methods used in this thesis to other aspects relevant for wolf conservation and management should be considered as a feasible way to improve the policy-making process regarding the conservation of wolves.

Conclusions

1. Wolves are considered a habitat generalist species. Nonetheless, habitat selection focused on breeding sites and breeding periods, a reduced spatio-temporal window where wolves are highly vulnerable, revealed that wolves show strong habitat selection across their range in order to minimize the chances of interaction with humans. Wolves locate their breeding sites far from areas where human activity is expected to be above the average within their home ranges, or compensate such risk by selecting secluded sites taking profit of refuge vegetation.

2. Despite the global patterns observed in homesite selection by wolves, remarkable sources of variation have been identified. The strength of the selection towards refuge is proportional to human population density as a surrogate for the predation risk in each study area. In Eurasia the effect of human avoidance is stronger than in North America at the homesite level. Continental differences may be explained by different persecution histories and because wolf-human coexistence in Eurasia has been longer and tighter than in North America.

3. Wolf breeding sites are neither conspicuous nor easily detectable by the general public. The sole reactive protection based on just prohibiting its destruction or disturbance does not seem enough to effectively protect wolf breeding sites. Preventive measures and regulation of potential sources of disturbance at breeding sites are expected to be more appropriate. Nonetheless, these measures rarely appear in wolf management and action plans in Europe.

4. The necessary generalization of broad-scale regulations including multiple taxa is expected to be effectively transferred to lower levels of political decision through species and site-specific adjustments. This is not the general case with breeding sites of wolves. Despite the principal international agreements and legislation at the European level on biodiversity conservation (Bern Convention and Habitats Directive) mandate the protection of wolf breeding sites, effective protection of these sites is not properly transposed to operational management instruments at the local level.

5. The management of the wolf-livestock conflict is frequently undertaken assuming a positive correlation between the number of wolves and attacks on livestock. A test of this hypothesis using data from wolf populations and livestock depredations in Europe and North America indicates that such positive correlation is not a general pattern. This relationship tends to be observed in areas where wolf has temporarily disappeared during the last decades, but not in areas where wolf occurrence has been continuous.

6. One plausible explanation to this source of uncertainty is that traditional practices of livestock husbandry, oriented to protect livestock from large carnivore attacks, are generally discontinued soon after wolves disappear. On the contrary, in areas where wolves persisted traditional practices were maintained, disassociating the number of attacks on livestock from wolf abundance.

7. Abundant literature suggests that depredations on livestock by wolves depends on the abundance of wild prey, assuming a preference for wild over domestic prey. Although the generality of this hypothesis has not been formally tested, this idea has been incorporated to some wolf management plans. The scarcity of direct actions aiming to increase wild prey populations as a measure to alleviate wolf-livestock conflict among wolf plans from Europe and North America suggests that caution prevails regarding this issue.

8. In a particular area of Northwestern Spain characterized by a recent and ongoing increase in wild prey and a sharp decrease of the staple prey of wolves (free-ranging horses), no increase in consumption of wild prey was detected in wolf diet along a 12yr period. We used these results to illustrate that, as a result of context-dependence and local particularities, policy-making under general assumptions or transferred evidence needs to be carefully evaluated to be effective and to avoid unexpected outcomes.

9. This thesis demonstrates that compiling and processing evidence from different sources can assist policy-making in conservation, reducing or identifying large-scale sources of uncertainty. Nonetheless caution must prevail regarding the role of site-specific particularities.

References

Adams W.M., Sandbrook, C. (2013). Conservation, evidence and policy. *Oryx* 47: 329–335.

Agarwala, M., & Kumar, S. (2009). Wolves in agricultural landscapes in western India. Tropical Resources, *Bulletin of the Yale Tropical Resources Institute* 28: 48–53.

Ahmadi, M., Kaboli, M., Nourani, E., Shabani, A.A., & Ashrafi, S. (2013). A predictive spatial model for gray wolf (*Canis lupus*) denning sites in a human-dominated landscape in western Iran. *Ecological Research* 28:513-521.

Ahmadi M., López-Bao, J.V., Kaboli, M. (2014). Spatial Heterogeneity in Human Activities Favors the Persistence of Wolves in Agroecosystems. *PLoS ONE* 9: e108080.

Athreya, V., Odden, M., Linnell, J., Krishnaswamy, J., & Karanth, K. (2016). A cat among the dogs: Leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx* 50: 156-162.

Balme, G. A., Lindsey, P. A., Swanepoel, L. H. and Hunter, L. T. (2014), Failure of research to address the rangewide conservation needs of large carnivores: leopards in South Africa as a case study. *Conservation Letters* 7: 3-11.

Barnosky, Hadly, E.A. Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J.,Hastings, A.,Marquet, P.A.,Martinez, N.D.,Mooers, A., Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D.P., Revilla, E., & Smith, A.B. (2012). Approaching a state shift in Earth's biosphere. *Nature* 486:52–58.

Barral, M.P., Rey-Benayas, J.M., Meli, P., & Maceira, N.O. (2015). Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: A global meta-analysis. *Agriculture, Ecosystems & Environment* 202: 223-231.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D., Odden, J., Andersen, R., Arild Høgda, K., & Gaillard, J. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32: 683-691.

Bax, N.J., Cleary, J., Donnelly, B., Dunn, D.C., Dunstan, P.K., Fuller, M., & Halpin, P.N. (2016). Results of efforts by the Convention on Biological Diversity to describe ecologically or biologically significant marine areas. *Conservation Biology* 30: 571-581.

Beschta, R.L., Ripple, W.J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142: 2401-2414.

Biagini, B., Bierbaum, R., Stults, M., Dobardzic, S., & McNeeley, S.M. (2014). A typology of adaptation actions: A global look at climate adaptation actions financed through the Global Environment Facility. *Global Environmental Change* 25: 97-108.

Biermann, F. (1996). "Common Concern of Humankind": The Emergence of a New Concept of International Environmental Law. *Archiv Des Völkerrechts 34*:426-481.

Blanco, J.C., & Cortés, Y. (2007). Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. *Journal of Zoology* 273: 114-124.

Boitani, L. (2000). Action plan for the conservation of Wolves (*Canis lupus*) in Europe. Strasbourg Cedex, Council of Europe (85pp.).

Bradley, E.H., Robinson, H.S., Bangs, E.E., Kunkel, K., Jimenez, M.D., Gude, J.A., & Grimm, T. (2015). Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. *Journal of Wildlife Management* 79: 1337-1346.

Breitenmoser, U. (1998). Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation* 83: 279-289.

Breitenmoser, U., Angst, C., Landry, J.M., Breitenmoser-Würsten,C., Linnell, J.D.C., & Weber, J.M. (2005). Non-lethal techniques for reducing depredation. Pp: 49-71 *In*: Woodroffe, R., Thirgood, S. & Rabinowitz, A. (Eds.). People and Wildlife, Conflict or Coexistence? Cambridge University Press, Cambridge, UK.

Brondizio, E.S., & Le Tourneau, F.M. (2016). Environmental governance for all. *Science* 352: 1272-1273.

Browne-Nuñez, C., Treves, A., MacFarland, D., Voyles, Z., & Turng, C. (2015). Tolerance of wolves in Wisconsin: A mixed-methods examination of policy effects on attitudes and behavioral inclinations. *Biological Conservation* 189: 59-71.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C. & Bruno, J. (2010). Global biodiversity: indicators of recent declines. *Science* 328: 1164-1168.

Butchart, S.H., Clarke, M., Smith, R.J., Sykes, R.E., Scharlemann, J.P., Harfoot, M. , Buchanan, G.M., Angulo, A., Balmford, A., Bertzky, B., Brooks, T.M., Carpenter, K.E., Comeros-Raynal, M.T., Cornell, J., Ficetola, G.F., Fishpool, L.D., Fuller, R.A., Geldmann, J., Harwell, H., Hilton-Taylor, C., Hoffmann, M., Joolia, A., Joppa, L., Kingston, N., May, I., Milam, A., Polidoro, B., Ralph, G., Richman, N., Rondinini, C., Segan, D. B., Skolnik, B., Spalding, M. D., Stuart, S. N., Symes, A., Taylor, J., Visconti, P., Watson, J. E., Wood, L. & Burgess, N.D. (2015). Shortfalls and Solutions for Meeting National and Global Conservation Area Targets. *Conservation Letters* 8: 329-337.

Capitani, C., Mattioli, L., Avanzinelli, E., Gazzola, A., Lamberti, P., Mauri, L., Scandura, M., Viviani, A., & Apollonio, M. (2006). Selection of rendezvous sites and reuse of pup raising areas among wolves *Canis lupus* of north-eastern Apennines, Italy. *Acta Theriologica* 51: 395-404.

Carter, N.H., & Linnell, J.D.C. (2016). Co-Adaptation Is Key to Coexisting with Large Carnivores. *Trends in Ecology & Evolution* 31: 575-578.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., & Palmer, T.M. (2015) Accelerated modern human-induced species losses: entering the Sixth Mass Extinction. *Science Advances* 1: e1400253.

Chamberlain, S.A., Bronstein J.L., Rudgers, J.A. (2014). How context dependent are species interactions? *Ecology Letters* 17: 881–890.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517-1519.

Chapron, G., Epstein, Y., Trouwborst, A. & López-Bao, J.V. (2017). Bolster legal boundaries to stay within planetary boundaries. *Nature Ecology & Evolution* 1: 0086.

Ciucci, P., Boitani, L., Falco, M., & Maiorano, L. (2018). Hierarchical, multi-grain rendezvous site selection by wolves in southern Italy. *Journal of Wildlife Management* 82: 1049-1061.

Clucas, B., McHugh, K., & Caro, T. (2008). Flagship species on covers of US conservation and nature magazines. *Biodiversity and Conservation* 17: 1517-1528.

Cook, C.N., Carter R.W., Fuller, R.A., & Hockings, M. (2012). Managers consider multiple lines of evidence important for biodiversity management decisions. *Journal of Environmental Management* 113: 341-346.

Cooke, S.J., Birnie-Gauvin, K., Lennox, R.J., Taylor, J.J., Rytwinski, T., Rummer, J.L., Franklin, C.E., Bennett, J.R., & Haddaway, N.R. (2017). How experimental biology and ecology can support evidence-based decision-making in conservation: avoiding pitfalls and enabling application, *Conservation Physiology* 5: cox043.

Costello, M. J., Vanhoorne, B. and Appeltans, W. (2015). Conservation of biodiversity through taxonomy, data publication, and collaborative infrastructures. *Conservation Biology* 29: 1094-1099.

Cubaynes, S., MacNulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W., Coulson, T. (2014). Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83:1344–1356.

Cvitanovic, C., Fulton, C.J., Wilson, S.K., & van Kerkhoff, L., Cripps, I.L., & Muthiga, N. (2014). Utility of primary scientific literature to environmental managers: An international case study on coral-dominated marine protected areas. *Ocean & Coastal Management* 102: 72-78.

Dawes, P., Elander, M., & Ericson, M. (1986). The Wolf (*Canis lupus*) in Greenland: A Historical Review and Present Status. *Arctic*, *39*: 119-132.

Dickman, A.J., Macdonald, E.A., & Macdonald, D.W. (2011). A review of financial instruments to pay for predator conservation and encourage human-carnivore coexistence. *Proceedings of the National Academy of Sciences* 201012972.

Dicks, L.V., Wright, H.L., Ashpole, J.E., Hutchison, J., McCormack G.C., Livoreil B., Zulka, K.P., & Sutherland. (2016). What works in conservation? Using expert assessment of summarised evidence to identify practices that enhance natural pest control in agriculture *Biodiversity and Conservation* 25: 1383-1399.

Duffy, J.E., Srivastava, D.S., McLaren, J., Sankaran, M., Solan, M.,Griffin, J.E.M. & Jones, K.E. (2009). Forecasting decline in ecosystem services under realistic scenarios of extinction. Pp: 60–77 *In*: Naeem, S., Bunker, D., Hector, A., Loreau, M., & Perrings, C. (Eds.). Biodiversity, ecosystem functioning, and human wellbeing: An ecological and economic perspective. Oxford University Press, Oxford, UK.

Dybing, N.A., Jacobson, C., Irwin, P., Algar, D., & Adams, P.J. (2018). Challenging the dogma of the 'Island Syndrome': a study of helminth parasites of feral cats and black rats on Christmas Island, Australasian Journal of Environmental Management, 25: 99-118.

Ehrlich, P.R., & Ehrlich, A.H. (2013). Can a collapse of global civilization be avoided? *Proceedings of the Royal Society B*. 280: 20122845.

Eklund, A., López-Bao, J.V., Tourani, M., Chapron, G., & Frank, J. (2017). Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Scientific reports* 7: 2097.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R. & Wardle, D.A. (2011). Trophic downgrading of planet Earth. *Science* 333: 301–306.

Ferraro, P.J., & Pattanayak, S.K. (2006). Money for Nothing? A Call for Empirical Evaluation of Biodiversity Conservation Investments. *PLoS Biology* 4: e105

Fritts, S.H., Stephenson, R.O., Hayes, R.D., & Boitani, L. (2003). Wolves and Humans. Pp: 289-316 *In:* Mech, L.D. & Boitani, L. (Eds.). Wolves, behavior, ecology, and conservation.The University of Chicago Press, Chicago.

Fuller, T.K. (1991). Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* **69**:283–287.

Geist, J. (2015). Seven steps towards improving freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25: 447-453.

Gross, L. (2005). Why Not the Best? How Science Failed the Florida Panther. *PLoS Biology* 3: e333.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., & Buckley, Y.M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters* 16: 1424–1435.

Gula, R. (2008). Wolf Depredation on domestic animals in the polish Carpathian Mountains. *The Journal of Wildlife Management* 72: 283-289.

Gutzat, F., Dormann, C.F. (2018). Decaying trees improve nesting opportunities for cavity-nesting birds in temperate and boreal forests: A meta-analysis and implications for retention forestry. *Ecology and Evolution* 2018; 00: 1–11.

Habib, B., & Kumar, S. (2007). Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. *Journal of Zoology* 272: 259-265.

Haddaway, N.R. & Pullin, A.S. (2014). The policy role of systematic reviews: past, present and future. *Springer Science Reviews* 2: 179-183.

Harris, R.B., & Loggers, C.O. (2003). Status of Tibetan plateau mammals in Yeniugou, China. *Wildlife Biology* 10:91-99.

Hill, R., Dyer, G.A., Lozada-Ellison, L.M., Gimona, A., Martin-Ortega, J., Munoz-Rojas, J., & Gordon, I.J. (2015). A social–ecological systems analysis of impediments to delivery of the Aichi 2020 Targets and potentially more effective pathways to the conservation of biodiversity. *Global Environmental Change* 34: 22-34.

Hindrikson, M., Remm, J., Pilot, M., Godinho, R., Stronen, A.V., Baltrūnaité, L., Czarnomska, S.D., Leonard, J.A., Randi, E., Nowak, C., Åkesson, M., López-Bao, J.V., Álvares, F., Llaneza, L, Echegaray, J., Vilà, C., Ozolins, J., Rungis, D., Aspi, J., Paule, L, Skrbinšek, T. & Saarma, U. (2017). Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. *Biological Reviews* 92: 1601-1629.

Iliopoulos, Y., Youlatos, D. & Sgardelis, S. (2014). Wolf pack rendezvous site selection in Greece is mainly affected by anthropogenic landscape features. *European Journal of Wildlife Research* 60: 23-34.

Isbell F., Calcagno V., Hector A., Connolly J., Harpole W.S., Reich P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta E.S., & Loreau, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202.

Iwu, M.M. (1996). Implementing the Biodiversity Treaty: how to make international co-operative agreements work. *Trends in Biotechnology*, 78-83.

Jackson, M.C., Loewen, C.J., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Global Change Biology* 22: 180-189.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., & Kowalczyk, R. (2007). Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography* 30: 66-76.

Jenkins, M. (2003). Prospects for Biodiversity. *Science* 302: 1175-1177.

Jordan, A., Rayner, T., Schroeder, H., Adger, N., Anderson, K., Bows, A., Le Quéré, C., Joshi, M., Mander, S., Vaughan N., & Whitmarsh, L. (2013). Going beyond two degrees? The risks and opportunities of alternative options. *Climate Policy* 13: 751-769.

Jumabay-Uulu, K., Wegge, P., Mishra, C., & Sharma, K. (2014). Large carnivores and low diversity of optimal prey: A comparison of the diets of snow leopards *Panthera uncia* and wolves *Canis lupus* in Sarychat-Ertash Reserve in Kyrgyzstan. *Oryx* 48: 529-535.

Kaartinen, S., Luoto, M., & Kojola, I. (2010). Selection of den sites by wolves in boreal forests in Finland. *Journal of Zoology* 281: 99-104.

Kark, S., Tulloch, A., Gordon, A., Mazor, T., Bunnefeld, N., & Levin, N. (2015). Cross-boundary collaboration: key to the conservation puzzle. *Current Opinion in Environmental Sustainability* 12: 12-24.

Kellert, S.R., Black, M., Rush, C.R. & Bath, A.J. (1996). Human Culture and Large Carnivore Conservation in North America. *Conservation Biology* 10: 977-990.

Kleiven, J., Bjerke, T. & Kaltenborn, B.P. (2004). Factors influencing the social acceptability of large carnivore behaviours. *Biodiversity and Conservation* 13: 1647-1658.

Krofel, M., Špacapan, M. & Jerina, K. (2017). Winter sleep with room service: denning behaviour of brown bears with access to anthropogenic food. *Journal of Zoology* 302: 8-14.

Kusak, J., Skrbinšek, A.M. & Huber, D. (2005). Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife Research* 51: 254-262.

Lagos, L. (2013). Ecología del lobo (*Canis lupus*), del poni salvaje (*Equus ferus atlanticus*) y del ganado vacuno semiextensivo (*Bos taurus*) en Galicia: interacciones depredador-presa. Ph.D Thesis, Santiago de Compostela University, Spain.

Larsen, H.O., & Olsen, C.S. (2007). Unsustainable collection and unfair trade? Uncovering and assessing assumptions regarding Central Himalayan medicinal plant conservation. *Biodiversity and Conservation* 16: 1679-1697.

LCIE (Large Carnivore Initiative for Europe). (2007). *Canis lupus*. The IUCN Red List of Threatened Species 2007: e.T3746A10048689.

Ledoux, L., Crooks, S., Jordan, A., Turner, R.K. (2000). Implementing EU biodiversity policy: UK experiences. *Land Use Policy* 17: 257-268.

Lim, M. (2016). Governance criteria for effective transboundary biodiversity conservation. *Internationaol Environmental Agreements* 16:797–813.

Linnell, J.D., Swenson, J.E. & Andersen, R. (2000). Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiversity and Conservation* 9: 857-868.

Llaneza, L., López-Bao, J.V., & Sazatornil, V. (2012). Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. *Diversity and Distributions* 18: 459-469.

Llaneza, L., García, E.J., Palacios, V., Sazatornil, V., & López-Bao, J.V. (2016). Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes. *Biodiversity and Conservation* 25: 1515-1528.

Llaneza, L., Sazatornil, V., & López-Bao, J.V. (2018). The importance of fine-scale breeding site selection patterns under a landscape-sharing approach for wolf conservation. *Biodiversity and Conservation* 27: 1239-1256.

López-Bao, J.V., Sazatornil, V., Llaneza, L. & Rodríguez, A. (2013). Indirect Effects on Heathland Conservation and Wolf Persistence of Contradictory Policies that Threaten Traditional Free-Ranging Horse Husbandry. *Conservation Letters* 6: 448-455.

López-Bao, J.V., Blanco, J.C., Rodríguez, A., Godinho, R., Sazatornil, V., Álvares, F., García, E.J., Llaneza, L., Rico, M., Cortés, Y., Palacios, V., & Chapron, G. (2015). Toothless wildlife protection laws. *Biodiversity and Conservation* 24: 2105-2108.

López-Bao, J.V., Bruskotter, J., & Chapron, G. (2017). Finding space for large carnivores. *Nature Ecology & Evolution* 1:0140.

López-Bao, J.V., & Margalida, A. (2018). Slow transposition of European environmental policies. *Nature Ecology & Evolution* 2: 914.

Madhusudan, M. D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* 41: 858-869.

Mateo-Tomás, P., Olea, P.P., & López-Bao, J.V. (2018). Europe's uneven laws threaten scavengers. *Science* 360: 612-613.

McCarthy, M.A., & Possingham, H.P. (2007). Active Adaptive Management for Conservation. *Conservation Biology* 21: 956-963.

Mech, L.D. & Boitani, L. (Eds.). (2003). *Wolves, behavior, ecology, and conservation*. The University of Chicago Press, Chicago.

Mech, L.D., & Boitani, L. (IUCN SSC Wolf Specialist Group). (2010). *Canis lupus*. The IUCN Red List of Threatened Species 2010: e.T3746A10049204.

Mech, L.D., Smith, D.W., & MacNulty, D.R. (2015). *Wolves on the hunt: the behavior of wolves hunting wild prey*. The University of Chicago Press. Chicago.

Meinecke, L., Soofi, M., Riechers, M., Khorozyan, I., Hosseini, H., Schwarze, S., Waltert, M. (2018). Crop variety and prey richness affect spatial patterns of human-wildlife conflicts in Iran’s Hyrcanian forests. *Journal for Nature Conservation* 43: 165-172.

Meli, P., Rey-Benayas, J.M., Balvanera, P., Martínez-Ramos, M. (2014). Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: A meta-analysis. *PLoS ONE* 9: e93507.

Mengersen, K., MacNeil, M.A., and Caley, M.J. (2015). The potential for meta-analysis to support decision analysis in ecology. *Research Synthesis Methods* 6: 111–121.

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33: 1561-1571.

Messier, F. (1984). Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63: 1068-1077.

Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L., & Stanley, E.H. (2004). Spatial Extrapolation: The Science of Predicting Ecological Patterns and Processes. *BioScience* 54: 310–320.

Muñoz-Fuentes, V., Darimont, C.T., Wayne, R.K., Paquet, P.C. and Leonard, J.A. (2009). Ecological factors drive differentiation in wolves from British Columbia. *Journal of Biogeography* 36: 1516-1531.

Murcia, C., Guariguata, M.R., Andrade, Á., Andrade, G.I., Aronson, J., Escobar, E.M., Etter, A., Moreno, F.H., Ramírez, W., & Montes, E. (2016). Challenges and Prospects for Scaling-up Ecological Restoration to Meet International Commitments: Colombia as a Case Study. *Conservation Letters* 9: 213-220.

Murie, A. (1944). The wolves of Mount McKinley. National Park Service, Fauna Series No. 5. United States Government Printing Office, Washington, D.C.

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., López-Bao, J.V., Peterson, R.O., Shores, C.R. Wirsing, A.J., Ripple, W.J. (2016). Food habits of the world's grey wolves. *Mammal Review* 46: 255–269.

Ngoprasert, D., Lynam, A., & Gale, G. (2007). Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx* 41: 343-351.

Ordiz, A., Støen, OG., Delibes, M. & Swenson, J.E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166: 59-67.

Ordiz, A., Bischof, R., Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? *Biological Conservation* 168: 128-133.

Oriol-Cotterill, A., Macdonald, D.W., Valeix, M., Ekwanga, S., & Frank, L.G. (2015a). Spatiotemporal patterns of lion space use in a human-dominated landscape. *Animal Behaviour* 101:27-39.

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015b). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* 124: 1263-1273.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., DeIongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., Maclennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O. and Okot-Omoya, E., Patterson, B.D., Plumptre, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., Polasky, S. (2013). Conserving large carnivores: Dollars and fence. *Ecology Letters* 16: 635–641.

Pimenta, V., Barroso, I., Boitani, L., & Beja, P. (2017). Wolf predation on cattle in Portugal: Assessing the effects of husbandry systems. *Biological Conservation* 207: 17-26.

Pimlott, D.H. (Ed.). (1975). Wolves: Proceedings of the First Working Meeting of Wolf Specialists and of the First International Conference on the Conservation of the Wolf. Stockholm, Sweden 5 - 6 September 1973 (IUCN Publications: Supplementary paper 43; International Union for Conservation of Nature and Natural Resources).

Post, E., Peterson, R.O., Stenseth, N.C., & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature* 401, 905–907.

Preisser, E.L., Bolnick, D.I., Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86: 501-509.

Primack, R.B., Miller-Rushing, A.J., Corlett, R.T., Devictor, V., Johns, D.M., Loyola, R., Maas, B., Pakeman, R.J., Pejchar, L. (2018). Biodiversity gains? The debate on changes in local- vs global-scale species richness. *Biological Conservation* 219: A1-A3.

Pullin, A.S., Knight, T.M., Stone, D.A., & Charman, K. (2004). Do conservation managers use scientific evidence to support their decision-making? *Biological Conservation* 119: 245-252.

Pullin, A.S., & Knight, T.M. (2009). Data credibility: a perspective from systematic reviews in environmental management. *New Directions for Evaluation* 122:65–74.

Pullin, A.S., Knight, T.M. & Watkinson, A.R. (2009). Linking reductionist science and holistic policy using systematic reviews: unpacking environmental policy questions to construct an evidence-based framework. *Journal of Applied Ecology* 46: 970-975.

Puyravaud, J., Davidar, P., Srivastava, R., & Wright, B. (2017). Modelling harvest of Asian elephants *Elephas maximus* on the basis of faulty assumptions promotes inappropriate management solutions. *Oryx* 51: 506-512.

Ran, J., Du, B., & Yue, B. (2009). Conservation of the endangered giant panda *Ailuropoda melanoleuca* in China: Successes and challenges. *Oryx* 43:176-178.

Randi, E. (2011). Genetics and conservation of wolves *Canis lupus* in Europe. *Mammal Review* 41: 99-111.

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., & Vira, B. (2010). Biodiversity conservation: challenges beyond 2010. *Science* 329: 1298–1303.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., and Wirsing, A.J. (2014). Status and Ecological Effects of the World’s Largest Carnivores. *Science* 343: 1241484.

Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P.A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A., Corlett, R.T., Darimont, C.T., Dickman, A.J., Dirzo, R., Dublin, H.T., Estes, J.A., Everatt, K.T., Galetti, M., Goswami, V.R., Hayward, M.W., Hedges, S., Hoffmann, M., Hunter, L.T.B., Kerley, G.I.H., Letnic, M., Levi, T., Maisels, F., Morrison, J.C., Nelson, M.P., Newsome, T.M., Painter, L., Pringle, R.M., Sandom, C.J., Terborgh, J., Treves, A., Van Valkenburgh, B., Vucetich, J.A., Wirsing, A.J., Wallach, A.D., Wolf, C., Woodroffe, R., Young, H., & Zhang, L. (2016). Saving the World's Terrestrial Megafauna. *BioScience* 66: 807–812.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B.H., Liverman, D., Richardson, K., Crutzen, P., & Foley, J.A. (2009). A safe operating space for humanity. *Nature* 461:472-475.

Rosendal, G.K. (2001). Impacts of overlapping international regimes: the case of biodiversity. *Global Governance* 7: 95-117.

Rueness, E.K., Asmyhr, M.G., Sillero-Zubiri, C., Macdonald, D.W., Bekele, A., Atickem,A., Stenseth, N.C. (2011). The cryptic African wolf: *Canis aureus lupaster* is not a golden jackal and is not endemic to Egypt. *PLoS ONE* 6: e16385.

Salafsky, N., Margoluis, R., Redford, K.H., Robinson, J.G. (2002). Improving the practice of conservation: A conceptual framework and research agenda for conservation science. *Conservation Biology* 16: 1469–1479.

Schwartz, M.E., Hellmann, J.J., McLachlan, J.S. (2009). The precautionary principle in managed relocation is misguided advice. *Trends in Ecology and Evolution* 24:474.

Shalmon, B. (1986). Wolves in the Southern Arava. *Re'em* 5: 60–74.

Sidorovich, V.E., Tikhomirova, L.L, & Jędrzejewska, B. (2003). Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. *Wildlife Biology* 9: 103-111.

Soltau, F. (2016). Common Concern of Humankind. Pp: 202-212 *In*: Carlarne, C., Gray, K.R., & Tarasofsky, R.G. The Oxford handbook of international Climate Change law. Oxford University Press.

Stanek, A.E., Wolf, N., Hilderbrand, G.V., Mangipane, B., Causey, D. & Welker, J.M. (2017). Seasonal foraging strategies of Alaskan gray wolves in a salmon subsidized ecosystem. *Canadian Journal of Zoology* 95: 555–563.

Stronen, A.V., Jędrzejewska, B., Pertoldi, C., Demontis, D., Randi, E., Niedziałkowska, M., Pilot, M., Sidorovich, V.E., Dykyy, I., Kusak, J., Tsingarska, E., Kojola, I., Karamanlidis, A.A., Ornicans, A., Lobkov, V.A., Dumenko, V., & Czarnomska, S.D. (2013). North-South differentiation and a region of high diversity in European wolves (*Canis lupus*). *PLoS ONE* 8: e76454.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., & Knight, T.M. (2004). The need for evidence-based conservation. *Trends in Ecology and Evolution* 19: 305-308.

Sutherland, W.J., Dicks, L.V., Ockendon, N., Petrovan, S.U., Smith, R.K. (Eds.). (2018). What Works in Conservation. Open Book Publishers. Cambridge, U.K.

Theuerkauf, J., Rouys, S., & Jędrzejewski, W. (2003). Selection of dens, rendezvous and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology* 81: 163–167.

Thomann, E., & Sager, F. (2017). Moving beyond legal compliance: innovative approaches to EU multilevel implementation, *Journal of European Public Policy* 24: 1253-1268.

Tinch, R., Schoumacher, C., & van den Hove, S. (2015). Exploring barriers to integration of biodiversity concerns across UE policy. Pp 309-340 *In*: Gasparatos, A., & Willis, K.J. (Eds.) Biodiversity in the green economy. Taylor & Francis, London.

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D., Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Höft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, J., Lojenga, R.K., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., Van Kolck, J., Visconti, P., Ye, Y. (2014). A mid-term analysis of progress toward international biodiversity targets. *Science* 346: 241-244.

Töpper, J.P., Meineri, E., Olsen S.L., Rydgren, K., Skarpaas, O., & Vandvik, V. (2018). The devil is in the detail: Nonadditive and context-dependent plant population responses to increasing temperature and precipitation. *Global Change Biology* 2018; 00:1-10.

Tourani, M., Moqanaki, E.M., Boitani, L., & Ciucci, P. (2014). Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78: 117-121.

Treves, A. & Karanth, K.U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* 17: 1491-1499.

Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science* 348: 571-573.

Valeix, M., Hemson, G., Loveridge, A. J., Mills, G. and Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology* 49: 73-81.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., & Melillo J.M. (1997). Human Domination of Earth's Ecosystems. *Science* 277: 494-499.

Vos, J. (2000). Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *Journal of Zoology* 251: 457-462.

Walton, L.R., Cluff, H.D., Paquet, P.C., Ramsay, M.A. (2001). Movement Patterns of Barren-Ground Wolves in the Central Canadian Arctic, *Journal of Mammalogy* 82: 867–876.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126-2128.

Yirga, G., Leirs, H., De Iongh, H.H., Asmelash, T., Gebrehiwot, K., Deckers, J., & Bauer, H. (2015). Spotted hyena (*Crocuta crocuta*) concentrate around urban waste dumps across Tigray, northern Ethiopia. *Wildlife Research* 42: 563–69.