

RESEARCH ARTICLE

Continuing recovery of wolves in Europe

Cecilia Di Bernardi¹*, Guillaume Chapron¹, Petra Kaczensky^{2,3}, Francisco Álvares^{4,5}, Henrik Andrén¹, Vaidas Balys⁶, Juan Carlos Blanco⁷, Silviu Chiriac⁸, Duško Čirović⁹, Nolwenn Drouet-Hoguet¹⁰, Djuro Huber¹¹, Yorgos Iliopoulos¹², Ilpo Kojola¹³, Miha Krofel¹⁴, Miroslav Kutal^{15,16}, John D. C. Linnell¹⁷, Aleksandra Majić Skrbinišek¹⁴, Peep Männil¹⁸, Francesca Maruccia¹⁹, Dime Melovski²⁰, Deniz Mengüllüoğlu²¹, Joachim Mergeay²², Robert W. Mysłajek²³, Sabina Nowak²³, Jānis Ozoliņš²⁴, Nathan Ranc²⁵, Ilka Reinhardt^{26,27}, Robin Rigg^{28,14}, Valeria Salvatori²⁹, Laurent Schley³⁰, Peter Sunde³¹, Aleksandër Trajçe³², Igor Trbojević^{33,34}, Arie Trouwborst^{35,36}, Manuela von Arx³⁷, Diana Zlatanova³⁸, Luigi Boitani³⁹

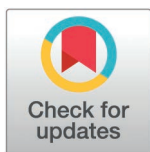
1 Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden, **2** Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Stor Elvdal, Norway, **3** University of Veterinary Medicine Vienna, Research Institute of Wildlife Ecology, Vienna, Austria, **4** CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus de Vairão, Universidade do Porto, Vairão, Portugal, **5** BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal, **6** Association for Nature Conservation "Baltijos vilkas", Vilnius, Lithuania, **7** Conservation Biology Consultants, Madrid, Spain, **8** Departement of Nature Protection, Vrancea Environmental Protection Agency, Vrancea, Romania, **9** Faculty of Biology, University of Belgrade, Belgrade, Serbia, **10** French Biodiversity Agency, Gières, France, **11** Faculty of Veterinary Medicine, University of Zagreb, Zagreb, Croatia, **12** CALLISTO Nature and Wildlife Conservation Society, Thessaloniki, Greece, **13** Natural Resources Institute Finland, Rovaniemi, Finland, **14** Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia, **15** Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic, **16** Carnivore Conservation Programme, Friends of the Earth Czech Republic, Olomouc, Czech Republic, **17** Norwegian Institute for Nature Research, Lillehammer, Norway, **18** Wildlife Department, Estonian Environment Agency, Tartu, Estonia, **19** Department of Life Sciences and Systems Biology, University of Torino, Torino, Italy, **20** Macedonian Ecological Society, Skopje, North Macedonia, **21** NEOM Nature Reserve, Gayal/Tabuk, Kingdom of Saudi Arabia, **22** INBO - Research Institute for Nature and Forest, Geraardsbergen, Belgium, **23** Department of Ecology, Faculty of Biology, University of Warsaw, Warszawa, Poland, **24** Latvian State Forest research institute SILAVA, Salaspils, Latvia, **25** Université de Toulouse, Castanet-Tolosan, France, **26** LUPUS - German Institute for Wolf Monitoring and Research, Spreetal, Germany, **27** Goethe-University Frankfurt am Main, Department of Biological Sciences, Frankfurt, Germany, **28** Slovak Wildlife Society, Liptovský Hrádok, Slovakia, **29** Istituto di Ecologia Applicata, Rome, Italy, **30** Administration de la nature et des forêts, Diekirch, Luxembourg, **31** Department of Ecoscience, Aarhus University, Aarhus C, Denmark, **32** Protection and Preservation of Natural Environment in Albania, Tirana, Albania, **33** Faculty of Natural Sciences and Mathematics, University of Banja Luka, Banja Luka, Bosnia and Herzegovina, **34** Ecology and Research Association, Banja Luka, Bosnia and Herzegovina, **35** Tilburg Law School, Tilburg University, Tilburg, the Netherlands, **36** Faculty of Law, North-West University, Potchefstroom, South Africa, **37** KORA Foundation – Carnivore Ecology and Wildlife Management, Ittigen, Switzerland, **38** Faculty of Biology, Sofia University, Sofia, Bulgaria, **39** Department of Biology and Biotechnologies 'Charles Darwin', Sapienza University, Rome, Italy

* These authors contributed equally to this work.

* cecilia.di.bernardi@slu.se

Abstract

The recovery of wolves (*Canis lupus*) across Europe is a notable conservation success in a region with extensive human alteration of landscapes and high human population densities. We provide a comprehensive update on wolf populations in Europe, estimated at over 21,500 individuals by 2022, representing a 58% increase over the past decade. Despite the challenges of high human densities and significant land use for agriculture, industry, and urbanization, wolves have demonstrated remarkable adaptability and increasing



OPEN ACCESS

Citation: Di Bernardi C, Chapron G, Kaczensky P, Álvares F, Andrén H, Balys V, et al. (2025) Continuing recovery of wolves in Europe. PLOS Sustain Transform 4(2): e0000158. <https://doi.org/10.1371/journal.pstr.0000158>

Editor: Jose Carlos Báez, Spanish Institute of Oceanography: Instituto Espanol de Oceanografia, SPAIN

Received: June 8, 2024

Accepted: December 18, 2024

Published: February 25, 2025

Copyright: © 2025 Di Bernardi et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data availability statement: The data is publicly archived in Dryad at <https://datadryad.org/stash/dataset/doi:10.5061/dryad.np5hqc03g>.

Funding: C. Di Bernardi was supported by the Large Carnivore Initiative for Europe through the Institute of Applied Ecology IEA and by Marie-Claire Cronstedt stiftelse. G. Chapron was supported by the Swedish Research Council VR (grants no. 2018-05203)

and 2020-04973). D. Čirović was funded by the Ministry of Science and Technological Development, Republic of Serbia (grant no. 451-03-65/2024-03/200178). M. Krofel was supported by the Slovenian Research and Innovation Agency (grant no. J1-50013 and P4-0059). J. D. C. Linnell was funded by the Research Council of Norway (grant no. 342821). R.W. Mysłajek was supported by the National Science Centre Poland (grant no. 2019/35/O/NZ8/01550). S. Nowak was supported by the National Science Centre Poland (grant no. 2020/39/B/NZ9/01829). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

population trends in most European countries. Improved monitoring techniques, although varying in quality and scope, have played a crucial role in tracking this recovery. Annually, wolves kill approximately 56,000 domestic animals in the EU, a risk unevenly distributed and differently handled across regions. Damage compensation costs 17 million EUR every year to European countries. Positive economic impacts from wolf presence, such as those related to reducing traffic accidents with wild ungulates or supporting wildlife tourism, remain under studied. Wolf recovery in Europe is supported by diverse policy and legal instruments such as LIFE programs, stakeholder platforms, as well as the EU Habitats Directive and the Bern Convention. Coexisting with newly established wolf populations in Europe entails managing impacts on human activities, including livestock depredation, competition for game, and fear of attacks on humans, amidst varying social and political views on wolf recovery. Sustainable coexistence continues to operate in evolving and complex social, economic, and political landscapes, often characterized by intense debates regarding wolf policies.

Author summary

We report that wolves are continuing to make a remarkable comeback across Europe, with their population growing to over 21,500 individuals by 2022—a 58% increase in a decade. This is a notable conservation success, particularly in a region heavily shaped by human activity, from agriculture to urbanization. Improved monitoring methods have helped us track their recovery, although these tools vary in quality and extent across countries. Annually, wolves kill around 56,000 domestic animals in the EU, leading to annual costs of about 17 million EUR for damage compensation. Yet, wolves may also bring potential benefits, such as reducing car accidents with wild ungulates and creating opportunities for ecotourism, though these positive impacts are often overlooked. Legal protections, including the EU Habitats Directive and the Bern Convention, along with conservation programs, such as the LIFE programs, have been key to supporting wolf recovery. However, the coexistence of wolves with human activities, notably farming and hunting, remains a challenge and requires navigating complex social, economic, and political contexts.

Introduction

While large carnivores and biodiversity are declining worldwide [1], an exception has been the recovery of large carnivores in Europe [2]. This positive trend is remarkable because Europe appears at first as an unlikely place for a large carnivore to recover. In Europe, wildlife has to share space with a human population of roughly 450 million people in a highly anthropized landscape where people grow crops, raise livestock, hunt wild game, and more broadly shape the landscape through urbanization, energy production, industries, and transport infrastructures [2–4]. Even more remarkable is that the predatory species recovering the most is the wolf (*Canis lupus*), which many people perceive as belonging to wilderness areas and which is often embroiled in conservation conflicts and political controversies [5].

An earlier continental overview revealed that permanent wolf ranges were characterized by a mean density of 36.7 human inhabitants/km² [2], which suggests a high degree of adaptation to human presence. This raised the question of whether Europe had found a recipe to

sustainably coexist with large predatory mammals [6], which could provide relevant insights for the conservation of many other species worldwide in the 21st century [7]. Here we provide an update of numbers, trends, monitoring methods, and conservation status of wolves across the European continent and discuss the ongoing conservation issues and challenges that will likely shape the future direction of wolf population development in Europe.

More than twenty thousand wolves in Europe

Our estimate based on monitoring reports and expert assessments in 34 countries (S1 Appendix) reveals that by 2022 at least 21,500 wolves inhabit Europe, 19,000 of which are found in the European Union (EU) [8], an increase of 58% from the 12,000 estimated 10 years ago [2]. In the EU, wolves share the landscape with millions of wild ungulates [4], 279 million head of livestock and 449 million people [9,10]. In most countries, wolf populations have continued to increase (Fig 1) and are now found in all but the smallest countries of mainland Europe (Fig 2). Several countries – Bulgaria, Greece, Germany, Italy, Poland, Spain, and Romania – now have more than 1,000 individuals each. For a variety of reasons including management goals (i.e., population caps) or the relatively recent recolonization of the species after a long absence, some countries have fewer than 100 individuals (Austria, Belgium, Denmark, Hungary, Luxembourg, Norway, and the Netherlands). The three microstates of Monaco, San Marino and The Vatican remain the only countries in mainland Europe not having experienced wolf recolonization.

Some countries that had very few wolves a decade ago now have large populations and continue to experience high growth rates. For example, wolves in Germany increased from 1 pack in 2000 to 184 packs and 47 pairs in 2022 [11]. Assessing wolf population dynamics in their respective countries, authors of the current paper reported that, during the last decade, wolf numbers increased in 19 countries (Austria, Belgium, Bulgaria, Czech Republic, Denmark, Finland,

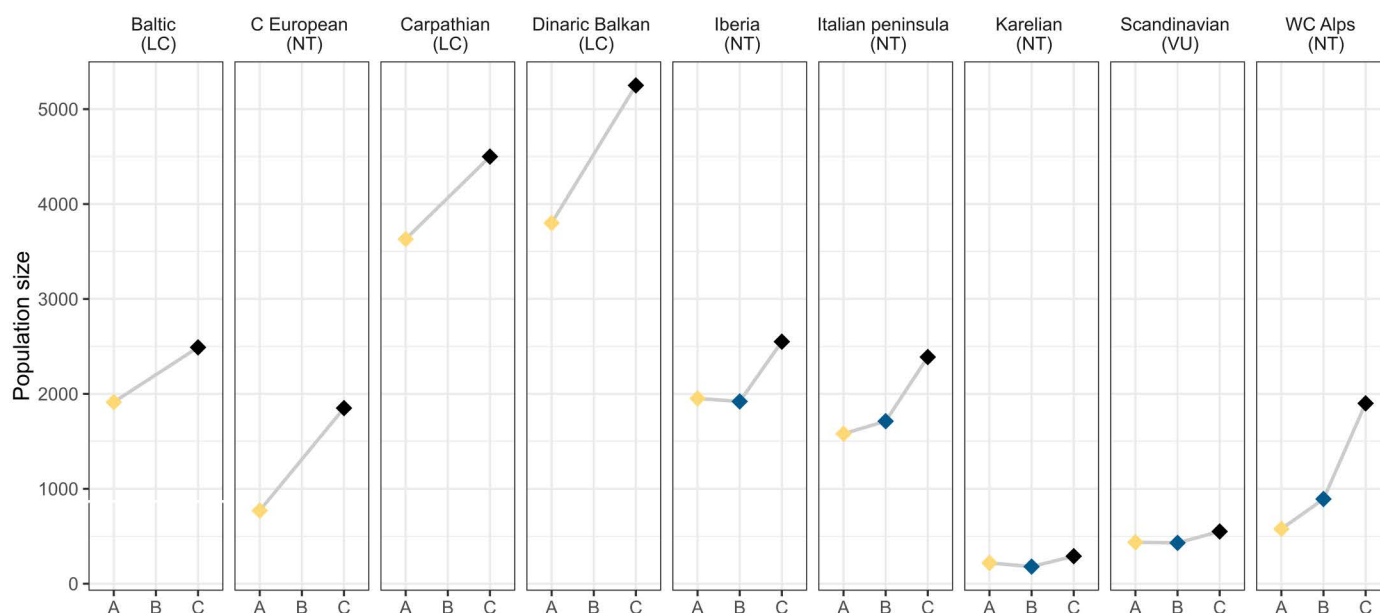


Fig 1. For the 9 European wolf populations defined by the Large Carnivore Initiative for Europe (LCIE), three population size estimates are shown, respectively for A) 2012–2016 from the LCIE [118] (in yellow), B) 2013–2018 from country reports in 2018 under Article 17 and Resolution No.8 [119] (in blue), and C) 2020–2022 from the LCIE [59] (in black). Red List categories from the assessment at the population level conducted by the LCIE are shown in brackets [59], where LC stands for Least Concern, NT for Near Threatened, VU for Vulnerable. A 10th population in Sierra Morena (Spain) is now extinct [17].

<https://doi.org/10.1371/journal.pstr.0000158.g001>

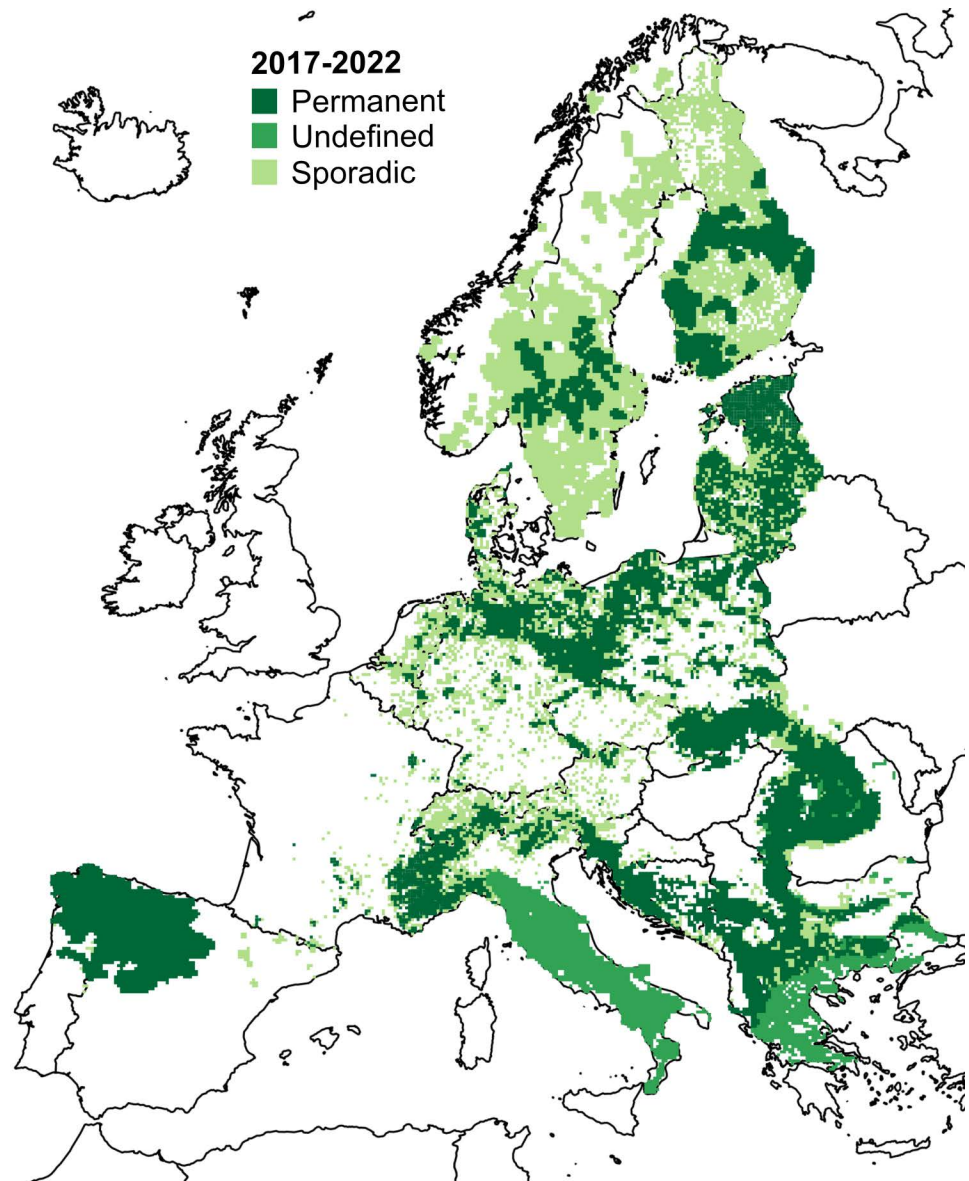


Fig 2. Wolf distribution in Europe reported for the period 2017–2022/23, as published by [120]. Permanent cells: established and reproducing populations, also including cells with continuous presence in the absence of documented reproduction. Sporadic cells: only occasional presence of dispersers or lone individuals. Undefined cells: confirmed presence but without distinction between permanent or sporadic presence, see [121] for details on, e.g., the use of an integrated spatial model for Italy [18]. Basemap is world map from QGIS (data source: Natural Earth 1:10 m detail level Cultural vectors <https://www.naturalearthdata.com/downloads/10m-cultural-vectors/>).

<https://doi.org/10.1371/journal.pstr.0000158.g002>

France, Germany, Greece, Hungary, Italy, Lithuania, The Netherlands, Poland, Slovak Republic, Slovenia, Sweden, Switzerland and the European part of Türkiye), remained broadly stable in 8 countries (Albania, Croatia, Luxembourg, Norway, Portugal, Romania, Spain, Ukraine), fluctuated in three countries (Estonia, Latvia, Serbia) and decreased in three countries (Bosnia & Herzegovina, Montenegro, North Macedonia) while the situation in Kosovo is unknown.

When assessing trends at the population level (*sensu* [12]), we find that the largest populations (Dinaric Balkan, Carpathian) are increasing, with smaller populations (e.g., Central

European, Western Central Alps) displaying even larger growth rates [13,14]. Some populations (i.e., Scandinavian and Karelian) have experienced slower growth, and even stagnation, because of intensive management actions (lethal control and hunter harvest). Only the Nordic countries (Finland, Norway, and Sweden) and Austria appear to have limited their recovering wolf populations (Fig 1). A small, isolated population in southern Spain is the only European wolf population to become extinct in recent years [15–17]. Overall, wolves have shown an ability to recover in highly-altered, multi-use landscapes on a continental scale when they are permitted to do so, confirming the extraordinary adaptability of this species [6].

Wolf monitoring has improved, but is still far from perfect

The methods used to estimate wolf numbers across Europe are diverse (S2 Appendix) and vary in quality and scale but have generally improved over the years. In 21 countries, the most recent wolf abundance estimates were based on a complete survey (most of the known wolf distribution area was surveyed), while in 13 countries the estimate was based on partial surveys (i.e., only in parts of the known wolf range). Typically, smaller or recently recovered populations are monitored more thoroughly (e.g., in the Alpine countries, Belgium, Denmark, Germany, the Netherlands, Norway, Slovenia, Sweden), while some larger populations are less intensively monitored (e.g., Bulgaria, Romania). However, it is worth noting the recent nation-wide estimate in Italy based on state-of-the-art methods combining systematic field surveys and integrated population modeling [18] that demonstrated the application of robust statistical methods across large scales. Some countries have very detailed monitoring, where almost every individual wolf is known and the genetic pedigree of the population is available (Denmark [19], Finland [20], Germany [21], the Italian Alps [22] and Scandinavia [23–25]). Genetic monitoring methods are diverse and serve a variety of goals: assignment of individuals to source populations, population size estimation, determining genome-wide inbreeding and diversity or detecting hybridization with other canids [26–28].

Monitoring is performed by a diversity of actors in different countries, including government agencies, research institutes, hunters, conservation NGOs and the general public. Funds for wolf monitoring are allocated for multiple reasons: wolves are a conflict-prone and controversial species, sometimes intensively hunted, potentially vulnerable to the impacts of some infrastructure development, so management agencies, interest groups and the broader public want to know how many wolves there are and where. In addition, within the EU, the wolf is a protected species and Member States have obligations to survey and report its status every 6 years under Article 17 of the Habitats Directive. A challenge typical of recovering wolf populations will be to maintain monitoring at a level that allows the reliable detection of trends in abundance and distribution as populations increase, while dealing with limited budgets. Moreover, considering that some wolf populations are regularly hunted and that the species' protection may soon be downgraded in EU law [29], it will be difficult to detect possible local decreases in wolf population density without annual and state-of-the-art monitoring. Furthermore, to avoid double counting individuals in populations shared between countries [30], monitoring would need to be coordinated among countries, with good examples being Norway and Sweden [24,31], the Alpine countries [13] and some countries sharing the Central European population (e.g., Belgium, Denmark, Germany, Luxembourg, The Netherlands [11,32]).

Challenges for coexistence

Wolf recovery in human-dominated landscapes implies accepting and managing a certain level of impact that wolves might have on people's livelihoods and the potential for conflicts among people over their differing views on how to manage wolves [33]. In Europe, conflicts

about wolves generally relate to depredation on domestic animals, competition for wild game, fear of attacks on humans, as well other socio-political issues of which the wolf has become the symbol [34–36].

Our data reveal that ca. 19,000 wolves in the EU killed ca. 56,000 domestic animals per year [8] out of a total of 279 million head of livestock, corresponding to ca. 3 killed livestock per wolf per year. From a population perspective, an average head of livestock in the EU faces a 0.02 percent annual risk of being killed by wolves. However, there is large spatial variation in this risk which considers the total number of livestock and not only those in areas inhabited by wolves. Sheep and goats accounted for roughly two thirds of losses but, locally, depredation also affected cattle, horses, semi-domestic reindeer and dogs (Fig 3). A few countries, such as Croatia, France, Greece, Italy, Norway, and Spain, had significantly more absolute losses than others (Figs 3, 4), possibly linked to different husbandry practices and/or different compensation systems. Most damage is caused to free-ranging livestock [37]. In some contexts, high levels of depredation do not automatically lead to widespread social conflicts, for example regarding depredation on horses by wolves in northwestern Spain [38] or in Albania [39], because in some cultures a certain level of depredation can be accepted as being “normal”. However, in other areas even low levels of depredation are the focus of intense social conflicts, for example with around 10 hunting dogs annually killed by wolves in Sweden [40–42]. The link between the number of wolves and the level of livestock depredation is not straightforward other than that, stating the obvious, there is no wolf depredation in the absence of wolves. No clear relationship was found when comparing either across countries [37,43] or longitudinally within a country, i.e., Germany [44]. A recent analysis of depredation in Europe found that damage typically increased as wolves recolonised new areas but subsequently decreased in association with the use of protection measures [45]. Regarding the connection between lethal control and levels of livestock depredation, different studies have produced contrasting findings (cf [46,47].) while research employing an experimental protocol is lacking, which precludes definitive answers.

Another challenge that wolves pose to human activities regards hunting of both wolves and other game species. This is also a complex issue due to multiple cultural, social, and political factors, rooted in concerns over competition for game, potential changes in behavior of game, interference with supplementary feeding of game during winter, concerns for hunters losing their status and role as regulators of wildlife populations [48–50], as well as the loss of hunting dogs [33,51]. The extent and character of wolf hunting differ widely among European countries, from full bans to regular license hunts or unregulated pest control (e.g., in North Macedonia), as a result of the local practices of wildlife management, the legal status of wolves and how it is translated into practical management, as well as the broader socio-political context.

Third, there is the fear of attacks by wolves on humans. Although wolf attacks are extremely rare in Europe [52] and reported cases were often found to be committed by human-habituated and food-conditioned individuals [53], many people fear the possibility of being attacked and their concerns are amplified by sensationalized and inaccurate media reports of wolf-human interactions [54–56]. For example, reported attacks on people in Italy [57] and Greece [58] were most likely by domestic dogs, not wolves. In some populations, hybridization with dogs is becoming a threat to wolf conservation with reported estimates possibly even including some hybrids [59–61]. Research has found limited evidence of jackal-wolf hybrids in Europe [62,63], but see [64] for putative gene flow between the species in the Caucasus. Wolf-jackal hybridization might become a future source of concern as wolf populations recover in human-dominated environments that jackals have already or will colonize as part of their ongoing, continental range expansion [65].

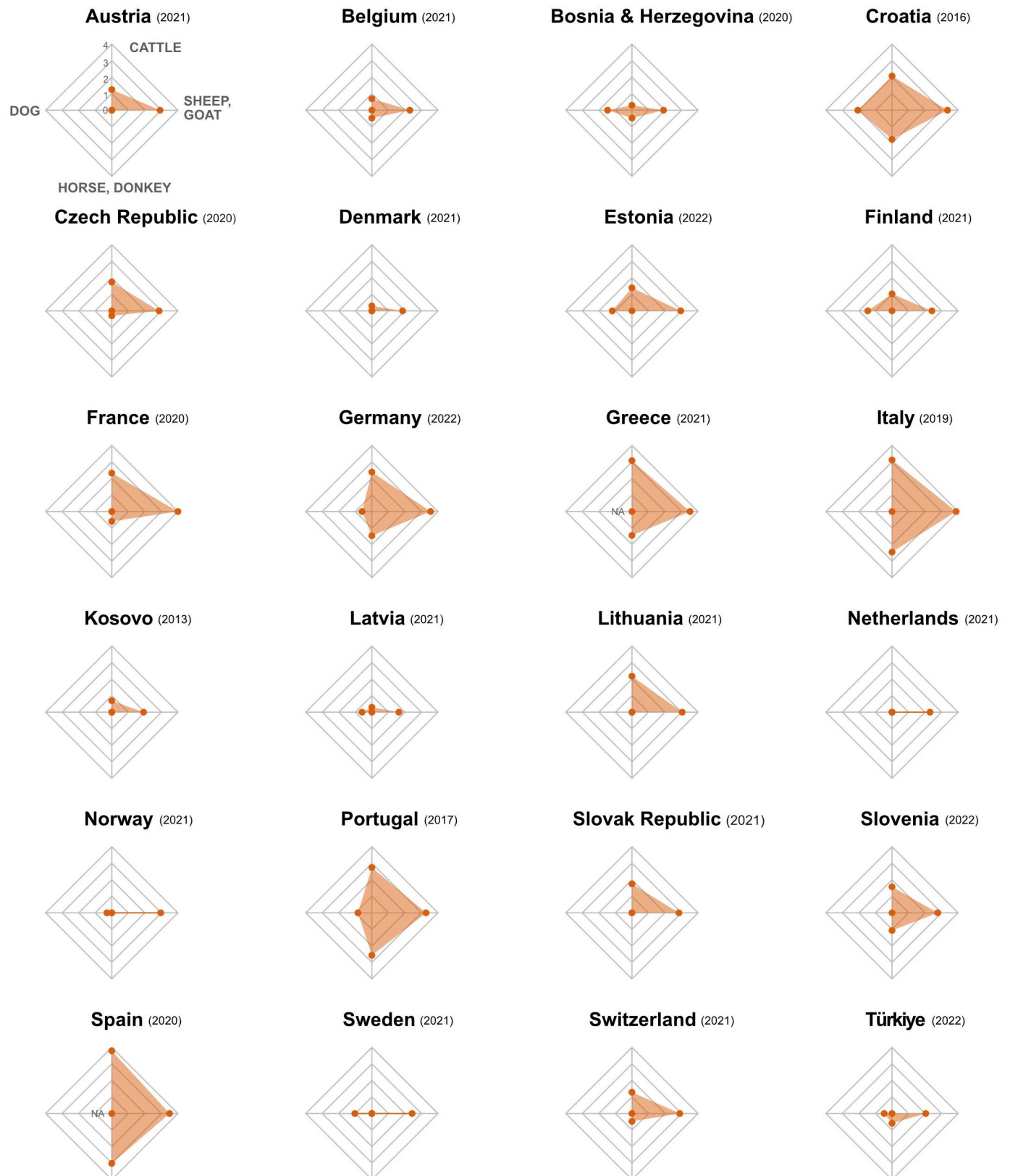


Fig 3. Depredation recorded in the most recent year (in brackets) for 24 countries, reported as the number of animals killed by wolves. The numbers in the graph are presented at the log10 scale, i.e., 1 stands for 10 animals, 2 for 100 animals, 3 for 1,000 animals, and 4 for 10,000 animals. Depredation on semi-domestic reindeer is not presented and is only reported by Norway (134 animals killed) and Finland (1,516 animals killed).

<https://doi.org/10.1371/journal.pstr.0000158.g003>

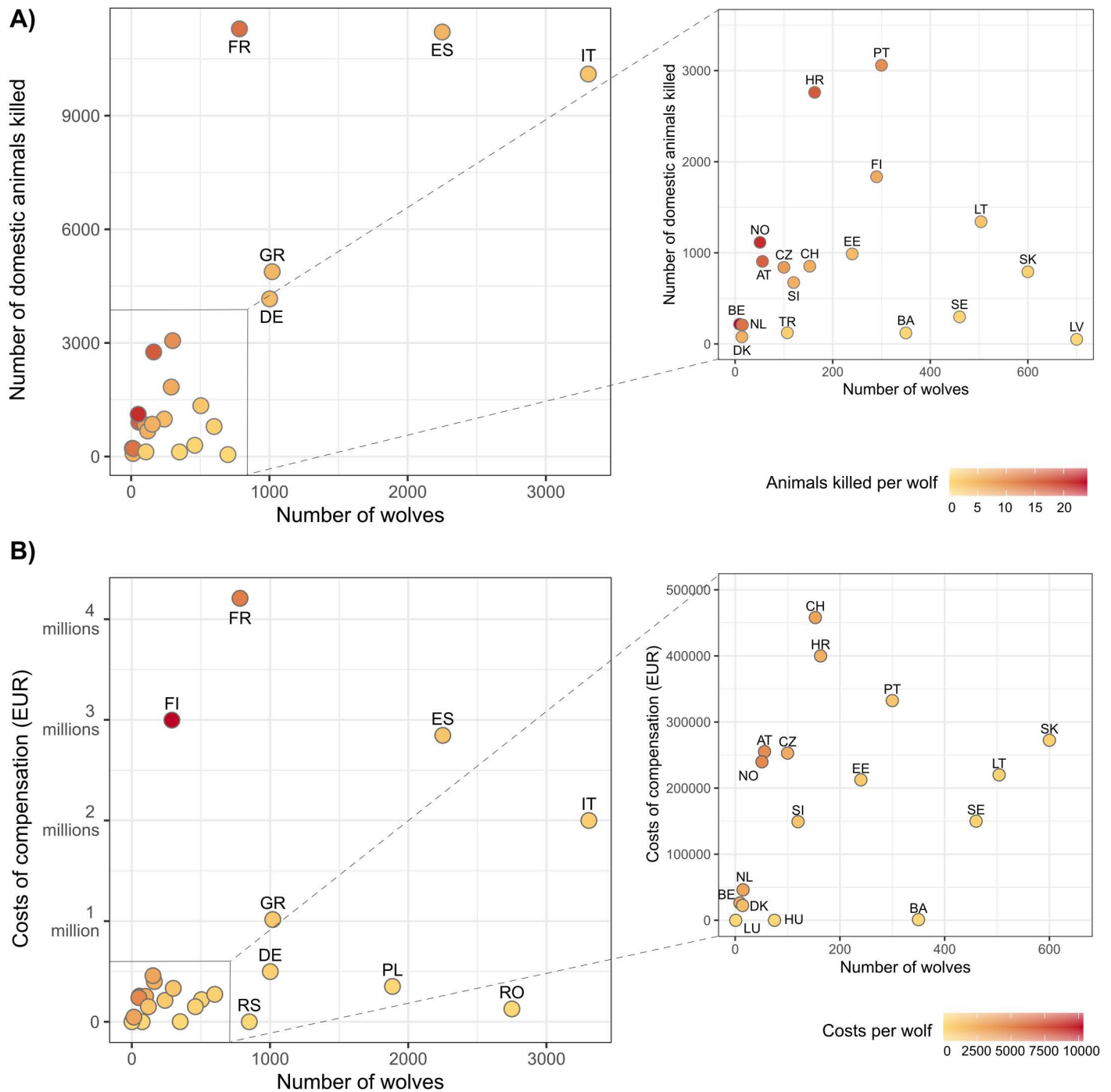


Fig 4. Number of A) domestic animals killed (depredation) and B) costs of compensation for livestock losses, according to the number of wolves from the latest annual update for each of the 23 countries reporting depredation data and 26 countries reporting compensation data (left: for the whole dataset, right: zoomed in) and wolf numbers. Each point is a country with country codes from ISO-3166 Alpha-2 classification (see [S3 Appendix](#)).

<https://doi.org/10.1371/journal.pstr.0000158.g004>

Complex socio-political conflicts regarding wolves stem from disagreements between diverse interest groups, stakeholders or segments of the public, where controversy about wolf management becomes symbolic for deeper divisions around value systems, power, influence,

class, knowledge, education, human activity and the very nature of the human-nature relationship [33,66,67]. Wolves are also increasingly symbolic for a range of wider social and political issues especially framed as a rural-urban divide in Europe [68]. For example, the far-right parties Alternative für Deutschland (AfD) in Germany and Dansk Folkeparti (DF) in Denmark have actively opposed wolf recovery by framing it as a threat to rural inhabitants abandoned by their governments [68,69].

Finally, like many other species, wolf conservation can also be affected by unrelated but complex political issues, often through unrelated geo-political events. For example, while wolves in France kill several thousand sheep per year, the decline of sheep farming in the country has been influenced by France's cessation of protective measures against New Zealand lamb imports to the European Union, a consequence of political fallout from the 1985 bombing of Greenpeace's boat in Auckland by the French special forces to prevent anti-nuclear protests in the French Pacific [70]. When the wolf came back to France in 1992, it served as a political scapegoat to highlight the decline of sheep farming without addressing the root economic issues. A second example of wolf conservation being linked to unrelated political issues is the recent construction of thousands of kilometers of border fences due to the human migration crises and military conflicts in eastern and southern Europe, which may in the future affect the size, dynamics, and genetic diversity of the Baltic and Dinaric Balkan wolf populations [71,72].

The economics of wolf recovery

One proxy for the economic costs of coexisting with wolves is the amount of money spent annually by countries for compensation of damages, although this is a rough way of estimating the overall costs of such coexistence (e.g., damage prevention, monitoring, law enforcement, and conservation projects can add significant costs). In total, European countries spent 17 million EUR annually on compensation for damage attributed to wolves. France paid the largest amount of any country (4.2 million EUR/year), although Finland paid the most per wolf (10,300 EUR/year) (Fig 4). As with wolf density and damages, when comparing across countries there does not appear to be a clear relationship between the number of wolves and the resulting economic costs, with larger or denser wolf populations not necessarily implying higher economic costs (Fig 4). Although compensation costs may be tolerable at the national level, the concentration of damages at a local level may put high pressure on individual livestock owners, local communities, or local activities, especially when combined with other sources of financial hardship. This underlines the importance of reducing damages with a diverse set of instruments that need to be adapted to local needs [73]. In general, electric fences, shepherding and livestock guarding dogs are the most commonly implemented damage prevention measures. In three quarters of European countries, mitigation measures are financially supported to different degrees by government authorities, NGOs, or in the framework of time-limited conservation projects (e.g., LIFE projects).

On the other hand, positive socio-economic impacts of wolf recovery include, for example, the reduction of ungulate damages on forestry (e.g., in Poland [74,75]). Recent studies have argued that the return of the wolf may reduce traffic accidents involving collisions between ungulates and vehicles [76]. For example, one study [77] suggests that wolves consuming roe deer and wild boar prevented between 2.4 and 7.8 million EUR in road collision-related injuries and property damage annually in France. Other positive aspects include wildlife tourism and commercial activities that directly or indirectly benefit from large carnivore presence [78,79]. However, potential economic benefits from wolf presence have been poorly investigated and quantified in Europe.

European policy instruments and controversies

The recovery of wolves in Europe has been made possible by broader social, economic, and historical processes, such as reforestation, rural-urban migration, and sustainable ungulate management [80], combined with generally favorable public opinion [81]. This recovery would, however, not have happened without a substantial institutional and political investment of European countries. Specifically, wolves have benefited from various degrees of legal protection at national and European levels [82]. The wolf has been listed in Appendix II (strictly protected) of the Bern Convention in most European countries, with the exception of some countries, mainly in the east, having made reservations (in December 2024, the Standing Committee of the Bern Convention approved a proposal by the EU to move the species to Appendix III (protected) [83]). EU Member States are obliged by the Habitats Directive (HD) to ensure that the wolf reaches and remains at a so-called Favorable Conservation Status (FCS) [84,85]. They must transpose the HD into their national laws. In most EU countries, the wolf is listed in HD Annex II (obligation to designate protected areas for the species) and Annex IV (killing allowed only under limited exceptions, referred to as derogations) although the wolf is listed in Annex V (hunting allowed) in several countries (Bulgaria, Estonia, northern part of Finland, northern part of Greece, Latvia, Lithuania, Poland, Slovakia, and northern part of Spain). Following the change of Appendix in the Bern Convention, the European Commission has announced it will implement a similar change in the HD to have the wolf no longer listed in Annex IV but instead in Annex V [29].

To facilitate achieving FCS, the EU has developed a portfolio of policy instruments. It has awarded substantial funding to promote wolf-human coexistence, through the LIFE program [86], although the program's effectiveness remains difficult to measure [87]. Properly implemented prevention measures, especially electric fences, have however demonstrated their efficacy [73,88], although more evidence is needed [89,90]. There is a need to invest in such measures, with a constant evaluation of their performance, to reduce the impact of wolf depredations to economically acceptable and socially tolerable levels. In parallel, the European Commission has also launched a unique initiative in the form of platforms for coexistence where stakeholders meet, debate and share best practices [67]. Initially launched at the European level, the idea has now expanded to include regional platforms [91]. Furthermore, Member States are able to avail themselves of substantial financial resources available within agricultural and rural development funds to cover the costs of livestock protection and compensation activities [92].

Conflicts over wolf management have regularly sparked intense political debates, in many countries and at the European level, especially regarding the long-term goal of wolf recovery, whether more liberal use of lethal control or hunting should be permitted [93] and also about the downgrading of wolf legal protection, as often demanded by farmer or hunter representatives [94]. The European Parliament passed a resolution in 2022 calling for more flexible wolf management and greater consideration of agricultural and rural interests [95]. In September 2023, the European Commission announced its intention to reassess the protection status of the wolf in Europe [96,97]. In December 2023, it filed a proposal to amend the legal status of the wolf in the Bern Convention from strictly protected to protected [98], which was voted by a majority of Member States in September 2024 [99] and approved by the Standing Committee of the Bern Convention in December 2024 [83]. Non-EU countries, which are not bound by the Habitats Directive, have experienced similar debates [100], with Norway adopting extremely limited population goals [101] and Switzerland aiming at reducing its wolf numbers through preventive regulation [102].

Conflicts about wolves have been litigated and there have been numerous court cases regarding wolves in national jurisdictions [103]. The Court of Justice of the European Union has also issued several rulings on what the Habitats Directive mandates regarding wolf conservation [104–108] and further rulings about wolves are pending [109,110]. In addition, there is a 12-year-old ongoing infringement case by the European Commission against Sweden and its annual wolf hunt [111].

Conclusions

The recovery of the wolf in Europe demonstrates that a large predatory species can successfully share landscapes with high densities of humans. There are other examples of such coexistence, notably the case of leopards (*Panthera pardus*) occurring and breeding at the edges of large urban and in densely populated agricultural areas in India [112,113]. Wolves in Europe have come back across a wide diversity of land uses. Their recovery has certainly benefited from their opportunistic ecology (in contrast, the Eurasian lynx (*Lynx lynx*) and brown bear (*Ursus arctos*) have not experienced the same extent of recovery). Favorable social, legal and institutional contexts have also contributed to this recovery. Among the predators listed in the EU Habitats Directive, the wolf has possibly experienced the strongest population growth [2]. This shows that, with appropriate policy instruments, land-sharing models can work, even for apex predators, on continental scales [6,114,115]. However, as controversies escalate, the challenge will be to adapt conservation policies as they transition from saving endangered populations to sustaining success [116]. An emerging but no less critical aspect will be to avoid wolf, and nature conservation at large, becoming embroiled in “culture wars” and being perceived as wedge issues that sharpen the divide between progressive versus conservative ideologies [68,69,117].

Supporting information

S1 Appendix. Material and methods.

(DOCX)

S2 Appendix. Estimates of the percentage of wolf range/ population covered by each monitoring method for 34 European countries. Empty cells indicate that the method was not considered relevant.

(DOCX)

S3 Appendix. Country codes based on the ISO-3166 Alpha-2 classification.

(DOCX)

Acknowledgments

We thank numerous contributors of data from governmental offices, universities and NGOs. All references to Kosovo, whether to the territory, institutions or population, in the main text, figure legends and supplementary material shall be understood in full compliance with United Nations Security Council Resolution 1244 and without prejudice to the status of Kosovo.

Author contributions

Conceptualization: Cecilia Di Bernardi, Guillaume Chapron, Petra Kaczensky, Luigi Boitani.

Data curation: Cecilia Di Bernardi, Guillaume Chapron, Petra Kaczensky, Luigi Boitani.

Formal analysis: Cecilia Di Bernardi, Guillaume Chapron.

Funding acquisition: Luigi Boitani.

Investigation: Cecilia Di Bernardi, Petra Kaczensky, Francisco Álvares, Henrik Andrén, Vaidas Balys, Juan Carlos Blanco, Silviu Chiriac, Duško Ćirović, Nolwenn Drouet-Hoguet, Djuro Huber, Yorgos Iliopoulos, Ilpo Kojola, Miha Krofel, Miroslav Kutal, John D. C. Linnell, Aleksandra Majić Skrbinišek, Peep Männil, Francesca Marucco, Dime Melovski, Deniz Mengüllüoğlu, Joachim Mergeay, Robert W. Mysłajek, Sabina Nowak, Jānis Ozoliņš, Nathan Ranc, Ilka Reinhardt, Robin Rigg, Valeria Salvatori, Laurent Schley, Peter Sunde, Aleksandër Trajçe, Igor Trbojević, Arie Trouwborst, Manuela von Arx, Diana Zlatanova, Luigi Boitani.

Project administration: Petra Kaczensky, Luigi Boitani.

Visualization: Cecilia Di Bernardi, Guillaume Chapron.

Writing – original draft: Cecilia Di Bernardi, Guillaume Chapron.

Writing – review & editing: Cecilia Di Bernardi, Guillaume Chapron, Petra Kaczensky, Francisco Álvares, Henrik Andrén, Vaidas Balys, Juan Carlos Blanco, Silviu Chiriac, Duško Ćirović, Nolwenn Drouet-Hoguet, Djuro Huber, Yorgos Iliopoulos, Ilpo Kojola, Miha Krofel, Miroslav Kutal, John D. C. Linnell, Aleksandra Majić Skrbinišek, Peep Männil, Francesca Marucco, Dime Melovski, Deniz Mengüllüoğlu, Joachim Mergeay, Robert W. Mysłajek, Sabina Nowak, Jānis Ozoliņš, Nathan Ranc, Ilka Reinhardt, Robin Rigg, Valeria Salvatori, Laurent Schley, Peter Sunde, Aleksandër Trajçe, Igor Trbojević, Arie Trouwborst, Manuela von Arx, Diana Zlatanova, Luigi Boitani.

References

1. Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, et al. Status and ecological effects of the world's largest carnivores. *Science*. 2014;343(6167):1241484. <https://doi.org/10.1126/science.1241484> PMID: 24408439
2. Chapron G, Kaczensky P, Linnell JDC, von Arx M, Huber D, Andrén H, et al. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*. 2014;346(6216):1517–9. <https://doi.org/10.1126/science.1257553> PMID: 25525247
3. Bautista C, Revilla E, Naves J, Albrecht J, Fernández N, Olszańska A, et al. Large carnivore damage in Europe: analysis of compensation and prevention programs. *Biological Conservation*. 2019;235:308–16. <https://doi.org/10.1016/j.biocon.2019.04.019>
4. Linnell JDC, Cretois B, Nilsen EB, Rolandsen CM, Solberg EJ, Veiberg V, et al. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*. 2020;244:108500. <https://doi.org/10.1016/j.biocon.2020.108500>
5. Convery I, Nevin OT, van Maanen E, Davis P, Lloyd K, editors. *The wolf: culture, nature, heritage*. Woodbridge: The Boydell Press; 2023.
6. Cretois B, Linnell JDC, Van Moorter B, Kaczensky P, Nilsen EB, Parada J, et al. Coexistence of large mammals and humans is possible in Europe's anthropogenic landscapes. *iScience*. 2021;24(9):103083. <https://doi.org/10.1016/j.isci.2021.103083> PMID: 34585121
7. IUCN SSC. IUCN SSC guidelines on human-wildlife conflict and coexistence. IUCN SSC Human-Wildlife Conflict and Coexistence Specialist Group. 1st ed; 2023. <https://doi.org/10.2305/ygik2927>
8. Di Bernardi C, Chapron G, Kaczensky P, Álvares F, Andrén H, Balys V. Continuing recovery of wolves in Europe. *Dryad*; 2025. <https://doi.org/10.5061/dryad.np5hqc03g>
9. Eurostat. Demography of Europe. LU: Publications Office; 2023. Available from: <https://data.europa.eu/doi/10.2785/083>
10. Eurostat. EU livestock population; 2023. Available from: https://ec.europa.eu/eurostat/web/agriculture/database?node_code=apro_mt_ls
11. DBBW. Wolf territories in Germany Development of territories since 2000; 2024 [cited 20 Sep 2024]. Available from: <https://www.dbb-wolf.de/wolf-occurrence/confirmed-territories/development-since-2000>
12. Linnell J, Salvatori V, Boitani L. Guidelines for population level management plans for large carnivores in Europe; 2008.

13. Marucco F, Reinhardt I, Avanzinelli E, Zimmermann F, Manz R, Potočník H, et al. Transboundary monitoring of the wolf alpine population over 21 years and seven countries. *Animals (Basel)*. 2023;13(22):3551. <https://doi.org/10.3390/ani13223551> PMID: 38003168
14. Reinhardt I, Kluth G, Nowak C, Szentiks CA, Krone O, Ansorge H, et al. Military training areas facilitate the recolonization of wolves in Germany. *Conservation Letters*. 2019;12(3):. <https://doi.org/10.1111/conl.12635>
15. Gómez-Sánchez D, Olalde I, Sastre N, Enseñat C, Carrasco R, Marques-Bonet T, et al. On the path to extinction: Inbreeding and admixture in a declining grey wolf population. *Mol Ecol*. 2018;27(18):3599–612. <https://doi.org/10.1111/mec.14824> PMID: 30074659
16. López-Bao JV, Blanco JC, Rodríguez A, Godinho R, Sazatornil V, Alvares F, et al. Toothless wildlife protection laws. *Biodivers Conserv*. 2015;24(8):2105–8. <https://doi.org/10.1007/s10531-015-0914-8>
17. Quevedo M, Echegaray J, Fernández-Gil A, Leonard JA, Naves J, Ordiz A, et al. Lethal management may hinder population recovery in Iberian wolves. *Biodivers Conserv*. 2018;28(2):415–32. <https://doi.org/10.1007/s10531-018-1668-x>
18. Gervasi V, Aragno P, Salvatori V, Caniglia R, De Angelis D, Fabbri E, et al. Estimating distribution and abundance of wide-ranging species with integrated spatial models: opportunities revealed by the first wolf assessment in south-central Italy. *Ecol Evol*. 2024;14(5):e11285. <https://doi.org/10.1002/ece3.11285> PMID: 38746543
19. Sunde P, Collet S, Nowak C, Thomsen PF, Hansen MM, Schulz B, et al. Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany. *Conservation Letters*. 2021;14(5). <https://doi.org/10.1111/conl.12812>
20. Mäntyniemi S, Helle I, Kojola I. Assessment of the residential Finnish wolf population combines DNA captures, citizen observations and mortality data using a Bayesian state-space model. *Eur J Wildl Res*. 2022;68(6). <https://doi.org/10.1007/s10344-022-01615-5>
21. Jarausch A, Harms V, Kluth G, Reinhardt I, Nowak C. How the west was won: genetic reconstruction of rapid wolf recolonization into Germany's anthropogenic landscapes. *Heredity (Edinb)*. 2021;127(1):92–106. <https://doi.org/10.1038/s41437-021-00429-6> PMID: 33846578
22. Marucco F, Boiani MV, Dupont P, Milleret C, Avanzinelli E, Pilgrim K, et al. A multidisciplinary approach to estimating wolf population size for long-term conservation. *Conserv Biol*. 2023;37(6):e14132. <https://doi.org/10.1111/cobi.14132> PMID: 37259636
23. Åkesson M, Danielsson A, Flagstad Ö, Svensson L. Sammanställning av släktträdet över den skandinaviska vargpopulationen fram till 2022; 2023. Available from: <https://res.slu.se/id/publ/122462>
24. Bischof R, Milleret C, Dupont P, Chipperfield J, Tourani M, Ordiz A, et al. Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. *Proc Natl Acad Sci U S A*. 2020;117(48):30531–8. <https://doi.org/10.1073/pnas.2011383117> PMID: 33199605
25. Wabakken P, Svensson L, Maartmann E, Nordli K, Flagstad Ø, Åkesson M. Inventering av varg vintern 2021–2022. Bestandsstatus for store rovdyr i Skandinavia. 2022 [cited 20 Sep 2024]. Available from: <https://res.slu.se/id/publ/120389>
26. Harmoinen J, von Thaden A, Aspi J, Kvist L, Cocchiararo B, Jarausch A, et al. Reliable wolf-dog hybrid detection in Europe using a reduced SNP panel developed for non-invasively collected samples. *BMC Genomics*. 2021;22(1):473. <https://doi.org/10.1186/s12864-021-07761-5> PMID: 34171993
27. Jarausch A, von Thaden A, Sin T, Corradini A, Pop MI, Chiriac S, et al. Assessment of genetic diversity, population structure and wolf-dog hybridisation in the Eastern Romanian Carpathian wolf population. *Sci Rep*. 2023;13(1):22574. <https://doi.org/10.1038/s41598-023-48741-x> PMID: 38114536
28. Smeds L, Aspi J, Berglund J, Kojola I, Tirronen K, Ellegren H. Whole-genome analyses provide no evidence for dog introgression in Fennoscandian wolf populations. *Evol Appl*. 2020;14(3):721–34. <https://doi.org/10.1111/eva.13151> PMID: 33767747
29. European Commission. EU proposal to adapt protection status of the wolf adopted by Bern Convention, paving the way to more flexibility in managing wolf populations. In: European Commission. European Commission [Internet]; 2024 [cited 19 Dec 2024]. Available from: https://ec.europa.eu/commission/presscorner/detail/en/ip_24_6202
30. Bischof R, Swenson JE. Linking noninvasive genetic sampling and traditional monitoring to aid management of a trans-border carnivore population. *Ecol Appl*. 2012;22(1):361–73. <https://doi.org/10.1890/11-0013.1> PMID: 22471096
31. Milleret C, Dupont P, Åkesson M, Brøseth H, Kindberg J, Bischof R. Estimates of wolf density, abundance, and population dynamics in Scandinavia, 2012 - 2021. Norwegian University of Life Sciences, Ås; 2021;30. Available from: <https://nmbu.brage.unit.no/nmbu-xmlui/handle/11250/2766059>

32. CEwolf consortium. CEwolf consortium. In: Senckenberg Society for Nature Research [Internet]. 2023 [cited 20 Sep 2024]. Available from: <https://www.senckenberg.de/en/institutes/senckenberg-research-institute-natural-history-museum-frankfurt/division-river-ecology-and-conservation/cewolf-consortium/>
33. Skogen K, Krange O, Figari H. Wolf conflicts: a sociological study. New York Oxford: Berghahn Books; 2017.
34. Kovařík P, Kutal M, Machar I. Sheep and wolves: Is the occurrence of large predators a limiting factor for sheep grazing in the Czech Carpathians?. *Journal for Nature Conservation*. 2014;22(5):479–86. <https://doi.org/10.1016/j.jnc.2014.06.001>
35. Redpath SM, Gutierrez RJ, Wood KA, Young JC, Evelyn A, Reed M. *Conflicts in Conservation*. Cambridge: Cambridge University Press; 2015.
36. Trajçe A, Ivanov G, Keçi E, Majić A, Melovski D, Mersini K, et al. All carnivores are not equal in the rural people's view. Should we develop conservation plans for functional guilds or individual species in the face of conflicts?. *Global Ecology and Conservation*. 2019;19:e00677. <https://doi.org/10.1016/j.gecco.2019.e00677>
37. Singer L, Wietlisbach X, Hickisch R, Schoell EM, Leuenberger C, Van den Broek A, et al. The spatial distribution and temporal trends of livestock damages caused by wolves in Europe. *Biological Conservation*. 2023;282:110039. <https://doi.org/10.1016/j.biocon.2023.110039>
38. López-Bao JV, Sazatornil V, Llaneza L, Rodríguez A. Indirect effects on heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters*. 2013;6(6):448–55. <https://doi.org/10.1111/conl.12014>
39. Trajçe A. The gentleman, the vagabonds and the stranger: cultural representations of large carnivores in Albania and their implications for conservation; 2017. Available from: <https://pure.roehampton.ac.uk/portal/en/studentTheses/the-gentleman-the-vagabonds-and-the-stranger-cultural-representat>
40. Frank J, Levin M, Nilsson L, Månsson J, Höglund L, Hensel H. Viltskadestatistik 2023 - Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda. Rapport från SLU Viltskadecenter. 2024 [cited 20 Sep 2024]. Available from: <https://res.slu.se/id/publ/129453>
41. Frank J, Levin M, Månsson J, Höglund L, Hensel H. Viltskadestatistik 2022 – Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda. Rapport från SLU Viltskadecenter. 2023 [cited 20 Sep 2024]. Available from: <https://res.slu.se/id/publ/122350>
42. Frank J, Levin M, Månsson J, Höglund L, Hensel H. Viltskadestatistik 2021 - Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda. Rapport från SLU Viltskadecenter. 2022 [cited 20 Sep 2024]. Available from: <https://res.slu.se/id/publ/117236>
43. Gervasi V, Linnell JDC, Berce T, Boitani L, Cerne R, Ciucci P, et al. Ecological correlates of large carnivore depredation on sheep in Europe. *Global Ecology and Conservation*. 2021;30:e01798. <https://doi.org/10.1016/j.gecco.2021.e01798>
44. Khorozyan I, Heurich M. Large-scale sheep losses to wolves (*Canis lupus*) in Germany are related to the expansion of the wolf population but not to increasing wolf numbers. *Front Ecol Evol*. 2022;10. <https://doi.org/10.3389/fevo.2022.778917>
45. Marsden K, Schwarz L, Froese I, Klusmann C, Eul J, Merzanis Y, et al. *Livestock depredation and large carnivores in Europe: Overview for the EU Platform*. Berlin: adelphi consult GmbH; 2023.
46. Grente O, Duchamp C, Bauduin S, Chamaille-Jammes S, Drouet-Hoguet N, Gimenez O. Tirs dérogatoires de loups en France : évaluation des effets sur les dommages aux troupeaux. *Naturae*. 2023;(5). <https://doi.org/10.5852/naturae2023a5>
47. Kutal M, Duľa M, Selivanova AR, López-Bao JV. Testing a conservation compromise: No evidence that public wolf hunting in Slovakia reduced livestock losses. *Conservation Letters*. 2023;17(1). <https://doi.org/10.1111/conl.12994>
48. Jonzén N, Sand H, Wabakken P, Swenson JE, Kindberg J, Liberg O, et al. Sharing the bounty—Adjusting harvest to predator return in the Scandinavian human–wolf–bear–moose system. *Ecological Modelling*. 2013;265:140–8. <https://doi.org/10.1016/j.ecolmodel.2013.05.017>
49. Lühtrath A, Schraml U. The missing lynx — understanding hunters' opposition to large carnivores. *Wildlife Biology*. 2015;21(2):110–9. <https://doi.org/10.2981/wlb.00068>
50. Wikenros C, Sand H, Månsson J, Maartmann E, Eriksen A, Wabakken P, et al. Impact of a recolonizing, cross-border carnivore population on ungulate harvest in Scandinavia. *Sci Rep*. 2020;10(1):21670. <https://doi.org/10.1038/s41598-020-78585-8> PMID: 33303844
51. Butler JR, Linnell JD, Marrant D, Athreya V, Lescureux N, McKeown A. Dog eat dog, cat eat dog: social-ecological dimensions of dog predation by wild carnivores. *Free-ranging dogs and wildlife conservation*. 2014;117–43.

52. Linnell JD, Kovtun E, Rouart I. Wolf attacks on humans: an update for 2002–2020. Norwegian Institute for Nature Research (NINA); 2021.
53. Nowak S, Szewczyk M, Tomczak P, Całus I, Figura M, Mysłajek RW. Social and environmental factors influencing contemporary cases of wolf aggression towards people in Poland. *Eur J Wildl Res*. 2021;67(4). <https://doi.org/10.1007/s10344-020-01455-1>
54. Arbieu U, Chapron G, Astaras C, Bunnefeld N, Harkins S, Iliopoulos Y, et al. News selection and framing: the media as a stakeholder in human–carnivore coexistence. *Environ Res Lett*. 2021;16(6):064075. <https://doi.org/10.1088/1748-9326/ac05ef>
55. Arbieu U, Mehring M, Bunnefeld N, Kaczensky P, Reinhardt I, Ansorge H, et al. Attitudes towards returning wolves (*Canis lupus*) in Germany: Exposure, information sources and trust matter. *Biological Conservation*. 2019;234:202–10. <https://doi.org/10.1016/j.biocon.2019.03.027>
56. Linnell JDC, Alleau J. Predators That Kill Humans: Myth, Reality, Context and the Politics of Wolf Attacks on People. In: Angelici FM, editor. *Problematic Wildlife: A Cross-Disciplinary Approach*. Cham: Springer International Publishing; 2016. p. 357–371. [doi:10.1007/978-3-319-22246-2_17](https://doi.org/10.1007/978-3-319-22246-2_17)
57. Caniglia R, Galaverni M, Delogu M, Fabbri E, Musto C, Randi E. Big bad wolf or man's best friend? Unmasking a false wolf aggression on humans. *Forensic Sci Int Genet*. 2016;24:e4–6. <https://doi.org/10.1016/j.fsigen.2016.06.009> PMID: 27353864
58. Iliopoulos Y, Astaras C, Chatzimichail E. Dogs, not wolves, most likely to have caused the death of a British tourist in northern Greece. *Nature Conservation*. 2022;50:115–43. <https://doi.org/10.3897/natureconservation.50.81915>
59. Boitani L, Kaczensky P, Alvares F, Andr  n H, Balys V, Blanco JC, et al. Assessment of the conservation status of the Wolf (*Canis lupus*) in Europe. Strasbourg, France: Council of Europe Publishing; 2022.
60. Donfrancesco V, Ciucci P, Salvatori V, Benson D, Andersen LW, Bassi E, et al. Unravelling the Scientific Debate on How to Address Wolf-Dog Hybridization in Europe. *Front Ecol Evol*. 2019;7. <https://doi.org/10.3389/fevo.2019.00175>
61. Salvatori V, Donfrancesco V, Trouwborst A, Boitani L, Linnell JDC, Alvares F, et al. European agreements for nature conservation need to explicitly address wolf-dog hybridisation. *Biological Conservation*. 2020;248:108525. <https://doi.org/10.1016/j.biocon.2020.108525>
62. Moura AE, Tsingarska E, D  browski MJ, Czarnomska SD, J  drzejewska B, Pilot M. Unregulated hunting and genetic recovery from a severe population decline: the cautionary case of Bulgarian wolves. *Conserv Genet*. 2013;15(2):405–17. <https://doi.org/10.1007/s10592-013-0547-y>
63. Stefanovi   M, Bogdanowicz W, Adavoudi R, Mart  nez-Sosa F, Doan K, Flores-Manzanero A, et al. Range-wide phylogeography of the golden jackals (*Canis aureus*) reveals multiple sources of recent spatial expansion and admixture with dogs at the expansion front. *Biological Conservation*. 2024;290:110448. <https://doi.org/10.1016/j.biocon.2024.110448>
64. Kazimirov PA, Belokon' YuS, Belokon' MM, Mishin AS, Stakheev VV, Yarovenko YuA, et al. Genetic identification of putative hybrids between grey wolf and golden jackal. *Russ J Genet*. 2024;60(6):763–70. <https://doi.org/10.1134/s1022795424700200>
65. Lanszki J, Schally G, Heltai M, Ranc N. Golden jackal expansion in Europe: first telemetry evidence of a natal dispersal. *Mammalian Biology*. 2018;88:1–4. <https://doi.org/10.1016/j.mambio.2017.11.011>
66. Hovardas T, Penteriani V, Trouwborst A, L  pez-Bao JV. Editorial: conservation and management of large carnivores—local insights for global challenges. *Front Ecol Evol*. 2021;9. <https://doi.org/10.3389/fevo.2021.682444>
67. Salvatori V, Balian E, Blanco JC, Carbonell X, Ciucci P, Demeter L, et al. Are large carnivores the real issue? solutions for improving conflict management through stakeholder participation. *Sustainability*. 2021;13(8):4482. <https://doi.org/10.3390/su13084482>
68. Leser J, Pates R. The framing of right-wing populism: Intricacies of 'populist' narratives, emotions, and resonance. *The Palgrave Handbook of Populism*. Springer; 2022. p. 437–50.
69. K  lvraa C. Wolves in Sheep's Clothing? The Danish Far Right and 'Wild Nature.' *The Far Right and the Environment*. Routledge; 2019.
70. Chapron G, L  pez-Bao JV. Conserving carnivores: politics in play. *Science*. 2014;343(6176):1199–200. <https://doi.org/10.1126/science.343.6176.1199-b> PMID: 24626913
71. Linnell JDC, Trouwborst A, Boitani L, Kaczensky P, Huber D, Reljic S, et al. Border Security Fencing and Wildlife: The End of the Transboundary Paradigm in Eurasia?. *PLoS Biol*. 2016;14(6):e1002483. <https://doi.org/10.1371/journal.pbio.1002483> PMID: 27331878

72. Trouwborst A, Fleurke F, Dubrulle J. Border fences and their impacts on large carnivores, large herbivores and biodiversity: an international wildlife law perspective. *Rev Euro Comp Intl Enviro*. 2016;25(3):291–306. <https://doi.org/10.1111/reel.12169>
73. Salvatori V, Marino A, Ciucci P, Galli C, Machetti M, Passalacqua E, et al. Managing wolf impacts on sheep husbandry: a collaborative implementation and assessment of damage prevention measures in an agricultural landscape. *Front Conserv Sci*. 2023;4. <https://doi.org/10.3389/fcsc.2023.1264166>
74. Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*. 2013;36(12):1263–75. <https://doi.org/10.1111/j.1600-0587.2013.00266.x>
75. Wójcicki A, Borowski Z. The presence of wolves leads to spatial differentiation in deer browsing pressure on forest regeneration. *Sci Rep*. 2023;13(1):17245. <https://doi.org/10.1038/s41598-023-44502-y> PMID: 37821647
76. Raynor JL, Grainger CA, Parker DP. Wolves make roadways safer, generating large economic returns to predator conservation. *Proc Natl Acad Sci U S A*. 2021;118(22):e2023251118. <https://doi.org/10.1073/pnas.2023251118> PMID: 34031245
77. Sèbe M, Briton F, Kinds A. Does predation by wolves reduce collisions between ungulates and vehicles in France? *Human Dimensions of Wildlife*. 2022;28(3):281–93. <https://doi.org/10.1080/10871209.2022.2036391>
78. Kavčič I, Álvares F, Boitani L, Borgna I, Iliopoulos Y, Krofel M, et al. Non-consumptive use of wolves in tourism: guidelines for responsible practices [Large Carnivore Initiative for Europe IUCN/SSC Specialist Group] Specialist Group. University of Ljubljana; 2022. Available from: <https://brage.inn.no/inn-xmliui/handle/11250/3021221>
79. Rode J, Flinzberger L, Karutz R, Berghöfer A, Schröter-Schlaack C. Why so negative? Exploring the socio-economic impacts of large carnivores from a European perspective. *Biological Conservation*. 2021;255:108918. <https://doi.org/10.1016/j.biocon.2020.108918>
80. Cimatti M, Ranc N, Benítez-López A, Maiorano L, Boitani L, Cagnacci F, et al. Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*. 2021;27(4):602–17. <https://doi.org/10.1111/ddi.13219>
81. Bele B, Skrbinišek T, Ambrogini C, Berzins R, Chioso C, Faure N, et al. Public attitudes toward wolves and wolf conservation in Austrian, French, Italian and Slovenian Alps. Project LIFE 18 NAT/IT/000972 WOLFALPS EU; 2022.
82. Trouwborst A. Managing the Carnivore comeback: international and EU species protection law and the return of lynx, wolf and bear to Western Europe. *Journal of Environmental Law*. 2010;22(3):347–72. <https://doi.org/10.1093/jel/eqq013>
83. Convention on the Conservation of European Wildlife and Natural Habitats Standing Committee. List of Decisions and Adopted Texts, 44th meeting, Strasbourg, 2–6 December 2024. 2024. Available from: <https://rm.coe.int/misc-e-44-standing-committee-final-draft/1680b2b2bbb>
84. Epstein Y, López-Bao JV, Chapron G. A legal-ecological understanding of favorable conservation status for species in Europe. *Conservation Letters*. 2015;9(2):81–8. <https://doi.org/10.1111/cons.12200>
85. Trouwborst A, Boitani L, Linnell JDC. Interpreting 'favourable conservation status' for large carnivores in Europe: how many are needed and how many are wanted? *Biodivers Conserv*. 2016;26(1):37–61. <https://doi.org/10.1007/s10531-016-1238-z>
86. Salvatori V, Mertens A. Damage prevention methods in Europe: experiences from LIFE nature projects. *Hystrix*. 2012;23(1):73–9. <https://doi.org/10.4404/hystrix-23.1-4548>
87. Oliveira T, Treves A, López-Bao JV, Krofel M. The contribution of the LIFE program to mitigating damages caused by large carnivores in Europe. *Global Ecology and Conservation*. 2021;31:e01815. <https://doi.org/10.1016/j.gecco.2021.e01815>
88. Menzano A, Marucco F, Simon RN, Berzins R, Berce T, Černe R, et al. The efficacy of prevention systems in the Alps in the framework of the LIFE projects. LIFE WolfAlps EU; 2023.
89. Eklund A, López-Bao JV, Tourani M, Chapron G, Frank J. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. *Sci Rep*. 2017;7(1):2097. <https://doi.org/10.1038/s41598-017-02323-w> PMID: 28522834
90. van Eeden LM, Eklund A, Miller JRB, López-Bao JV, Chapron G, Cejtin MR, et al. Carnivore conservation needs evidence-based livestock protection. *PLoS Biol*. 2018;16(9):e2005577. <https://doi.org/10.1371/journal.pbio.2005577> PMID: 30226872
91. European Commission. EU Regional large carnivore platforms. 2024 [cited 20 Sep 2024]. Available from: https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive/large-carnivores/eu-large-carnivore-platform/eu-regional-large-carnivore-platforms_en

92. Marsden K, Hovardas T. EU Rural Development Policy and the management of conflictual species: The case of large carnivores. *Biological Conservation*. 2020;243:108464. <https://doi.org/10.1016/j.biocon.2020.108464>
93. Kiffner C, Chapron G, König HJ. Germany's wolves in the crosshairs. *Science*. 2019;365(6458):1089. <https://doi.org/10.1126/science.aay8053> PMID: 31515376
94. Guillot L. Wolf 2 — von der Leyen 0: EU court insists on being careful with wolf hunting. POLITICO; 29 Jul 2024 [Cited 22 Aug 2024]. Available from: <https://www.politico.eu/article/wolf-hunting-protected-species-conservation-european-commission-president-ursula-von-der-leyen/>.
95. Foote N. EU Parliament votes to blow big, bad wolves' protection down. Available from: www.euractiv.com. 25 Nov 2022 [Cited 20 Sep 2024]. Available from: <https://www.euractiv.com/section/agriculture-food/news/eu-parliament-votes-to-decrease-big-bad-wolves-protection-status/>.
96. Chapron G, Epstein Y, Ouro Ortmark M, Helmius L, Ramírez Loza JP, Bétaille J, et al. European Commission may gut wolf protection. *Science*. 2023;382(6668):275. <https://doi.org/10.1126/science.adk7686> PMID: 37856592
97. European Commission. Commission urges local authorities to make full use of existing derogations and collects data for conservation status review. In: European Commission [Internet]. 2023 [cited 20 Sep 2024]. Available from: https://ec.europa.eu/commission/presscorner/detail/en/ip_23_4330
98. European Commission. Commission proposes to change international status of wolves from 'strictly protected' to 'protected' based on new data on increased populations and impacts. In: European Commission [Internet]; 2023 [cited 20 Sep 2024]. Available from: https://ec.europa.eu/commission/presscorner/detail/en/ip_23_6752
99. Guillot L. EU countries agree to downgrade the protection status of the wolf. POLITICO. 25 Sep 2024 [Cited 27 Sep 2024]. Available from: <https://www.politico.eu/article/eu-countries-agree-to-downgrade-the-protection-status-of-the-wolf/>.
100. Arlettaz R, Chapron G. Swiss law would weaken wildlife protection. *Science*. 2020;369(6511):1576. <https://doi.org/10.1126/science.abe6191> PMID: 32973024
101. Trouwborst A, Fleurke FM, Linnell JDC. Norway's wolf policy and the bern convention on European wildlife: avoiding the "Manifestly Absurd". *Journal of International Wildlife Law & Policy*. 2017;20(2):155–67. <https://doi.org/10.1080/13880292.2017.1346357>
102. Conseil fédéral. Loup: le Conseil fédéral met en vigueur la régulation préventive des meutes. 2023 [cited 20 Sep 2024]. Available from: <https://www.bafu.admin.ch/bafu/fr/home/documentation/communiqu%C3%A9s/annonce-sous-mediennachrichten.msg-id-98407.html>
103. Chapron G, Marfaing G, Bétaille J. Patterns of litigation in France during two decades of recovery of a large carnivore. *bioRxiv*; 2022;2022. <https://doi.org/10.1101/2022.10.11.511781>
104. Case C-342/05, Commission of the European Communities v Republic of Finland; 2007. Available from: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A62005CJ0342>
105. Case C-436/22, Asociación para la Conservación y Estudio del Lobo Ibérico (ASCEL) v Administración de la Comunidad de Castilla y León; 2024. Available from: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A62022CJ0436>
106. Case C-601/22, Umweltverband WWF Österreich and Others v Amt der Tiroler Landesregierung; 2024. Available from: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A62022CJ0601>
107. Case C-674/17, Luonnonsuojeluyhdistys Tapiola Pohjois-Savo – Kainu ry v Risto Mustonen and Others; 2019. Available from: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A62017CJ0674&qid=1735391359509>
108. Case C-88/19, Asociația "Alianța pentru combaterea abuzurilor" v TM and Others; 2020. Available from: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A62019CJ0088>
109. Case C-26/24, LNDC Animal Protection - I: Request for a preliminary ruling from the Tribunale regionale di giustizia amministrativa della Regione autonoma Trentino - Alto Adige/Südtirol (Italy) lodged on 15 January 2024 – LNDC Animal Protection v Provincia autonoma di Trento, Ministero dell'Ambiente e della Sicurezza energetica; 2024. Available from: <http://data.europa.eu/eli/C/2024/3298/oj/eng>
110. Case C-629/23, Eesti Suurkiskjad: Request for a preliminary ruling from the Riigikohus (Estonia) lodged on 16 October 2023 — MTÜ Eesti Suurkiskjad v Keskkonnaamet; 2023. Available from: <http://data.europa.eu/eli/C/2023/1439/oj/eng>
111. Laikre L, Allendorf FW, Aspi J, Carroll C, Dalén L, Fredrickson R, et al. Planned cull endangers Swedish wolf population. *Science*. 2022;377(6602):162. <https://doi.org/10.1126/science.add5299> PMID: 35857558

112. Athreya V, Srivathsa A, Puri M, Karanth KK, Kumar NS, Karanth KU. Spotted in the News: using media reports to examine leopard distribution, depredation, and management practices outside protected areas in Southern India. *PLoS One*. 2015;10(11):e0142647. <https://doi.org/10.1371/journal.pone.0142647> PMID: 26556229
113. Odden M, Athreya V, Rattan S, Linnell JDC. Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS One*. 2014;9(11):e112044. <https://doi.org/10.1371/journal.pone.0112044> PMID: 25390067
114. López-Bao JV, Bruskotter J, Chapron G. Finding space for large carnivores. *Nat Ecol Evol*. 2017;1(5):140. <https://doi.org/10.1038/s41559-017-0140> PMID: 28812694
115. López-Bao JV, Kaczensky P, Linnell JDC, Boitani L, Chapron G. Carnivore coexistence: wilderness not required. *Science*. 2015;348(6237):871–2. <https://doi.org/10.1126/science.348.6237.871-b> PMID: 25999497
116. Carter NH, Linnell JDC. Building a resilient coexistence with wildlife in a more crowded world. *PNAS Nexus*. 2023;2(3):pgad030. <https://doi.org/10.1093/pnasnexus/pgad030> PMID: 36896129
117. Clemm von Hohenberg B, Hager A. Wolf attacks predict far-right voting. *Proc Natl Acad Sci U S A*. 2022;119(30):e2202224119. <https://doi.org/10.1073/pnas.2202224119> PMID: 35858455
118. Linnell JDC, Cretois B. The revival of wolves and other large predators and its impact on farmers and their livelihood in rural regions of Europe. European Parliament; 2018.
119. Eionet. Article 17 - Species assessments at Member State level (Mammals); 2024 [cited 20 Sep 2024]. Available from: <https://nature-art17.eionet.europa.eu/article17/species/report/?period=5&group=Mammals>
120. Kaczensky P, Ranc N, Hatlauf J, Payne JC, Acosta-Pankov L, Álvares F, et al. Large carnivore distribution maps for Europe 2017 – 2022/23. Dryad;2024. 2620878 bytes. <https://doi.org/10.5061/DRYAD.3XSJ3TXRC>
121. Kaczensky P, Ranc N, Hatlauf J, Payne JC, Acosta-Pankov L, Álvares F, et al. Large carnivore distribution maps and population updates 2017 – 2022/23; 2024. Available from: <https://circabc.europa.eu/ui/group/3f466d71-92a7-49eb-9c63-6cb0fadf29dc/library/97829710-878b-4bf7-95a1-f135b00dd8f7/details>