Title: Should hunters fear the wolf? Effects of wolf recolonization on ungulate harvests in a multi-species European landscape

Authors: Jacopo Cerri[1]*, Maéva Bibal-Mazoyer[2], Lucas Cock-Bocanegra[3], Marcello Franchini[4], Ibra Edoardo Monti[5], Oliwia Józefowicz[1], Luca Corlatti[6,7]

Affiliations:

1. Mammal Research Institute, Polish Academy of Sciences, Stoczek 1D, 17-230, Bialowieza, Poland
2. Edinburgh Napier University, Sighthill Campus, EH11 4BN Edinburgh, Scotland
3. Asociación Iberozoa, Avenida de Bruselas 48, 28028, Madrid, España
4. Dipartimento di Scienze Agroalimentari, Ambientali e Animali, Università degli Studi di Udine, Via delle Scienze 206, 33100, Udine, Italy
5. Dipartimento di Medicina Veterinaria, Università degli Studi di Sassari, Via Vienna 2, 07100, Sassari, Italy
6. Parco Nazionale dello Stelvio – Ersaf Lombardia, Via De Simoni 42, 23020, Bormio, SO, Italy
7. Chair of Wildlife Ecology and Management, University of Freiburg, Stefan Meier-Str. 76, 79104, Freiburg, Germany

Corresponding author: Jacopo Cerri, Mammal Research Institute, Polish Academy of Sciences, Stoczek 1, 17-230, Bialowieza, Poland. Email: j.cerri@ibs.bialowieza.pl

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Abstract

1. The recolonization of European landscapes by the gray wolf *Canis lupus* raises questions about the ecological effects of predators and their impact on human interests such as large-game hunting bags, leaving room for alarmism among hunters.

2. We investigated the impact of wolf on recreational hunting by using long-term (2006-2023) and high-resolution (234 hunting districts) hunting bag data on four species of wild ungulates harvested in the Friuli Venezia Giulia Region (Italy), before and after the wolf recolonization. Species included the roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, wild boar *Sus scrofa* and Northern chamois (*Rupicapra rupicapra*). We used Bayesian Generalized Linear Models to control for spatiotemporal correlation, landscape composition and yearly climate.

3. For all the game species we did not detect any meaningful difference in the temporal evolution of hunting bags, with respect to the history of wolf recolonization. This may reflect several - and not mutually exclusive - mechanisms: the relatively small size of wolf population compared to the overall abundance of wild prey, predation impacts concentrated on juveniles, prey switching by wolves, or management decision to maintain hunting bags more or less consistent through time, irrespective of wolf presence.

4. Hunting bags for the roe deer suggested a decline in areas of the Po Plain with more than 7 years of wolf presence, possibly due to synergistic effects of predatory impacts and environmental quality.

5. Our findings do not rule out the possibility of long-term reductions in the hunting bags of wild ungulates, in response to the progressive increase in wolf numbers and thus the impact of predation. However, they do not support the idea that hunting bags decline rapidly following wolf recolonization of an area.

5. ***Policy implications***: In the absence of detectable effects of wolf recolonization on ungulate hunting bags, accurate and transparent information becomes particularly important for effective wildlife management. Clear communication helps avoid alarmism and misleading management practices, while sustained dialogue among stakeholders - including hunters, scientists, and communication managers - is essential for understanding and anticipating the long-term consequences of predator recolonization.

Introduction

Following severe reductions across much of their historical range in the Northern Hemisphere during the 19th and 20th centuries, gray wolf *Canis lupus* populations have been steadily recolonizing an increasing portion of that range in recent decades (Chapron et al., 2014; Mech, 1995). This recolonization has important consequences for mammal communities and ecosystem processes, which have been extensively investigated in North America (Wilmers et al., 2025).

Much more uncertain are the potential ecological and social implications of wolf expansion in Europe (Kuijper et al., 2024), largely because European landscapes differ fundamentally from those in North America in terms of ecosystem spatial scales, human influence and wolf behavior. Europe is not only more anthropized overall, but human activities are also far more pervasive and tightly interwoven with natural ecosystems, reflecting a long history of land use within comparatively small and fragmented landscapes. As a result, wildlife is exposed to a dense mosaic of human pressures - including lethal activities such as hunting and culling, as well as non-lethal disturbances associated with tourism, infrastructure, and recreation - that may exert stronger and more spatially diffuse effects on populations and ecological processes than wolf recolonization itself (Bassi et al., 2020; Sand et al., 2025). In parallel, the widespread presence of animal husbandry across much of Europe (Malek et al., 2024) creates additional, human-mediated trophic pathways that can sustain wolf populations through access to livestock, carrion, or animal by-products (Ćirović and Penezić, 2019; Ciucci et al., 2020; Singer et al., 2023), potentially reducing their reliance on wild ungulates and further entangling wolf ecology with human land-use systems. The size of wolf packs is also significantly smaller in Europe than in North America, with consequences over the choice of prey species and hunting efficiency (Ciucci et al., 2026). Finally, hybridization rates between wolves and domestic dogs are extremely high in some areas of Europe (Lorenzini et al., 2026), with potentially important consequences on wolf behavior (Amici et al., 2024).

Recently several studies have investigated the potential consequences of the return of the wolf in Europe, for example by comparing ungulate densities between areas with and without wolves (Melis et al., 2009; Van Beeck Calkoen et al., 2023), assessing changes in ungulate populations before and after wolf recolonization (Kojola et al., 2009; Lazzeri et al., 2024a,b; Orazi et al., 2025; Randon et al., 2020; Wikenros et al., 2015, 2025), or quantifying behavioral changes in prey species (Gerber et al., 2024) and assessing indirect impacts on vegetation (Bubnicki et al., 2019; Kuijper et al., 2013, 2015). However, significant uncertainty still remains regarding the consequences of wolf recolonization in Europe for human activities. In particular, the extent to which wolf predation on wild ungulates may indirectly affect hunting bags, also due to its interplay with different wildlife management practices remains poorly understood (Corlatti and Ciuti, 2026).

Hunting is crucial for the management of European wild ungulates (Carpio et al., 2021), with millions of animals being culled every year (Cerri et al., 2025) and hunters are key stakeholders for wildlife and environmental policies. However, in many European countries hunters are also involved in social conflicts about wolves and their management (Kuijper et al., 2019; Mech, 2017), as well as in wolf persecution (Liberg, 2012; Musto et al., 2021; Nowak et al., 2021; Sunde, 2021; Suutarinen and Kojola, 2017), often due to hunters' concerns about competition with wolves over game species (Bisi et al., 2010; Gangaas et al., 2013; Højberg et al., 2017). Understanding the impact of predation by wolves on the hunting bags of wild ungulates is therefore crucial to create an informed debate and avoid misinformation (e.g., on social media, Nanni et al., 2020). Furthermore, understanding impacts of wolves on the hunting bags of wild ungulates is important because some hunters believe it to be a valuable justification for wolf culling (e.g. in Sweden, Sjölander-Lindqvist, 2015), a practice whose implementation is non-trivial (Treves et al., 2016), and whose impacts on wolf mortality can add up to those of poaching (Oliynyk, 2023; Santiago-Avilá and Treves, 2022) and jeopardize conservation efforts. Despite European countries not currently authorizing wolf culling for safeguarding hunting bags, as the management of wolves is becoming increasingly politicized (Kutal et al., 2025), the absence of any scientific evidence might make this argument more and more influential in the near future.

In this study we aimed to address this gap by quantifying the impact of recolonizing wolves on the hunting bags of four species of wild ungulates (roe deer, red deer, wild boar and northern chamois) in the Friuli Venezia Giulia Region (Italy), an area of North-Eastern Alps which have been recolonized by wolves around 2013.

Methods

Study area and populations

The study was conducted in Friuli Venezia Giulia (Italy, Fig. 1), a Region that lies at the intersection between Italy, Austria and Slovenia, extending over an area of 7,924 km². The study area hosts a variety of different ecosystems within the four ecoregions of the Alpine and pre-Alpine area, the Po Plain and the Karst. Lowlands are characterized by the presence of intensive croplands and human settlements, while the remaining three ecoregions have lower levels of anthropization, a higher degree of terrain roughness and greater forest cover (Poldini et al., 2006)

The study area hosts most of the main species of ungulates found in Italy, the red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, Alpine chamois *Rupicapra rupicapra* (herein, chamois) , Alpine ibex *Capra ibex*, fallow deer *Dama dama* and mouflon *Ovis aries*. Except for the Alpine ibex, all these species are subject to recreational hunting, with major differences in their overall hunting bags (Fig. S1, Appendix 1). In this study we focused only on harvest data of the roe deer, red deer, wild boar and chamois. We did not consider the mouflon and the fallow deer as the two species have a relatively limited distribution in the region, being limited to a very low number of hunting reserves.

The wildlife management system is based on 243 hunting reserves (Fig. 1), with a size of 32.7 ± 34.7 km^2 (mean ± s.d.). Each year, typically in spring/summer, ungulate populations are monitored in hunting reserves through a combination of point counts, drive counts and spotlight counts (Regione Friuli Venezia Giulia, 2015). Based on such counts, the maximum number of individuals which can be hunted in the following season (hunting quota) is defined (Fig. S2, Appendix 1), following recommendations from the Institute for Environmental Protection and Research (ISPRA, Raganella Pelliccioni et al., 2013). Only part of the hunting quotas is effectively realized (Fig. S3, Appendix 1). Hunting typically occurs from September to January.

Four species of carnivores are also present: the brown bear *Ursus arctos*, all males attempting to disperse between the Dinaric and Alpine populations; the Eurasian lynx *Lynx lynx*, mostly individuals dispersing from the Dinaric population (Serva et al., 2025); the golden jackal *Canis aureus* (Frangini et al., 2025), which have increased in number and distribution in the last two decades; and the gray wolf. As for the gray wolf, the first records of the species date back to 2013 (Marucco et al., 2018), and the first confirmed reproduction was in 2018 (Franchini et al., 2019). Population surveys, conducted within the WolfAlps and WolfAlpsEU LIFE projects (Avanzinelli et al., 2024), indicate a rapid increase in the distribution and size of wolf populations (Fig. S4, Appendix 1), which by 2023/2024 included five packs and four reproductive pairs (Boiani et al., 2025).

Data collection and environmental covariates

To quantify changes in the hunting bags of the four wild ungulates, after the recolonization of wolves, we used the total number of individuals that were harvested each year in the 234 hunting reserves.

Hunting quotas (Fig. S2, Appendix 1) and their realization rate (Fig. S3, Appendix 1), they had remained stable between 2006 and 2023. In other words, the percentage of spring/summer counts of roe deer, red deer, wild boar and chamois which in the subsequent year was hunted was constant: any change in harvests would have therefore arisen mostly from changes in their number in the environment, also because the number of hunters has declined through time (Fig. S5, Appendix 1). Moreover, harvests showed a strong correlation with the number of individuals observed during spring/summer counts in the previous year (Fig. S6, Appendix 1): although it was not formally possible to estimate ungulate density, this point suggests that the number of harvested ungulates reflected well their abundance in the environment.

With regards to environmental covariates, we included both landscape attributes and climatic indexes, reflecting seasonal conditions, which could potentially confound the relationship between wolves and wild ungulates. Landscape attributes included, for each hunting reserve: i) the proportion of urbanized areas, ii) the proportion of coniferous and iii) broad-leaved forests, iv) the proportion of grasslands, v) the proportion of agricultural areas, as well as the proportion of vi) lowlands (0 -300 m), vii) hills (300 – 600 m) or viii) mountains (areas with an elevation of 600 m or more).

Urbanized areas and forest cover were included because urbanization can decrease the potential suitability of landscape for ungulates and wolves by increasing human disturbance and mortality from collisions and persecution. Conversely, forest cover provides ungulates and wolves with food resources and shelter from human disturbance, promoting their presence at the landscape scale (ungulates: Carpio et al., 2020, Cerri et al., 2025; wolves: Cimatti et al., 2021; Louvrier et al., 2017; Planillo et al., 2024). Finally, croplands can benefit some ungulates and wolves by providing additional plant biomass to ungulates (Brunot et al., 2025; Calosi et al., 2025; Vannini et al., 2021) or alternative prey to wolves (e.g. the coypu, *Myocastor coypus*, Canova and Meriggi, 2025; Cerri et al., 2024). Grasslands can also benefit some ungulates by providing nutritious herbaceous species, particularly when actively managed (Mysterud et al., 2023). The proportion of urbanized areas was estimates identifying them from the 2015 built-up surface map with a 10 m resolution of the Global Human Settlement Layer (https://human-settlement.emergency.copernicus.eu/download.php?ds=bu). Forests and grasslands were identified from the Copernicus Forest Type map (https://land.copernicus.eu/en/products/high-resolution-layer-forests-and-tree-cover/forest-type-2018-raster-10-m-100-m-europe-3-yearly) and the Copernicus Grassland layer (https://land.copernicus.eu/en/products/high-resolution-layer-grasslands/grassland-2018-raster-10-m-100-m-europe-yearly) at a resolution of 100 m. Agricultural areas were identified by differencing, by subtracting to the area of each hunting reserve that was not covered by forests, urbanized areas and grasslands, and by subsequently discarding also areas covered by ice or water bodies according to the 2018 Corine Land Cover (https://land.copernicus.eu/en/products/corine-land-cover/clc2018). Lowlands, Hills and Mountains were identified by using a 250 m Digital Elevation Model provided by Amazon Web Service, through the "elevatr" package in R.

To simplify the interpretation of different landscape attributes, linking them to broadly different environmental conditions, we carried out Partitioning Around Medoids (PAM) cluster analysis (Kassambara et al., 2017). Cluster analysis aimed to identify groups of hunting reserves characterized by homogeneous environmental conditions. Landscape attributes were standardized and centered, before being used for clustering, and we selected the optimal number of clusters based on the Silhouette width, the elbow method and the gap statistics method (Kassambara et al., 2017; Fig. S7, Appendix 2). PAM cluster analysis, based on Euclidean distances, identified two groups of hunting districts (Fig. S8, Appendix 2), with environmental conditions corresponding to those of the Po Plain and the mountains (Prealps, Alps, Karst, Fig. S9, Appendix 2). Lowlands were characterized by higher landscape anthropization, a higher amount of croplands and a lower amount of forests than mountains (Fig. S10, Appendix 2).

These two groups of hunting districts were converted into a dichotomous variable for the Generalized Linear Model (GLM).

As for climatic conditions, for each district and every year we considered the temperatures and rainfall in winter, spring and summer. By acting on vegetation phenology and quality, food acquisition and thermoregulation, these variables affect the life history of wild ungulates, and therefore their population dynamics (e.g. chamois: Corlatti et al., 2022a,b; e.g. deer: De Marinis et al., 2022; Felton et al., 2024; Lorenzini et al., 2022; Mattioli et al., 2022; e.g. wild boar: Scandura et al., 2022). Daily mean temperatures and total rainfall, at a 30 km resolution, were downloaded from the ERA5 post-processed daily statistics dataset (https://cds.climate.copernicus.eu/datasets/derived-era5-single-levels-daily-statistics), then associated to each reserve and finally aggregated on a seasonal basis. Due to the correlation between these measures, we graphically explored their relationships with the harvests of the four species of ungulates and then we included the mean daily temperature in summer as a predictor in the GLMs.

Finally surveys allowed us to classify hunting reserves in terms of their history of wolf recolonization. For each district we calculated a time-invariant gradient of prolonged wolf presence, ranging from 0 to 10 years and reflecting the number of years elapsed since the first detection of wolves and 2023 (e.g. if a district was colonized in 2013, in 2023 would have experienced 10 years of wolf recolonization). We did not quantify the years since wolf recolonization as a time-varying covariate because surveys were not carried out on each year (Fig. S4, Appendix 1), and they did not account for imperfect detectability (Gervasi et al., 2024). Moreover, it is also possible that wolves settled down in the study area slightly before 2013. Due to the fact that ungulate harvests in a certain year are based on hunting quotas derived from population monitoring in the previous year, it would have been impossible to detect any ecological effect of wolves in districts where the species was recorded only in 2023 (1 year of presence). We therefore treated these districts (n = 11) as areas from where wolves were absent.

Statistical analyses

To quantify changes in harvests we fit Bayesian Generalized Linear Mixed Models, modeling the total number of harvested individuals in each hunting reserve according to a set of covariates and accounting for spatio-temporal correlations between neighbouring reserves through random effects.

For the roe deer, the wild boar and the chamois we used data collected between 2006 and 2023, while for the red deer between 2009 and 2023. For the chamois we only considered data from 80 hunting reserves in the Alps, as the species is absent from lowlands. Due to these differences, we fit separate models for harvests of roe deer, red deer, wild boar and chamois. For all the four models we used a negative binomial distribution. Considering that 16.0% of roe deer, 63.8% of red deer, 33.9% of wild boar and 55.2% of chamois harvests were zeroes we used a hierarchical formulation accounting for zero inflation (Zuur et al., 2017).

Covariates included: *i*) a temporal label indicating the year of each harvest, *ii*) a dichotomous variable, obtaining from PAM cluster analysis, indicating whether harvests in a certain year belonged to a district in lowlands or mountains, *iii*) the mean daily summer temperature, *iv*) a variable indicating the years elapsed since wolf recolonization. We assessed the impact of the time elapsed since wolf recolonization over harvests, by means of a three-wayinteraction term between his variable, the environment of each district and the year of each observation.

Moreover, as the red deer outcompetes the roe deer (Franchini et al., 2023; Richard et al., 2010) and the chamois (Corlatti et al., 2019), while at the same time being one of the main prey of gray wolves (Newsome et al., 2016), for red deer and chamois we also controlled for the number of red deer that were harvested in the same year. Finally, as the number of harvested individuals could simply depend upon the spatial extent of a certain hunting reserve, we also controlled for this offset variable through a second-order random walk term (Smith, 2024).

We controlled for spatial, temporal and spatio-temporal correlations by using the approach suggested by Zuur et al. (2017). First, we fit a full model with all potential covariates, choosing a basic spatial structure for neighboring hunting districts, by comparing between the iCAR the Besag-York and Mollié and the BYM2 structure (see Zuur et al., 2017 for an overview). Then we compared different forms of spatio-temporal interactions (Knorr-Held, 2000), as suggested by Blangiardo and Cameletti (2015) and Zuur et al. (2017). Once we identified the best full model, in terms of its spatio-temporal structure, we removed redundant covariates through backward model selection. Model selection was based by comparing the Widely Applicable Information Criterion (WAIC), the Deviance Information Criterion (DIC) and the sum of the log-converted Conditional Predictive Ordinates (CPO), while also checking the scale of model predictions against observed harvests and assessing real effect size through marginal effects (Kruschke and Liddell, 2018). During model selection we inspected model residuals to detect potential non-linear effects and overdispersion.

For all the four species of wild ungulates, model selection highlighted that complex spatio-temporal correlation structures did not improve model fitness over easier model structures. For all the four species, we used an iCAR correlation structure to account for spatial correlation between neighboring hunting reserves. For the roe deer, the red deer and the wild boar, we accounted for the temporal trends in hunting bags by simply considering the year of each harvest through a linear term. For the northern chamois we controlled for the effect of time by means of a second-order random walk term, and allowed this term to vary in each district (see Appendix 3).

Models were implemented in INLA (Lindgren and Rue, 2015), through R (R Core Team, 2025). A complete overview of model selection is provided in Appendix 3.

Results

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Model selection highlighted differences in harvests, between mountains and lowlands. Roe deer harvests increased in lowlands and decreased in the Alps (Fig. 2), while harvests of the red deer and the wild boar increased in both the two environments, although with a different magnitude (Fig. 3, Fig. 4).

As for the gradient of wolf recolonization, this variable was not retained by model selection for the red deer and the chamois (Fig. 5), while it seemed to somehow improve model predictions for the roe deer and the wild boar (Appendix 3). However, when inspecting marginal effects, we did not detect any clear difference in the temporal evolution of wild boar harvests, between areas with a different gradient of wolf recolonization (Fig. 4).

The only species for which temporal dynamics in harvests were slightly different between hunting reserves with a different gradient of wolf recolonization was the roe deer. Namely, in lowland hunting reserves, where wolves have been present for at least six years, roe deer harvests progressively decreased, although with a considerable degree of uncertainty (Fig. 2; Appendix 4). However, no effect of wolf recolonization on roe deer harvests was observed in the Alps, where it showed a constant decline through time.

Discussion

The rapid recolonization of Europe by wolves has progressively raised questions about their ecological role as apex predators (Kuijper et al., 2024) and therefore on their potential capacity to impact human activities, including the reduction of the hunting bags of game species, especially wild ungulates, thereby resulting in a competition with recreational hunters.

Our findings indicate that in areas where wolf recolonization is recent and wolf populations are still relatively small compared to the abundance of prey species, their predatory impact on the hunting bags of wild ungulates appear to be negligible. In the Friuli Venezia Giulia Region, a decade after the wolf recolonization - which so far resulted in the establishment of five packs and four reproductive pairs over almost 7,924 km² (Avanzinelli et al., 2024; Boiani et al., 2025) - we did not detect any change in the temporal trend of wild ungulate harvests. This could have multiple, non-exclusive explanations.

First, although less likely under a strict predation-risk framework (Gaynor et al., 2019), demographic compensation through spatial redistribution cannot be entirely excluded. Given the fragmented distribution of wolves, localized increases in predation pressure may create population sinks that are partially offset by immigration from adjacent areas, driven by density-dependent processes or dispersal rather than by active selection of high-risk habitats. If present, such compensation could dampen detectable effects on harvest trends.

Another explanation could be that a significant share of wolf predations in the Alps involves juveniles (Gazzola et al., 2005; Palmegiani et al., 2013). Juveniles play a minor contribution to short-term population dynamics, because high survival in adults can maintain recruitment high and because mortality from predation can be compensatory to mortality from starvation (Sand, 2012) or collisions with vehicles (Kautz et al., 2022). This would mitigate the effect of predation on total harvests, at least across 10 years. Nevertheless, sustained predation on juveniles could reduce ungulate populations and hunting bags, over longer time-scales (Gaillard, 1998). In this study we did not analyze temporal trends in harvests between different age classes, because of the lack of age-specific data until 2021. However, future studies should collect and analyze age-specific harvests through time, as this might reveal age-specific reductions in hunting bags and species-specific differences (Gervasi et al., 2012).

Impacts on ungulate harvests could have also been offset by the rapid development of anti-predatory behavior in ungulates (Lazzeri et al., 2024b; Orazi et al., 2025) and prey shifting. When multiple prey species are available and predators adaptively shift between them, in response to their behavior, predation impacts on single prey might be buffered. While in the long-term wolves could change their hunting behavior and focus on specific prey (Gable et al., 2018), the effect of this process might not be observable in a decade.

Finally, ongoing impacts on wild ungulate populations could have simply gone undetected, due to the nature of our data and their spatial resolution. Despite hunting quotas (Fig. S2, Appendix 1) and realizations (Fig. S3, Appendix 1) had remained stable in time, the lack of measures of hunting effort certainly introduced noise in the data (Imperio et al., 2010). Further noise was also introduced by the relatively low resolution of wolf monitoring (100 km^2), which also did not provide a comprehensive gradient of wolf abundance (Wikenros et al., 2025). Therefore, in core areas of wolf packs the number of wild ungulates could have already been lowered, but this process went undetected.

An additional, non-mutually exclusive, explanation concerns the role of hunters in shaping harvest dynamics. Harvest levels may - at least partially - be driven by management decisions towards conservatism, whereby hunting quotas are maintained relatively constant within given management periods, despite short-term decreases in wildlife densities. For example, after wolf recolonization, increased predation on ungulates should decrease their spring/summer counts and therefore harvest levels. Yet hunters might fail to identify predation as a driver of ungulate decrease, attributing it to a random short-term decrease, and therefore decide to maintain consistent hunting quotas. While in the long term these two additive sources of mortality reduce the number of individuals and therefore harvests, it is plausible that, in the short-term, sustained harvesting by hunters could mask the effect of predator return on harvest levels. Under this interpretation, any trophic cascade effect - if present - may be largely socially filtered in human-dominated systems, rather than directly driven by wolf predation (Corlatti and Ciuti, 2026).

All in all, our results suggest that wolves either act as weak numerical regulators in this multi-prey system, or their effects fail to propagate through the ecosystem because humans function as dominant co-regulators of ungulate populations - with intermediate scenarios also possible.

Our findings have several important consequences from a conservation standpoint. Wolves are currently persecuted throughout Europe by hunters, due to their concerns about competition over wild ungulates. Similar concerns are probably mounting also in areas that have been recently colonized by wolves, such as the Central and Eastern Alps. While our study does not exclude the possibility that wolves could somehow reduce the hunting bags of wild ungulates in the long term, it certainly rules out the occurrence of fast and wide-spread reductions in hunting bags in areas that have been recently colonized by wolves. There is therefore enough time for wildlife agencies to: *i*) develop communication campaigns tailored to hunters, *ii*) adapt the monitoring of wild ungulate populations to detect emerging predatory impact of wolves in specific environments, *iii*) conceive adaptive management policies for wild ungulates, which could safeguard their harvesting by hunters without jeopardizing wolf conservation.

Developing communication campaigns should provide hunters with accurate and impartial information about the lack of any immediate decrease in hunting bags of wild ungulates , while at the same time disclosing our uncertainty about long-term changes (Blastland et al., 2020).

While communication campaigns will not entirely solve the issue of wolf persecution by hunters, which can have deeper roots (Skogen and Krange, 2020), they would be a useful starting point to avoiding alarmism and preventing the circulation of misinformation (Nanni et al., 2020). This would be particularly valuable considering that wolf population in the study area will most likely increase, as happened in other sectors of the Alps (Marucco et al., 2023a,b), resulting in a much higher exposure of local communities (Brogi et al., 2025).

Adapting the monitoring of wild ungulate populations to detect the emerging predatory impact of wolves, also with respect to environmental quality (Lennox et al., 2025), is another priority. Namely, it would be particularly valuable to assess long-term trends in ungulate populations and their harvests in lowlands, as our data suggest the emergence of predatory impacts by wolves in the roe deer. Although ungulates can thrive in agricultural landscapes (Brunot et al., 2025; Calosi et al., 2025; Mysterud et al., 2022; Vannini et al., 2021), the Po Plain is generally characterized by intensive croplands with few patches of small woodlands and hedgerows. These small patches of permanent cover are highly used by both the roe deer (Morellet et al., 2011) and wolves (Torretta et al., 2022). It is therefore plausible that in lowlands, the limited availability of permanent cover could paradoxically facilitate predation, making these environments the first to potentially experience reductions in wild ungulates.

Finally, the last point is to conceive adaptive management policies for wild ungulates that also account for predation by wolves. The interplay between wolf predation and hunting might not necessarily be compensatory but additive (Gehr et al., 2017), with potentially important consequences over the long-term population dynamics of ungulates. Population models accounting for an increase in wolf populations, changes in predation rates and other sources of variation, might be a useful tool to inform wildlife agencies and design sustainable culling plans for ungulates preventing overharvesting (Marrotte et al., 2022).

Figures

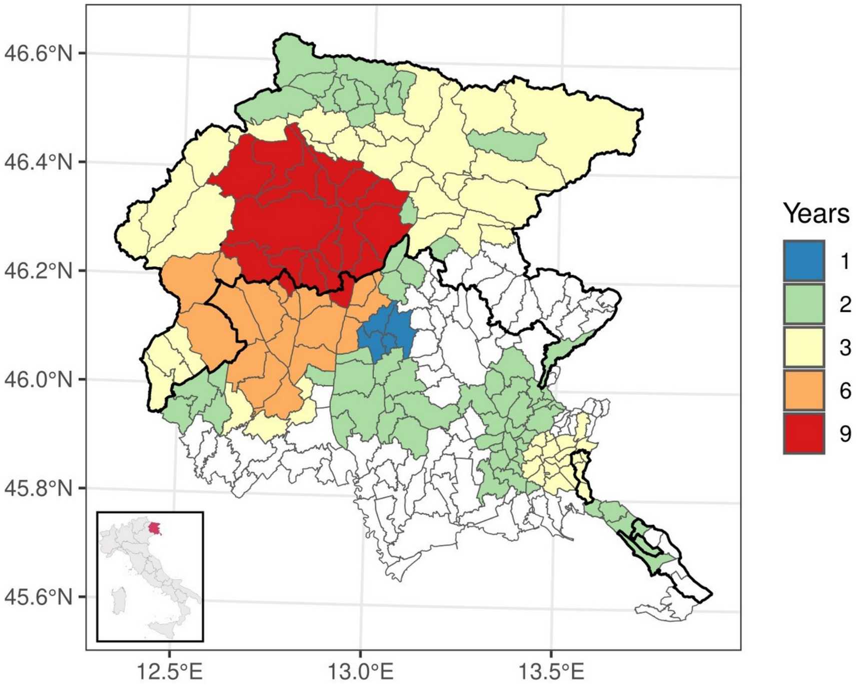

Fig. 1. Map of the study area: overview of hunting districts, altogether with the number of years elapsed since wolf recolonization. By 2023, white districts had not been recolonized by wolves yet. Districts with a mountainous environment are bolded.

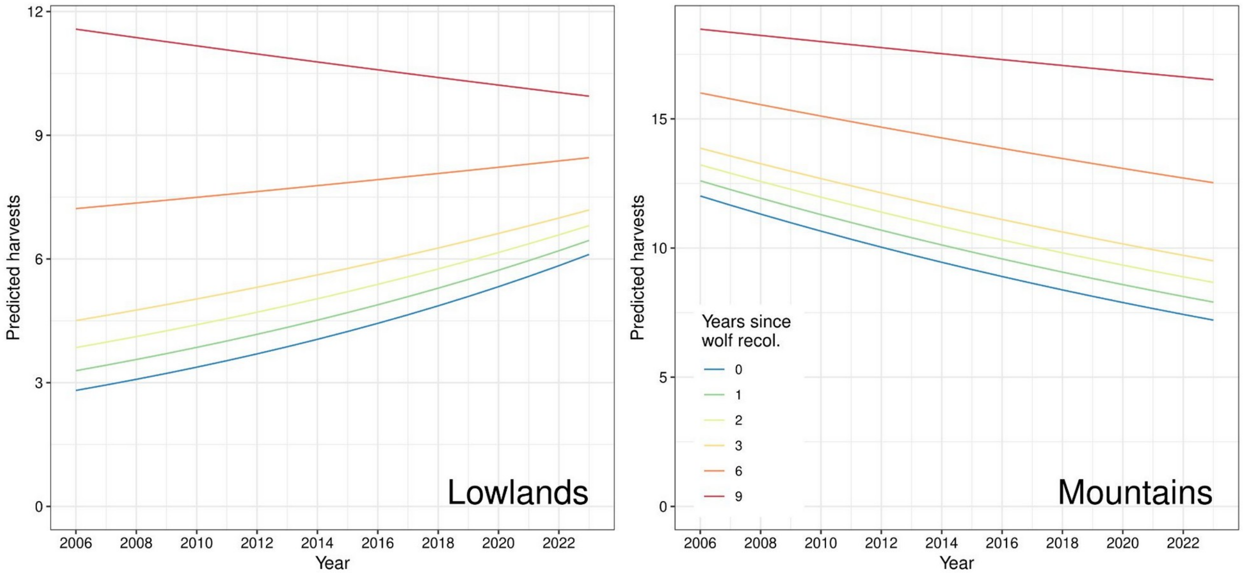

Fig. 2. Marginal effects for the best candidate model for the roe deer, displaying predicted harvests in time, between hunting districts with a different history of wolf recolonization.

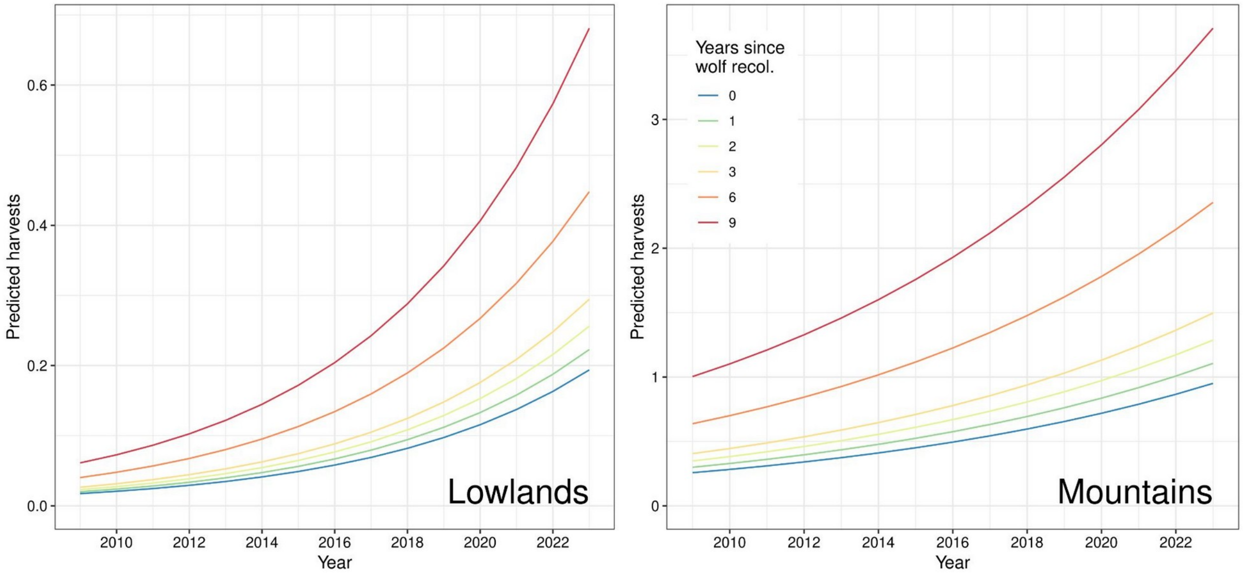

Fig. 3. Marginal effects for the best candidate model for the red deer, displaying predicted harvests in time, between hunting districts with a different history of wolf recolonization.

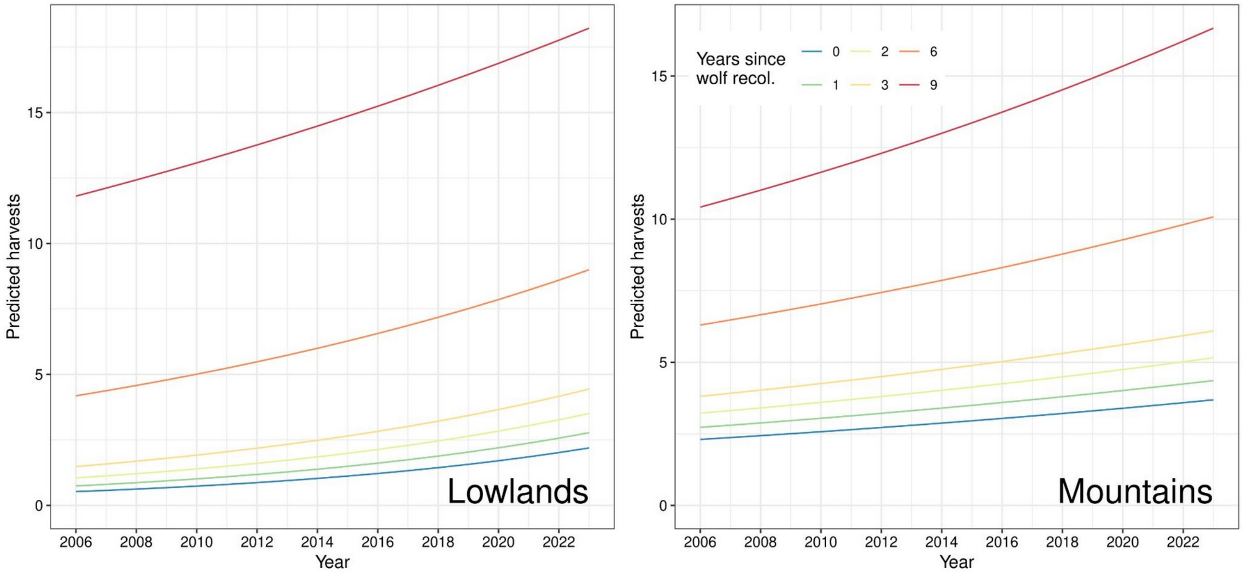

Fig. 4. Marginal effects for the best candidate model for the wild boar, displaying predicted harvests in time, between hunting districts with a different history of wolf recolonization.

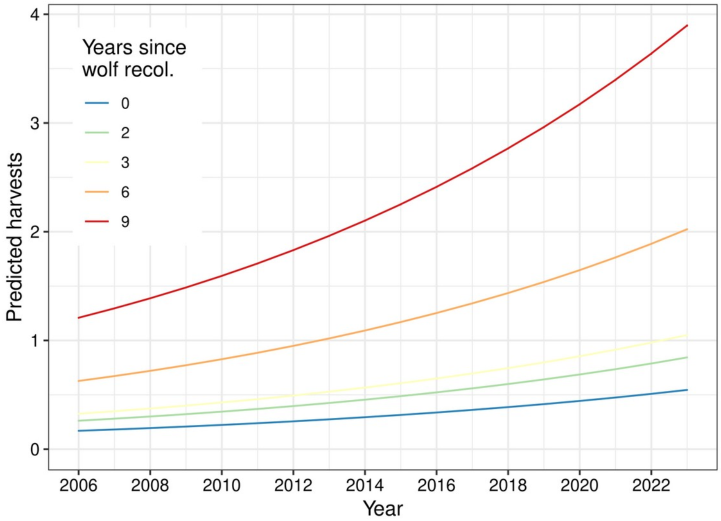

Fig. 5. Marginal effects for the best candidate model for the chamois, displaying predicted harvests in time, between hunting districts with a different history of wolf recolonization.

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Data availability statement

The reproducible data and software code, as well as Appendix1, Appendix2, Appendix3 and Appendix 4 are available on OSF: https://osf.io/w3gah and GitHub: https://github.com/JacopoCerri7/HuntersWolvesFVG

Author contribution (CRediT)

Conceptualization - JC, LCr; **Data curation** - LCk, IEM, MBM, MF, OJ; **Formal analysis** - JC, MBM, LCr; **Funding acquisition** - JC, LCr; **Investigation** - JC, IEM, LCk, LCr, MBM, MF, OJ **Methodology** - JC, LCr; **Project administration** - JC, LCr; **Resources** - JC, LCr; **Software** - JC, MBM; **Supervision** - JC, LCr, MF; **Validation** - LCk, IEM, MBM, MF, OJ; **Visualization** - JC, MBM; **Writing – original draft** - JC, LCr, MF; **Writing –** review & editing - JC, IEM, LCk, LCr, MBM, MF, OJ

References

Amici, F., et al. (2024). A first exploratory comparison of the behaviour of wolves (*Canis lupus*) and wolf-dog hybrids in captivity. Animal Cognition, 27(1), 9. https://doi.org/10.1007/s10071-024-01849-7

Avanzinelli, E., et al. (2024). La distribuzione del lupo nelle regioni alpine 2020-2024. Progetto LIFE WOLFALPS EU. https://www.lifewolfalps.eu/wp-content/uploads/2025/01/CAMPIONAMENTO-2020-2024_REGIONI-ALPINE-LWA-EU-1.pdf

Bassi, E., et al. (2020). Relative impact of human harvest and wolf predation on two ungulate species in Central Italy. Ecological Research, 35(4), 662-674. https://doi.org/10.1111/1440-1703.12130

Bisi, J., et al. (2010). The good bad wolf—wolf evaluation reveals the roots of the Finnish wolf conflict. European Journal of Wildlife Research, 56(5), 771-779. https://doi.org/10.1007/s10344-010-0374-0

Blangiardo, M., & Cameletti, M. (2015). Spatial and spatio-temporal Bayesian models with R-INLA. John Wiley & Sons. https://doi.org/10.1002/9781118950203

Blastland, M., et al. (2020). Five rules for evidence communication. Nature, 587(7834), 362-364. https://doi.org/10.1038/d41586-020-03189-1

Boiani, M.V., et al. (2025). The wolf in the Friuli Venezia Giulia Region (2023–2024). Technical Report (in Italian, https://www.regione.fvg.it/rafvg/export/sites/default/RAFVG/ambiente-territorio/tutela-ambiente-gestione-risorse-naturali/FOGLIA51/allegati/Relazione_tecnica_Il_lupo_in_regione_FVG_2023-2024.pdf)

Brogi, R., et al. (2025). Wolves on the phone: Public calls reveal a rise in urban concerns as wolves recolonize human-dominated areas. Ambio, 1-12. https://doi.org/10.1007/s13280-025-02264-z

Brunot, M., et al. (2025). Access to agricultural crops promotes first-year growth in a wild herbivore. European Journal of Wildlife Research, 71(2), 25. https://doi.org/10.1007/s10344-025-01899-3

Bubnicki, J. W., et al. (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. Elife, 8, e44937. https://doi.org/10.7554/eLife.44937

Brunot, M., et al. (2025). Access to agricultural crops promotes first-year growth in a wild herbivore. European Journal of Wildlife Research, 71(2), 25. https://doi.org/10.1007/s10344-025-01899-3

Calosi, M., et al. (2025). Starving or Stuffing? Plasticity in Wild Boar Body Mass Variations During Summer in a Mediterranean Area. Integrative Zoology. https://doi.org/10.1111/1749-4877.13012

Canova, L., & Meriggi, A. Reclaiming the man-made plain: ecological factors influencing the colonization of the wolf *Canis lupus* in the western Po Plain (NW Italy). Hystrix, the Italian Journal of Mammalogy. http://www.italian-journal-of-mammalogy.it/pdf-205330-125425?filename=125425.pdf

Carpio, A. J., et al. (2021). Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. Mammal Review, 51(1), 95-108. https://doi.org/10.1111/mam.12221

Cerri, J., et al. (2024). Dietary studies provide a partial picture of the feeding ecology of grey wolves across different environments. Archived on EcoEvoRxiv. https://doi.org/10.32942/X2FC8G

Cerri, J., et al. (2025). Trends of ungulate species in Europe: not all stories are equal. https://doi.org/10.32942/X26642

Cerri, J., et al. (2024). Dietary studies provide a partial picture of the feeding ecology of grey wolves across different environments. https://doi.org/10.32942/X2FC8G

Chapron, G., et al. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346(6216), 1517-1519. https://doi.org/10.1126/science.1257553

Cimatti, M., et al. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. Diversity and Distributions, 27(4), 602-617. https://doi.org/10.1111/ddi.13219

Ćirović, D., & Penezić, A. (2019). Importance of slaughter waste in winter diet of wolves (*Canis lupus*) in Serbia. North-Western Journal of Zoology, 15(2).

Ciucci, P., et al. (2020). Anthropogenic food subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in human-modified landscapes. Global Ecology and Conservation, 21, e00841. https://doi.org/10.1016/j.gecco.2019.e00841

Ciucci, P., et al. (2026). Wolf *Canis lupus* Linnaeus, 1758. In Carnivora (pp. 279-341). Cham: Springer Nature Switzerland.

Corlatti, L. et al. (2022). Northern Chamois *Rupicapra rupicapra* (Linnaeus, 1758) and Southern Chamois Rupicapra pyrenaica Bonaparte, 1845. In: Corlatti, L., Zachos, F.E. (eds) Terrestrial Cetartiodactyla. Handbook of the Mammals of Europe. Springer, Cham. https://doi.org/10.1007/978-3-030-24475-0_30

Corlatti, L., et al. (2019). Long-term dynamics of Alpine ungulates suggest interspecific competition. Journal of Zoology, 309(4), 241-249. https://doi.org/10.1111/jzo.12716

Corlatti, L., & Ciuti, S. (2026). Indirect effects of hunting on wildlife. Wildlife Biology, https://doi.org/10.1002/wlb3.01691

De Marinis, A.M., et al. (2022). Common Fallow Deer *Dama dama* (Linnaeus, 1758). In Corlatti, L. and F. Zachos (Eds): Terrestrial Cetartiodactyla – Handbook of the Mammals of Europe, pp. 115-154. Springer Nature Switzerland, Cham. https://doi.org/10.1007/978-3-030-24475-0_21

Donini, V., et al. (2021). Disentangling demographic effects of red deer on chamois population dynamics. Ecology and Evolution, 11(12), 8264-8280. https://doi.org/10.1002/ece3.7657

Felton, A. M., et al. (2024). Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions. Global Change Biology, 30(9), e17505. https://doi.org/10.1111/gcb.17505

Franchini, M., et al. (2019). “Interazione tra grandi carnivori e sistemi zootecnici alpini: stato dell'arte e implicazioni future. In: I servizi ecosistemici: opportunità di crescita per l'allevamento in montagna? Quaderni SoZooAlp N.10, 205–222 (in Italian).

Franchini, M., et al.(2023). You're stressing me out! Effect of interspecific competition from red deer on roe deer physiological stress response. Journal of Zoology, 320(1), 63-74. https://doi.org/10.1111/jzo.13058

Frangini, L., et al. S. (2025). An Uncomfortable Neighborhood: Presence Evolution of Two Competing Carnivores in North-Eastern Italy. Ecology and Evolution, 15(10), e72368. https://doi.org/10.1002/ece3.72368

Gable, T. D., et al. (2018). Do wolves ambush beavers? Video evidence for higher-order hunting strategies. Ecosphere, 9(3), e02159. https://doi.org/10.1002/ecs2.2159

Gaillard, J. M., et al. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in ecology & evolution, 13(2), 58-63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gangaas, K. E., et al. (2013). Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. PloS one, 8(7), e68849. https://doi.org/10.1371/journal.pone.0068849

Gaynor, K. M., et al. (2019). Landscapes of fear: spatial patterns of risk perception and response. Trends in ecology & evolution, 34(4), 355-368. https://doi.org/10.1016/j.tree.2019.01.004

Gazzola, A., et al. (2005). Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. Journal of Zoology, 266(2), 205-213. https://doi.org/10.1017/S095283690500680

Gehr, B., et al. (2018). Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. Ecology and evolution, 8(1), 109-119. https://doi.org/10.1002/ece3.3642

Gervasi, V., et al. (2024). Estimating distribution and abundance of wide-ranging species with integrated spatial models: Opportunities revealed by the first wolf assessment in south-central Italy. Ecology and Evolution, 14(5), e11285. https://doi.org/10.1002/ece3.11285

Gervasi, V., et al.(2012). Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. Journal of Animal Ecology, 81(2), 443-454. https://doi.org/10.1111/j.1365-2656.2011.01928.x

Gerber, N., et al. (2024). Do recolonising wolves trigger non-consumptive effects in European ecosystems? A review of evidence. Wildlife Biology, 2024(6), e01229. https://doi.org/10.1002/wlb3.01229

Højberg, P. L., et al. (2017). Fear, economic consequences, hunting competition, and distrust of authorities determine preferences for illegal lethal actions against gray wolves (*Canis lupus*): a choice experiment among landowners in Jutland, Denmark. Crime, Law and Social Change, 67(4), 461-480. https://doi.org/10.1007/s10611-016-9670-2

Imperio, S., et al. (2010). Investigating population dynamics in ungulates: do hunting statistics make up a good index of population abundance?. Wildlife Biology, 16(2), 205-214. https://doi.org/10.2981/08-051

Kassambara, A. (2017). Practical guide to cluster analysis in R: Unsupervised machine learning (Vol. 1). Sthda.

Kautz, T. M., et al. (2022). Compensatory human and predator risk trade-offs in neonatal white-tailed deer. Global ecology and conservation, 36, e02089. https://doi.org/10.1016/j.gecco.2022.e02089

Kojola, I., et al. (2009, December). European wild forest reindeer and wolves: endangered prey and predators. In Annales Zoologici Fennici (Vol. 46, No. 6, pp. 416-422). Finnish Zoological and Botanical Publishing Board. https://doi.org/10.5735/086.046.0602

Knorr-Held, L. (2000). Bayesian modelling of inseparable space-time variation in disease risk. Statistics in medicine, 19(17-18), 2555-2567. https://doi.org/10.1002/1097-0258(20000915/30)19:17/18%3C2555::AID-SIM587%3E3.0.CO;2-%23

Kruschke, J. K., & Liddell, T. M. (2018). The Bayesian New Statistics: Hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. Psychonomic bulletin & review, 25(1), 178-206. https://doi.org/10.3758/s13423-016-1221-4

Kuijper, D. P., et al. (2019). Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes?. Biological Conservation, 235, 102-111. https://doi.org/10.1016/j.biocon.2019.04.004

Kuijper, D. P., et al. (2013). Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography, 36(12), 1263-1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x

Kuijper, D. P., et al. (2024). Wolves recolonize novel ecosystems leading to novel interactions. Journal of Applied Ecology, 61(5), 906-921. https://doi.org/10.1111/1365-2664.14602

Kuijper, D. P., et al. (2014). What cues do ungulates use to assess predation risk in dense temperate forests?. PLoS One, 9(1), e84607. https://doi.org/10.1371/journal.pone.0084607

Kutal, M., et al. (2025). Deeply Political and Populist Decisions on Large Carnivores in Europe in Recent Times. Conservation Letters, 18(4). https://doi.org/10.1111/conl.13125

Lazzeri, L., et al. (2024). Beyond ungulate density: Prey switching and selection by the wolf in a recolonised area. Global Ecology and Conservation, 54, e03069. https://doi.org/10.1016/j.gecco.2024.e03069

Lazzeri, L., et al. (2024). Switch or perish? Prey–predator interactions in a Mediterranean area. Animal Conservation, 27(6), 830-850. https://doi.org/10.1111/acv.12973

Lennox, R. J., et al. (2025). The role of habitat in predator–prey dynamics with applications to restoration. Restoration Ecology, 33(3), e14354. https://doi.org/10.1111/rec.14354

Liberg, O., et al. (2012). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proceedings of the Royal Society B: Biological Sciences, 279(1730), 910-915. https://doi.org/10.1098/rspb.2011.1275

Lindgren, F., & Rue, H. (2015). Bayesian spatial modelling with R-INLA. Journal of statistical software, 63, 1-25. https://doi.org/10.18637/jss.v063.i19

Lorenzini, R., et al. (2022). European Roe Deer *Capreolus capreolus* (Linnaeus, 1758). In Corlatti, L. and F. Zachos (Eds): Terrestrial Cetartiodactyla – Handbook of the Mammals of Europe, pp. 165-1

Lorenzini, R., et al. (2026). Genetic evidence reveals extensive wolf-dog hybridisation in peninsular Italy: warnings against ineffective management. Biological Conservation, 313, 111615. https://doi.org/10.1016/j.biocon.2025.111615

Louvrier, J., et al. (2018). Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. Ecography, 41(4), 647-660. https://doi.org/10.1111/ecog.02874

Malek, Ž., et al. (2024). A harmonized data set of ruminant livestock presence and grazing data for the European Union and neighbouring countries. Scientific data, 11(1), 1136. https://doi.org/10.1038/s41597-024-03983-w

Marucco, F., et al. 2018. "La popolazione di lupo sulle Alpi Italiane 2014-2018. Relazione tecnica, Progetto LIFE 12 NAT/IT/00080 WOLFALPS – Azione A4 e D1." (in Italian, https://www.lifewolfalps.eu/wp-content/uploads/2020/10/Report_monitoraggio_Alpi_completo.pdf)

Marrotte, R. R., et al. (2022). Harvest and density‐dependent predation drive long‐term population decline in a northern ungulate. Ecological Applications, 32(6), e2629. https://doi.org/10.1002/eap.2629

Marucco, F., et al. (2023). Transboundary monitoring of the wolf alpine population over 21 years and seven countries. Animals, 13(22), 3551. https://doi.org/10.3390/ani13223551

Mattioli, S., et al. (2022). Red Deer *Cervus elaphus* Linnaeus, 1758. In Corlatti, L. and F. Zachos (Eds): Terrestrial Cetartiodactyla – Handbook of the Mammals of Europe, pp. 51-86. Springer Nature Switzerland, Cham. https://doi.org/10.1007/978-3-030-24475-0_19

Mech, L. D. (1995). The challenge and opportunity of recovering wolf populations. Conservation biology, 9(2), 270-278. https://doi.org/10.1046/j.1523-1739.1995.9020270

Mech, L. D. (2017). Where can wolves live and how can we live with them?. Biological conservation, 210, 310-317. https://doi.org/10.1016/j.biocon.2017.04.029

Melis, C., et al. (2009). Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global ecology and biogeography, 18(6), 724-734. https://doi.org/10.1111/j.1466-8238.2009.00480.x

Morellet, N., et al. (2011). Landscape composition influences roe deer habitat selection at both home range and landscape scales. Landscape Ecology, 26(7), 999-1010. https://doi.org/10.1007/s10980-011-9624-0

Musto, C., et al. (2021). Men and wolves: Anthropogenic causes are an important driver of wolf mortality in human-dominated landscapes in Italy. Global Ecology and Conservation, 32, e01892. https://doi.org/10.1016/j.gecco.2021.e01892

Mysterud, A., et al. (2023). Agricultural grasslands buffer density effects in red deer populations. The Journal of wildlife management, 87(3), e22357. https://doi.org/10.1002/jwmg.22357

Nanni, V., et al. (2020). Social media and large carnivores: Sharing biased news on attacks on humans. Frontiers in Ecology and Evolution, 8, 71. https://doi.org/10.3389/fevo.2020.00071

Newsome, T. M., et al.. (2016). Food habits of the world's grey wolves. Mammal Review, 46(4), 255-269. https://doi.org/10.1111/mam.12067

Nowak, S., et al. (2021). The illegal shooting and snaring of legally protected wolves in Poland. Biological Conservation, 264, 109367. https://doi.org/10.1016/j.biocon.2021.109367

Oliynyk, R. T. (2023). Human-caused wolf mortality persists for years after discontinuation of hunting. *Scientific Reports*, *13*(1), 11084. https://doi.org/10.1038/s41598-023-38148-z

Orazi, V., et al. (2025). Antipredator behaviour as a major determinant of prey altitudinal movements: the wolf and the chamois. Frontiers in Zoology, 22(1), 1-15. https://doi.org/10.1186/s12983-025-00559-1

Palmegiani, I.,et al. (2013). Wolf diet and its impact on the ungulates community in a new recolonized area of Western Alps: Gran Paradiso National Park. Folia Zoologica, 62(1), 59-66. https://doi.org/10.25225/fozo.v62.i1.a9.2013

Planillo, A., et al. (2024). Understanding habitat selection of range-expanding populations of large carnivores: 20 years of grey wolves (*Canis lupus*) recolonizing Germany. Diversity and Distributions, 30(1), 71-86. https://doi.org/10.1111/ddi.13789

Poldini, L., et al. (2006). "Manuale degli habitat del Friuli Venezia Giulia. Strumento a supporto della valutazione d'impatto ambientale (VIA), ambientale strategica (VAS) e d'incidenza ecologica (VIEc)." Regione Autonoma Friuli Venezia Giulia – Direzione Centrale ambiente e lavori pubblici—Servizio Valutazione Impatto Ambientale, Università degli Studi di Trieste—Dipartartimento di Biologia, 1078 pp. (in Italian).

Raganella Pelliccioni, E., et al. (2013). Linee guida per la gestione degli ungulati. Istituto Superiore per la Protezioni e la Ricerca Ambientale. https://www.isprambiente.gov.it/files/pubblicazioni/manuali-lineeguida/MLG_91_2013.pdf

Randon, M., et al. (2020). Population responses of roe deer to the recolonization of the French Vercors by wolves. Population Ecology, 62(2), 244-257. https://doi.org/10.1002/1438-390X.12043

Regione Friuli Venezia Giulia (2015). Piano Faunistico Venatorio Regionale. https://www.regione.fvg.it/rafvg/export/sites/default/RAFVG/ambiente-territorio/tutela-ambiente-gestione-risorse-naturali/gestione-venatoria/FOGLIA12/allegati/Piano_Faunistico_Regionale.pdf

Richard, E., et al. (2010). High red deer density depresses body mass of roe deer fawns. Oecologia, 163(1), 91-97. https://doi.org/10.1007/s00442-009-1538-z

Sand, H., et al. (2012). Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality. Canadian Journal of Zoology, 90(3), 403-412. https://doi.org/10.1139/z2012-007

Sand, H., et al. (2025). Quantifying large carnivore predation relative to human harvest on moose in an intensively managed boreal ecosystem. *Ecological Applications*, 35(1), e70000. https://doi.org/10.1002/eap.70000

Santiago-Ávila, F. J., & Treves, A. (2022). Poaching of protected wolves fluctuated seasonally and with non-wolf hunting. *Scientific Reports*, *12*(1), 1738. https://doi.org/10.1038/s41598-022-05679-w

Scandura, M., Podgórski, T., Vicente, J., and L. Iacolina. 2022. Wild Boar *Sus scrofa* Linnaeus, 1758. In Corlatti, L. and F. Zachos (Eds): Terrestrial Cetartiodactyla – Handbook of the Mammals of Europe, pp. 1-27. Springer Nature Switzerland, Cham. https://doi.org/10.1007/978-3-030-24475-0_17

Singer, L., et al. (2023). The spatial distribution and temporal trends of livestock damages caused by wolves in Europe. Biological Conservation, 282, 110039. https://doi.org/10.1016/j.biocon.2023.110039

Sjölander-Lindqvist, A. (2015). Targeted removal of wolves: analysis of the motives for controlled hunting. Wildlife Biology, 21(3), 138-146. https://doi.org/10.2981/wlb.00011

Skogen, K., & Krange, O. (2020). The Political dimensions of illegal wolf hunting: Anti-elitism, lack of trust in institutions and acceptance of illegal wolf killing among Norwegian hunters. Sociologia ruralis, 60(3), 551-573. https://doi.org/10.1111/soru.12309

Smith, J. A. (2024). Offset or not: guidance on accounting for sampling effort in generalized linear models. Archived on EcoEvoRxiv. https://doi.org/10.32942/X2CP8Z

Sunde, P., et al. (2021). Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany. Conservation Letters, 14(5), e12812. https://doi.org/10.1111/conl.12812

Torretta, E., et al. (2022). Hide-and-seek in a highly human-dominated landscape: Insights into movement patterns and selection of resting sites of rehabilitated wolves (*Canis lupus*) in northern Italy. Animals, 13(1), 46. https://doi.org/10.3390/ani13010046

Treves, A., et al. (2016). Predator control should not be a shot in the dark. Frontiers in Ecology and the Environment, 14(7), 380-388. https://doi.org/10.1002/fee.1312

Van Beeck Calkoen, S. T., et al. (2023). Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe. Journal of Applied Ecology, 60(12), 2625-2635. https://doi.org/10.1111/1365-2664.14526

Vannini, C., et al. (2021). Land cover and weather jointly predict biometric indicators of phenotypic quality in a large herbivore. Ecological Indicators, 128, 107818. https://doi.org/10.1016/j.ecolind.2021.107818

Wilmers, C. C., et al. (2025). The Ecological Impacts of Large-Carnivore Recovery in North America. Annual Review of Ecology, Evolution, and Systematics, 56(1), 337-363. https://doi.org/10.1146/annurev-ecolsys-102722-021139

Wikenros, C., et al. (2015). Response of moose hunters to predation following wolf return in Sweden. PloS one, 10(4), e0119957. https://doi.org/10.1371/journal.pone.0119957

Wikenros, C., et al. (2025). Retrospective analyses to understand how wolf territory density impacts moose quotas, harvest and observation rate. European Journal of Wildlife Research, 71(3), 1-13. https://doi.org/10.1007/s10344-025-01920-9

Zuur, A. F., et al. (2017). Spatial, temporal and spatial-temporal ecological data analysis with R-INLA. Highland Statistics Ltd, 1.